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FACTORS INFLUENCING ARTHROPOD DIVERSITY IN THE CITRUS LANDSCAPE IN TSHIPISE, LIMPOPO PROVINCE, SOUTH AFRICA

By

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Declaration

I, Manamela Thakgatso Rosina, hereby declare that this thesis submitted to the University of Venda for the degree of MSc in Biological Sciences: Zoology has not been submitted previously for any other degree at this or any other institution and that it is my work in design and execution and that all materials contained therein have been duly acknowledged.

Signature:  Date: 08 May 2025

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Abstract

Citrus plants play a crucial role in global food and nutrient supplies. South Africa exported 165.1 million cartons of citrus during the 2023 season and projected growth to 200 million cartons within four years. However, citrus crops are vulnerable to pest infestations, leading to a heavy reliance on chemical pesticides. Different pesticide types and dosages leave varying residue levels on treated citrus, with strict maximum residue limits (MRLs) enforced by global markets. Ongoing shifts in MRL standards and concerns over chemical dependence have pressured Southern African citrus producers to adopt Integrated Pest Management (IPM) approaches that balance effective pest control with minimised chemical use. This study investigated the factors influencing arthropod diversity in citrus agroecosystems, focusing on how landscape heterogeneity influences IPM. Using a landscape context approach, it quantified arthropod diversity within citrus orchards and surrounding habitats and edges to understand how these areas support beneficial arthropods like predators and parasitoids (**Chapter 2**). Results showed that diverse landscapes supported higher populations of beneficial arthropods in natural habitats, enhancing natural pest control, whereas croplands harboured more pest species.

Additionally, the study evaluated the effects of excluding insectivorous vertebrates to assess their roles in pest suppression, crop damage reduction, and the spatial distribution of *Thaumatotibia leucotreta* **(Chapter 3**). By elucidating arthropod population dynamics, the role of landscape structure and context, and insectivorous vertebrates, this study highlights the importance of landscape heterogeneity in enhancing natural pest control within citrus agroecosystems.

Findings show that maintaining diverse, non-crop habitats near croplands can support natural enemy populations, reducing reliance on chemical pesticides in IPM. The study also reveals that landscape context, especially proximity to natural habitats, influences the distribution and impact of crucial pests like *T. leucotreta* within citrus orchards. These insights offer practical guidance for optimising IPM approaches, suggesting that incorporating elements of natural habitats within agricultural landscapes can improve pest suppression and align with evolving global standards for pesticide residue limits.

Keywords: landscape heterogeneity; integrated pest management; conservation biological control; arthropod diversity; *Thaumatotibia leucotreta*; insectivorous vertebrates

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CHAPTER ONE

Introduction and Literature Review

1.1. Overview of the study

In South African citrus industries, conventional chemical control methods are widely utilised, although growers have adopted cultural, biocontrol, and Integrated Pest Management (IPM) strategies to control field pest populations (Urquhart, 1999). These practices have partially succeeded because field insect pest populations proliferate under favourable conditions. Despite the availability of multiple control methods, citrus growers prefer chemical control options because they get the desired results instantly. Like any other pests, citrus insects have parasitoids and predators. Even though data on insect assemblages in citrus orchards are limited, some studies have reported the presence of efficient parasitoids and predators in citrus to control these pests (Galloway et al., 2021). However, the periodic application of chemical pesticides affects permanent fluctuating relationships between insect pests, parasitoids and predators. This disruption could cause insect pest populations to recover without a check, resulting in some damage by these insects to citrus.

Nonetheless, the European Union's (EU) regulation on citrus black spot (CBS) *Phyllosticta citricarpa* mandates a calendar-based spray program, which may have unintended impacts on the beneficial insect assemblage that naturally control citrus pest populations. This is an unsustainable situation, placing growers on a chemical treadmill. However, export markets, particularly the EU, increasingly demand reduced chemical inputs and increased IPM implementation. Strengthening IPM programmes requires thoroughly understanding arthropod (*viz.,* important insects: insect pests, parasitoids, and predators) assemblages in citrus orchards. Additionally, documenting the role of seasonal climate in shaping these insects' dynamics is essential for effectively guiding IPM programs.

This thesis comprises four chapters. The first chapter is the general introduction to the present study. Chapter 2 discusses the diversity of arthropods between the citrus orchards and the surrounding natural vegetation landscapes. This chapter highlights what could be implemented in citrus orchards to improve the standard ecological fluctuation patterns between the potential insect pests and their respective natural enemies. Then, Chapter 3 discusses the impact of potential insect pests on citrus fruits in the absence of vertebral predators (*viz.,* birds, bats, etc.).

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This chapter explored the importance of vertebral over invertebrate predators (ants, beetles, etc.) or parasitoids in controlling insect pests infesting citrus fruits. We excluded vertebrate predators by caging the experimental citrus trees to investigate their role in controlling insect pests that threaten the fruits of these plants. Lastly, Chapter 4 provides a general discussion of the entire study and offers conclusions and recommendations for improving the management of insect pests associated with citrus orchards.

1.2. Background of the study

The citrus industry plays a vital role in global food and nutrient supplies, primarily through its decadent array of nutrients found in citrus fruits; hence, understanding the intricate interactions within citrus agroecosystems becomes essential. In the 2023 export season, South African citrus growers traded 165.1 million cartons globally, and this industry intends to export 200 million cartons by 2027 and possibly 260 million cartons by 2032 (Erasmus, 2024). However, citrus fruits are susceptible to pests, necessitating the need to be treated with chemical pesticides to reduce the effects of these pests (Urquhart, 1999; Urbaneja et al., 2020). Aerial application of these chemicals could result in different residual levels in citrus fruits (Grout and Moore, 2015). Various trading markets have acceptable maximum residual levels (MRLs) traced from the exported citrus products treated with chemical pesticides (Grout and Moore, 2015). Due to ongoing changes to MRLs from citrus-importing countries, pest management strategies in Southern Africa remain contentious.

Several contra versions have surfaced among the targeted markets for citrus fruit export; some markets support the use of Plant Protection Products (PPPs), while some dispute such practices and task citrus farmers to reduce the usage of the chemical pesticides to the lowest possible levels (Grout and Moore, 2015). Applying low levels of chemicals against these insect pests could not be effective, and this could cause massive outbreaks of these pests (Urbaneja et al., 2020). Thus, integrating other sustainable pest control methods with the recommended low levels of chemical pesticides could help maintain these pests under crop injury levels (Colloff et al., 2013).

Therefore, understanding arthropod population dynamics in citrus agroecosystems can help gain insights into the fluctuating patterns of these insect pests kept under control by their enemies and seasonal climatic factors.

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1.3. *Citrus* spp.

The citrus plants, *Citrus* spp. (Rutaceae), originating from Southeast Asia's subtropical regions, are widely cultivated for their fruit production, producing the most traded fruits worldwide (Habermann and de Souza, 2014; Grout and Moore, 2015). The commonly commercialised citrus plant species, *Citrus sinensis* (L.) Osbeck (sweet orange), *C. aurantium* Osbeck (sour orange), *C. reticulata* Blanco (mandarin), *C. paradisi* Macf. (grapefruit), *C. limon* (L.) Osbeck (lemon), *C. aurantifolia* Swingle (lime), and other hybrids are cultivated worldwide, including in South Africa (Hussain et al., 2021). Citrus plants are evergreen perennials and can grow up to 4 - 8 m tall (Barden et al., 1987). Citrus plants are easily propagated through cuttings (Bain, 1958). These plants produce medium-sized, white, and intensely fragrant flowers ranging between 2 and 3 cm. Most citrus flowers are self-pollinating; a single flower has male and female reproductive organs (Mesejo et al., 2007). These flowers produce fruits that develop and hang on their trees for approximately 8 to 10 months (Bain, 1958). In most citrus cultivars, except for limes and lemons, flowering and fruit occur annually during spring in subtropical regions. However, flowering is a continuous process in tropical areas, primarily influenced by adequate rainfall or water supply (Schneider, 1968). The hesperidium berry fruit forms from a single ovary composed of carpels covered by a leathery peel. The fruit's shape ranges from oblate to prolate spheroid, while the peels contain numerous oil glands and vary in colour, including green-yellow to red-orange and deep orange (Schneider, 1968).

1.4. The Citrus Sector in South Africa

In South Africa, the citrus industry exports approximately 54% of its total fruit production (FPEF, 2024). The sector spans around 96,277 ha of land across the country (Erasmus, 2024). Limpopo Province is the leading citrus-growing region, accounting for 48% of the total citrus in the country, followed by the Eastern Cape (23%) and Western Cape (14%) provinces (CGA, 2023). This industry produces a variety of citrus fruits, including oranges, limes, lemons, grapefruits, mandarins, and navels. Among these, oranges are the most traded fruit (31%), followed by lemons (22%), mandarins (20%), navels (17%), and grapefruits (10%) (CGA, 2023). South Africa's citrus industry is renowned for its high-quality produce, attributed to favourable climatic conditions, well-drained soils, and advanced farming practices (Ntombela et al., 2022). The cooler climates of the Western Cape and Eastern Cape are favoured for producing navel oranges, lemons, and easy peelers such as *C. Clementina* (Clementines) and *C. unshiu* (Satsumas) (USDA, 2023). In contrast, the warmer climates of Mpumalanga,

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Limpopo, and KwaZulu-Natal provinces are more conducive to cultivating *C. paradisi* and *C. sinensis* (USDA, 2023). Despite this cultivating and trading success, the citrus industry faces various challenges, including adverse threats from insect pests and diseases, which threaten its overall competitiveness (Meintjes, 2024). Although the threat of these pests has been maintained under the injury levels by applying pesticides, recent export regulations (Annex VII to Implementing Regulation (EU) 2019/2072) have mandated the use of lower pesticide concentrations on citrus fruits, and this could potentially cause outbreaks of some insect pests and pathogens (Grout and Moore, 2015).

1.5. Arthropods in Citrus

Citrus agroecosystems are associated with rich diversity and abundance of arthropods, including both pests (Table 1.1) and beneficial species (Table 1.2) (Urbaneja et al., 2023). Although beneficial arthropods (i.e., primarily pollinators) are valued, they do not play a significant role in the citrus industry because citrus flowers are autogamous (Karmakar, 2013) (see Section 1.3). Nonetheless, the primary interest in citrus production is the establishment of sustainable management strategies against the potential insect pests of citrus trees (Urquhart, 1999). However, natural enemies—particularly insectivorous predators and parasitoids—are of considerable interest within Integrated Pest Management (IPM) frameworks due to their potential to reduce pest populations and reliance on chemical controls.

Notably, approximately 20 insect species have been identified as critical pests in citrus orchards globally, categorised into three concerned statuses: phytosanitary, production, and cosmetic pests (Nepagan et al., 2018; Urbaneja et al., 2020). Among these insects, phytosanitary pests are considered the most destructive, as they pose significant threats to local citrus industries and foreign ranges through the global trade of infested citrus fruits (Follett and Neven, 2006; Moore, 2021).

The False codling moth (FCM), *Thaumatotibia leucotreta* (Meyrick)(Lepidoptera: Tortricidae) is the primary phytosanitary pest threatening South African citrus growers (Grout and Moore., 2015; Moore, 2021). This insect pest moth is native to Sub-Saharan Africa, extending its distribution range to some Indian and Atlantic Ocean islands, such as Mauritius and Cape Verde. The distribution of *T. leucotreta* occurs wherever citrus is produced in southern Africa (Grout and Moore, 2015). The moth thrives in warm, humid climates with mild winters, producing multiple generations throughout the year. Its life cycle includes egg, larval, pupal,

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and adult stages (Grout and Moore, 2015). The adult females of *T. leucotreta* deposit eggs on the surface of citrus fruits. When the larvae hatch, they bore and burrow into the fruit for feeding and development (Grout and Moore, 2015). Damage caused by the larvae of *T. leucotreta* results in the rejection of citrus fruits in export markets, causing massive economic losses (Grout and Moore, 2015; Moore, 2021). This insect moth is most active during warm seasons and can reproduce all year round, making it a persistent threat in citrus agroecosystems (Grout and Moore, 2015).

Furthermore, the carob moth *Ectomyelois ceratoniae* Zeller (Lepidoptera: Pyralidae) is another significant insect pest, although it is considered a minor pest in South Africa's citrus industry (Grout and Moore, 2015). *Ectomyelois ceratoniae* is a substantial pest since it causes similar fruit damage to *T. leucotreta. E. ceratoniae* is originally from the Mediterranean basin and is widespread in southern Africa (Grout and Moore, 2015), and thrives in warm, dry climates (Morland, 2015). The eggs of both *T. leucotreta* and *E. ceratoniae* are small, saucer-shaped, flattened, and initially translucent, turning reddish brown before hatching (Grout and Moore, 2015). The larvae of *E. ceratoniae* bore into the rind and albedo or enter through the navel to feed on the pulp of the citrus fruit (Grout and Moore, 2015; Morland, 2015). The body colour of the larvae of *E. ceratoniae* is pale pink with a brown head and can be confused with the larvae of *T. leucotreta* (Grout and Moore, 2015). Although the present study focused on sampling diverse arthropods, it was more critical to understand the population dynamics of these insect pests and their respective natural enemies in natural and citrus landscapes.

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Table 1.1: Examples of major insect pests of citrus fruits.

Order	Family	Scientific Name	Plant damage	Current distribution	Reference
Diptera	Tephritidae	*Ceratitis capitata*, *Ceratitis rosa*	Internal fruit feeder	Sub-Saharan Africa	(Grout and Moore, 2015)
Hemiptera	Pseudococcidae	*Planococcus citri*, *Nipaecoccus viridis*, *Paracoccus burnerae*,	Fruit sap sucking	Southeast Asia, South Asia, Southern Africa	(Grout and Moore, 2015)
Hemiptera	Triozidae	*Tripza erytreae*	Fruit greening disease	Eastern and Southern African	(Grout and Moore, 2015)
Hemiptera	Coccidae	*Coccus hesperidum*, *Aonidiella aurantii*	Sap-sucking	Cosmopolitan, Southeast Asia	(Grout and Moore, 2015)
Hemiptera	Aphididae	*Aphis gossypii*, *Toxoptera citricida*	Leaf sap-sucking	Asia	(Grout and Moore, 2015)
Hemiptera	Aleyrodidae	*Dialeurodes citri*, *Bemisia tabaci*	Leaf yellowing	Asia	(Grout and Moore, 2015)
Lepidoptera	Gracillariidae	*Phyllocnistis citrella*	Leaf miner	South Asia	(Grout and Moore, 2015)
Lepidoptera	Tortricidae	*Ecdytolopha aurantiana*	Stem borer	South America	(Grout and Moore, 2015)
Lepidoptera	Noctuidae	*Helicoverpa armigera*	Flower and fruit feeder	Africa and Asia	(Grout and Moore, 2015)

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Thysanoptera	Thripidae	*Scirtothrips citri*, *Frankliniella occidentalis*	Fruit scarring; leaf distortion	Western North America	(Grout and Moore, 2015)

Table 1.2: Examples of beneficial arthropods in citrus orchards.

Order	Family	Scientific Name	Insect purpose	Reference
Arachnida	Phytoseiidae	*Phytoseiulus persimilis*	Predatory Mite	(Grout and Moore, 2015)
Coleoptera	Carabidae	*Calosoma* spp., *Pterostichus* spp.	Predatory ground beetles	(Grout and Moore, 2015)
Coleoptera	Coccinellidae	*Hippodamia convergens*	Predatory Beetle	(Grout and Moore, 2015)
Coleoptera	Coccinellidae	*Stethorus punctillum*	Spider Mite Destroyer	(Grout and Moore, 2015)
Coleoptera	Staphylinidae	*Aleochara* spp., *Staphylinus* spp.	Predator	(Grout and Moore, 2015)
Collembola	Tomoceridae	*Tomocerus*	Decomposer	(Hore and Banerjee, 2017)
Dermaptera	Forficulidae	*Forficula auricularia*	Predator	(Grout and Moore, 2015)
Diptera	Syrphidae	*Episyrphus balteatus*	Predator	(Grout and Moore, 2015)
Diptera	Syrphidae	*Eumerus tuberculatus*	Pollinator	(Haq et al., 2016)
Hymenoptera	Trichogrammatidae	*Trichogramma* spp.	FCM, Fruit fly, Bollworm parasitoid	(Grout and Moore, 2015)
Hymenoptera	Aphelinidae	*Eretmocerus spp.*	Whitefly parasitoid	(Grout and Moore, 2015)
Hymenoptera	Braconidae	*Aphytis melinus*	California Red Scale Parasitoid	(Grout and Moore, 2015)
Hymenoptera	Eulophidae	*Tamarixia radiata*	Asian citrus psyllid parasitoid	(Grout and Moore, 2015)
Hymenoptera	Apidae	*Apis florea*	Pollinator	(Haq et al., 2016)

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Neuroptera	Chrysopidae	*Chrysoperla carnea*	Predator	(Grout and Moore, 2015)

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1.6. Importance of landscape structure and functional biodiversity on arthropod dynamics

Functional biodiversity is a fundamental component of agroecosystems, consisting of communities of fauna and flora interacting within diverse ecosystems (Moonen and Bàrberi, 2008). Functional biodiversity is crucial for maintaining ecological interactions between insect and plant species, particularly in crop production industries. Until recently, pest management programs focused on reducing insecticide use and maintaining functional biodiversity, contributing toward the balanced fluctuating patterns of insect pests and their respective enemy populations (Bianchi et al., 2019). Such programs emphasise the role of functional biodiversity in supporting diverse insect communities, including pollinators, natural enemies of pests, and decomposers, in habitats adjacent to crop orchards. These adjacent habitats, such as natural vegetation strips, hedgerows, or riparian zones, provide critical resources such as nectar, pollen, alternative prey, and refuge sites. They also serve as essential population sinks or reservoirs, enabling natural enemy populations to recolonise orchards after insecticide applications have reduced their numbers. This, in turn, enhances ecosystem services like pollination, biological pest control, and nutrient cycling, ultimately contributing to improved crop yields and reduced dependence on chemical inputs (Kremen et al., 2007). For example, the study by Munyuli et al. (2007) highlights the positive effects of habitat manipulation on natural enemy abundance and pest control in agricultural systems. In cowpea crops, intercropping with green gram enhanced arthropod predator abundance significantly. This habitat manipulation strategy increased natural predator populations, lowering pest pressure and crop yields.

Additionally, the study by Cividanes and Barbosa (2001) examined the effects of intercropping soybean with maize on natural enemy populations and pest dynamics. This habitat manipulation strategy led to an increased abundance of natural enemies, including predatory insects such as *Geocoris* sp. (Hemiptera: Geocoridae) and *Orius* sp. (Hemiptera: Anthocoridae), as well as parasitoid wasps from the families Braconidae and Scelionidae. However, the findings also revealed that while natural enemy populations increased, some pest species became more severe under this intercropping system.

A meta-analysis shows high populations of predatory and parasitoid insects have been observed in biodiverse landscapes near crop orchards, contributing to the reduction of insect pest populations in the orchards (Korányi et al., 2022). Efforts in fostering functional biodiversity

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in Indonesia have enhanced arthropod diversity (natural enemies, pollinators, and detritivores) on Chilli *Capsicum annuum* L. (Solanaceae) farms, particularly by leveraging refugia (Reksiana et al., 2023). These studies' findings suggest that maintaining high landscape heterogeneity can support arthropod diversity within agroecosystems and could reduce the critical insect pests in crop fields. Additionally, diverse habitats help mitigate harsh environmental conditions, resulting in the protection of crop production (Tscharntke et al., 2005). In line with these landscape-level strategies, the use of cover crops in citrus orchards presents a promising on-farm practice to enhance sustainability. Although their adoption in South African citrus systems remains limited, cover crops—particularly legumes—have been shown to improve soil microbial activity, suppress weeds, and enhance nitrogen input through biological fixation (67 to 209 kg N ha−1) (Silwana et al., 2022). They further highlight that this practice not only reduces dependence on synthetic fertilisers but also increases fruit yield by 7.6 to 64% and improves fruit quality by 2.3 to 12.4% in weight and 2.4 to 5.8% in °Bx. Such benefits align with broader goals of increasing agrobiodiversity, climate resilience, and economic sustainability for citrus growers.

Diverse heterogeneous landscapes support the diverse recruitment of arthropods (Ali et al., 2022). For example, Tscharntke et al. (2005) demonstrated that landscapes comprising a mix of semi-natural habitats and crops harbour more diverse arthropod communities than homogeneous agricultural landscapes. The species richness and community composition associated with landscape heterogeneity are essential for conserving biological diversity (Darvishi et al., 2024). A study conducted in the Cape Floristic Region, South Africa, highlighted how the extent of natural vegetation, specifically herbaceous plants, influences how local practices affect the composition of arthropods, including Araneae and Coleoptera, in vineyard ecosystems (Gaigher and Samways, 2010; Eckert et al., 2019; Geldenhuys et al., 2022,). Similarly, Eckert et al. (2020) found that native cover crops enhance foliar arthropod diversity more effectively than exotic cover crops, contributing to area-scale compositional heterogeneity. Diverse native crops can improve arthropod diversity and populations in agricultural regions, encouraging more resilient agroecosystems. Nonetheless, non-native (*viz.,* alien invasive species) plant species in ecosystems adjacent to focal crop fields have been found to frequently change the composition and structure of the native vegetation communities (Litt et al., 2014). Such alteration can reduce arthropod populations, particularly among monophagous and oligophagous phytophagous species, which depend on specific native host

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plants for nectar (as a food source) and oviposition (reproduction). In contrast, polyphagous species may be less affected due to their broader dietary and reproductive host range.

1.7. Arthropod management in citrus

Arthropod management in citrus orchards relies on scouting, collection, identification, and treatment methods to maintain pest populations below economic injury thresholds. These approaches are critical during pest outbreaks and are integral to Integrated Pest Management (IPM) strategies (Citrus Academy, 2017). Chemical, cultural, and biological control methods are the most frequently employed techniques, with monitoring and scouting as fundamental components of pest management systems (Urquhart, 1999).

1.7.1. The role of scouting in arthropod management

Monitoring and scouting are indispensable for effective arthropod management. They provide essential data on pest populations, infestation levels, and the activity of beneficial organisms. Regular scouting allows for early detection of pest outbreaks, enabling timely interventions to minimise crop damage (Citrus Academy, 2017). Pests pose significant challenges in citrus production, and their management relies heavily on robust monitoring systems. Scouting methods in citrus orchards include visual inspections, systematic field walks, and random tree sampling, allowing for direct observation of pests and crop health assessment. Pheromone traps targeting male pests, such as *T. leucotreta*, and sticky traps capturing flying insects like Aphidoidea are valuable for quantifying pest activity and guiding control measures (Adom et al., 2021). Sticky traps also effectively monitor parasitoid activity and estimate their densities, providing insights into natural biological control potential. Monitoring fallen fruit for pest infestations also helps assess damage levels and potential post-harvest risks.

1.7.2. Chemical control

Chemical control methods have been foundational in pest management strategies, particularly in the citrus industry. These methods have demonstrated high efficacy in rapidly reducing pest populations, contributing significantly to crop protection and yield improvement (Urquhart, 1999). The most significant disadvantage of using pesticides is their unintended impacts on non-target insect populations, including insect predators and parasitoids of potential insect pests (Boina and Bloomquist, 2015; see Table 1.3). Insect pests often rebuild their populations more rapidly than their natural enemies, resulting in severe outbreaks that significantly impact

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citrus (Pimentel et al., 1992). Thus, chemical pesticides should be applied to the population levels of these insect pests. Conversely, excessive application of chemical pesticides could cause insect pests to become resistant. Therefore, low chemical treatment levels could be applied with other control methods (*viz.,* cultural, biological, and integrated management controls) to prolong their effectiveness against insect pests and reduce the chance of these insects' outbreak.

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Table 1.3: Examples of typical insecticides used to control insect pests in citrus orchards.

Insecticide	Active Ingredient	Target Insect Pest	Some potentially vulnerable Insect species
Walker 240 SC	Methoxyfenozide (diacylhydrazine)	*Thaumatotibia leucotreta*	Apis spp., Coccinellidae spp., Chrysopidae spp., Trichogramma spp., Aphidius spp., Carabidae spp., Lycosidae spp.
MAINTAIN 200 SP	Acetamiprid (acetamidine)	*Scirtothrips citri*, *Frankliniella occidentalis*	Apidae spp.
IMIDOR 350 SC	Imidacloprid (chloronicotinyl)	*Aonidiella aurantii, Aphis gossypii*, *Diaphorina citri*	Apidae spp.
HARRIER 500 EC	Mercaptothion (organophosphate)	*Ceratitis capitata, Ceratitis rosa Karsch, Planococcus citri, Lepidosaphes beckii, Toxoptera aurantii, Scirtothrips citri,*	Coccinellidae spp., Syrphidae spp., Carabidae spp.
SPIROFEN 240 SC	Spirodiclofen (tetronic acid)	*Panonychus citri, Tetranychus urticae*	Aphidius spp., Coccinellidae spp., Phytoseiidae., Trichogramma spp., Apidae spp.
TIVOLI 240 SC	Spirotetramat (tetramic acid)	*Planococcus citri, Phyllocoptruta oleivora, Scirtothrips citri, Aleurothrixus floccosus*	Aphidius spp., Coccinellidae spp., Phytoseiidae., Trichogramma spp., Apidae spp.

https://www.villacrop.co.za/product-category/insecticide

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1.7.3. Cultural control

Cultural control manipulates agroecosystems to create environmental conditions that are less favourable for insect pests; these conditions often disrupt life cycles, resulting in the reduction of their field populations (Grout, 2019). In the citrus industry, orchard sanitation and tree pruning are essential cultural control methods to reduce insect pests (Citrus Academy, 2017). For example, dry fruits left hanging in the citrus trees were found to attract a fruit weevil pest, *Araecerus fasciculatus* (De Geer)(Coleoptera: Anthribidae), which then multiplies and threatens the young and mature fruits of this plant (Grout et al., 2023). Additionally, Moore and Kirkman (2008) demonstrated that weekly citrus orchard sanitation conducted from December to June could decrease *T. leucotreta* fruit infestation by an average of 75%.

A favoured cultural control method in citrus orchards involves planting tree varieties resistant to insect pests and diseases (Grout, 2019). This approach discourages potential insect pests from attacking the concerned trees and reduces the chemical pesticides applied against these insects (Grout, 2019). For example, resistant citrus varieties have been found to discourage attacks by insect pests like Aphididae spp. and Aleyrodidae spp. (Urbaneja et al., 2020). Further, diseases like citrus canker and greening can be discouraged by planting resistant citrus plants (Ali et al., 2023); these resistant citrus varieties can reduce up to 70% of field populations of *Diaphorina citri* Kuwayama (Hemiptera: Liviidae).

1.7.4. Biological control

Biological control is the most preferred method for managing pests, and it encompasses several approaches, with classical and augmentative methods (Moore, 2021). In the South African citrus industry, augmentative biological control programs against potential insect pests have been practised for several decades with a good record of success (IAEA, 2021; see Table 1.4). An iconic augmentative biocontrol program in other parts of the world involved the introduction of the predatory *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) and a parasitoid, *Lestophonus iceryae* Williston (Diptera: Cryptochetidae), against *Icerya purchasi* Maskell (Hemiptera: Monophlebidae), which is a significant pest of citrus trees in California (Malek, 2020). Although augmentative biological control methods offer environmentally sustainable solutions to the management of insect pests in crop farms, the success of this approach lies in the continuous release of insect natural enemies (Moore and Hattingh, 2004).

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Interestingly, conservation biological control (CBC) has been gaining attention and is considered an alternative approach to strengthen augmentative release efforts. Conservation Biological Control is an ancient approach to managing and preserving functional ecosystems (Perfecto and Vandermeer, 2015). In CBC programs, diverse vegetation is either conserved or introduced (Johnson, 2008). Most importantly, diverse plant species that support the high recruitment of insect parasitoids and potential insect pest predators in agricultural lands are maintained (Johnson, 2008). For example, introducing floral resources and non-crop habitats in Quebec apple orchards increased the abundance of predatory insects, causing a reduction in insect pest populations, including codling moths (Bostanian et al., 2004).

Similarly, a study in olive groves showed that increased natural vegetation landscape complexity resulted in higher densities of beneficial arthropods against the populations of olive fruit flies (Albertini et al., 2017). In Spain, the introduction of wildflower strips in citrus orchards significantly increased predatory insects, which controlled field populations of *Tetranychus urticae* Koch (Arachnida: Trombidiformes: Tetranychidae) (Aguilar-Fenollosa et al., 2011). Lastly, a study conducted in China found that orchards with companion plants showed a 65% increase in the biodiversity of natural enemies compared to orchards without such plantings. This finding highlights the critical role that refuge habitats, such as companion weeds, play in sustaining predator populations and reducing the need for repeated introductions of biological control agents (Niu et al., 2014). Further, Irvin et al. (2021) showed that incorporating plants, such as alyssum and buckwheat, into citrus orchards attracted predators to control populations of *D. citri*. Complementary research by Irvin and Hoddle (2021) found that buckwheat attracted beneficial insects and enhanced the longevity and reproductive success of *Tamarixia radiata* Waterston (Hymenoptera: Eulophidae), a parasitoid critical for controlling *D. citri*.

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Table 1.4: Some examples of biological control programs in citrus production orchards.

Insect pest	Biological control agent	Control status	References
Pseudococcidae spp.	*Coccidoxenoide peregrinus*	Partially Controlled	(Wakgari and Giliomee, 2003)
Thaumatotibia leucotreta	*Cryptophlebia leucotreta* granulovirus (CrleGV)	Partially Controlled	(Moore et al., 2002)
Ectomyelois ceratoniae	*Trichogramma cacoeciae*	Partially controlled	(Hached et al., 2021)
Aleurothrixus floccosus (Maskell)	*Cales noacki*	Partially controlled	(Sakin and Ulusoy, 2009)
Toxoptera citricida (Kirkaldy),	*Chrysopidae, Coccinellidae, Syrphidae*	Partially controlled	(López Arroyo, 2009)
Aonidiella aurantia	*Aphytis* spp.	Under control	(Grout and Richards., 1991)

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Another biocontrol effort that has recently gained attention is the predation of insect pests by insectivorous volant vertebrates, including birds and bats (Kolkert et al., 2020). When niche habitats of these vertebrates are well maintained, their populations thrive, increasing predation pressure on potential insect pests (Kolkert et al., 2020). This biocontrol contribution could lead to fewer requirements for chemical pesticide application in crop farms. For example, bats have been found to reduce the field populations of major insect pest, the two-spotted stink bugs *Bathycoelia distincta* Distant (Hemiptera: Pentatomidae), threatening macadamia fruits (Weier et al., 2018). Linden et al. (2019) estimated that birds and bats contribute approximately USD 5,000 per hectare per year through their role in biological control, reducing pest populations of macadamia in the Levubu area, Limpopo, South Africa. A recent study conducted in the Tshipise citrus area, Limpopo, analysed bat diets and revealed that bats consume a wide range of insect species, with a particular preference for lepidopterans. Significant citrus pests were consumed, including *T. leucotreta* and *Ectomyelois ceratoniae*, both of which were present in the diets of all bat foraging groups. These findings suggest that insectivorous bats likely play a crucial role during moth pest outbreaks, providing valuable pest control services that offer ecological and economic benefits across different landscapes (Khavheli, 2024).

1.7.5. Integrated Pest Management

Pest management plans improved as researchers sought better solutions to insects like *Aonidiella aurantii* Maskell (Hemiptera: Diaspididae) and *T. leucotreta* developing resistance to chemical pesticide treatments (Grout, 2015). This need for effective control methods led to the testing and implementation of Integrated Pest Management (IPM) plans. IPM is a decision-making process involving the coordinated use of multiple strategies to optimise pest control, ecologically and economically sustainable (Ehler, 2006). This approach integrates techniques such as biological control (See section 1.7.4), habitat modification, adjustments in cultural practices (section 1.7.3), and the deployment of pest-resistant rootstock cultivars (Ehler, 2006). As part of IPM, insecticides are selected and applied to minimise risks to human health, beneficial and non-target organisms, and the environment (Mehmood et al., 2016).

In South Africa, *T. leucotreta* is managed before harvest through strategies, including weekly removal of infested fruit (sanitation), application of a genus-specific granulovirus (Moore et al., 2004), and mating disruption techniques. Additional control methods involve attract-and-kill tactics, augmentative releases of the egg parasitoid *Trichogrammatoidea cryptophlebiae*

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Nagaraja (Hymenoptera: Trichogrammatidae), and the use of spinetoram or chlorantraniliprole sprays (Moore and Hattingh, 2012). Furthermore, the Sterile Insect Technique (SIT) has been implemented in parts of the Western Cape and Eastern Cape provinces, involving the release of sterilised adults of this moth in large numbers. Historically, *T. leucotreta* control in citrus orchards focused on preventing economic losses by using pheromone traps to monitor pest levels and applying treatments when pest counts exceeded specific thresholds (Coombes et al., 2024. By adhering to established thresholds, growers can optimise their pest management strategies, balancing the need for effective control with environmental considerations and preserving beneficial insect populations. For example, a study by Malan et al. (2011, 2018) in citrus orchards of the Western Cape, Eastern Cape, and Mpumalanga demonstrated an Integrated Pest Management approach for False codling moth, combining pheromone trapping, entomopathogenic nematodes, and cultural sanitation to reduce pest populations by up to 75% without extensive chemical intervention.

This study aimed to quantify arthropod diversity in citrus orchards and analyse their interactions with other species and the surrounding landscape to inform the development of IPM strategies. To our knowledge, no prior research has quantified arthropod diversity in this region of South Africa. Our approach builds on existing landscape ecology studies (e.g., Tscharntke et al., 2005; Fahrig et al., 2011) by focusing on perennial crop systems, where knowledge gaps persist despite advances in ecological intensification.

The specific objectives were to:

- Quantify arthropod diversity in citrus orchards across different habitat types and spatial scales.
- Examine the influence of landscape heterogeneity (compositional and configurational) on arthropod community structure.
- Assess the ecological role of insectivorous flying vertebrates, using exclusion experiments to evaluate their impact on pest control and citrus fruit damage.

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CHAPTER TWO

THE INFLUENCE OF LANDSCAPE HETEROGENEITY ON CITRUS AGROBIODIVERSITY AND ITS ROLE IN CONSERVATION BIOLOGICAL CONTROL

Abstract

Agricultural intensification and expansion have driven landscape fragmentation and homogenisation, rapidly decreasing farmland biodiversity and compromising essential ecosystem services like natural pest control, pollination, and nutrient cycling. Enhancing landscape heterogeneity has been proposed to counteract these effects, as diverse landscapes can support more varied arthropod communities. However, the relationship between landscape structure and arthropods within monoculture perennial crops is complex, with landscape and local-scale factors playing important roles. This study examined the influence of landscape diversity and spatial configuration on arthropod richness and abundance. The study analysed landscape-scale diversity metrics and the configuration of dominant habitats within a landscape context, focusing on both landscape and local scales. Generalised linear mixed-effect models showed that landscape heterogeneity positively affected species richness and abundance at a broader scale. However, habitat patch size also mattered, with larger crop fields positively affecting richness but larger woodlands negatively impacting abundance. At the local scale, sites dominated by riparian and edge habitats supported higher species richness, while landscapes transitioning from cropland to woodland had lower abundance. These findings highlight the importance of maintaining landscape heterogeneity, particularly edge and riparian zones, to enhance arthropod diversity within citrus agroecosystems. The study's approach provided a comprehensive analysis of how landscape elements contribute to biodiversity, demonstrating that tailored management strategies could promote ecological resilience in agricultural settings. This study contributes significant insights into agroecological management, highlighting the need for balanced habitat diversity to support beneficial arthropod communities and ecosystem services in South African citrus landscapes.

Keywords: integrated pest management; agricultural landscapes; habitat fragmentation; arthropod diversity; ecosystem services and disservices; conservation biological control

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2.1. Introduction

Changes in land use, particularly the intensification and expansion of agriculture, have been closely linked to the rapid decline in biodiversity across numerous landscapes (Benton et al., 2003; Bianchi et al., 2006). This biodiversity loss is driven primarily by habitat fragmentation and landscape homogenisation (Gossner et al., 2016). Simplified and fragmented agricultural landscapes often compromise critical ecosystem services, such as pollination, nutrient cycling, and pest control (Altieri, 1999; Bianchi et al., 2006; Losey and Vaughan, 2006; Zhang et al., 2007; Power, 2010; Dainese et al., 2019). In the citrus industry, several chemical-based and non-chemical (cultural and biological) control strategies have a good track record of success, but have some limitations in controlling insect pests. Despite this control success, conservation biological control (CBC) measures were never integrated into these control strategies. It entails several insect pest control benefits from the native biodiversity, and this control approach is more compatible with cultural and augmentative insect release control measures (Ehler, 1998; Pell et al., 2010; Seastedt, 2014). Importantly, CBC seeks to complement the management of insect pests by supporting populations of natural enemies readily available in the agroecosystem (Ehler, 1998; Pell et al., 2010; Seastedt, 2014). When the densities of insects' natural enemies are increased, their effectiveness as either predators, parasitoids or pathogens is enhanced (Ehler, 1998; Pell et al., 2010; Seastedt, 2014). Besides the cultivated citrus plants in South Africa, citrus are usually off the bare ground; thus, the little patches of wild plants and some aquatic sources could contribute to CBC practice unattended. For instance, the augmentative release of natural enemies can be implemented effectively in relatively small areas, while it becomes challenging (but not impossible) for large-scale applications (Moore, 2021a).

Thus, conserving naturally occurring predators and parasitoid populations remains attractive, practical, and universally applicable (Moore, 2021). Despite the potential of CBC in reducing field insect populations (Ehler, 1998; Pell et al., 2010; Seastedt, 2014), this control measure has never been explored in the South African citrus production systems. Interestingly, researchers have also explored CBC in citrus systems through habitat manipulation techniques, including intercropping (Hazarika et al., 2001; Zhou et al., 1994; Olkowski and Zhang, 1998), cover cropping (Mailloux et al., 2010), structural changes (Van Mele and Cuc, 2000), weed tolerance (Van Mele, 1998), and the provision of alternative food resources (e.g. Powder milk and sugar; López Arroyo, 2009), to enhance the efficacy of natural enemies in citrus orchards.

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These targeted interventions highlight the potential of CBC to strengthen pest control and promote biodiversity within citrus systems. Moreover, the potential of CBC could be derived from the success of organic citrus orchards with diverse understory herbaceous species (Silwana et al., 2023).

While local-scale interventions have been tested, the interaction between local management practices and broader landscape structures in shaping arthropod communities and the effectiveness of CBC still needs to be better understood. A comprehensive understanding of CBC requires adopting a landscape-scale perspective to evaluate the role of habitat composition, connectivity, and heterogeneity in supporting natural enemies and enhancing ecosystem services (Tscharntke et al., 2007). Incorporating this broader perspective is crucial for developing sustainable pest management strategies in citrus orchards. Increasing farmland heterogeneity offers a promising approach to enhancing biodiversity without compromising agricultural productivity (Batáry et al., 2011). Diverse landscapes provide complementary resources and habitats across space and time, allowing more species to persist by fulfilling their varied and seasonally extended resource needs or accommodating their distinct ecological niches (Fahrig et al., 2011; Kremen et al., 2012; Rusch et al., 2013; Schellhorn et al., 2015). Functional diversity ensures ecosystem stability and resilience, maintaining essential pest regulation and pollination maintenance under environmental stress levels (Elmqvist et al., 2003; Tilman et al., 2014). Effectively managed crop and non-crop habitats create stable environments that promote biodiversity and agricultural sustainability (Sattler et al., 2020; Tscharntke et al., 2021).

Therefore, this study examines the status of CBC in the present nature of landscape heterogeneity associated with citrus orchards by quantifying and comparing the abundance of arthropods (pests, predators, parasitoids, pollinators, etc). It evaluates how landscape heterogeneity and context shape arthropod diversity. Landscape structure impacts arthropod communities differently across spatial scales (Gabriel et al., 2010; Jackson and Fahrig, 2015). While landscape-scale studies focus on broader spatial arrangements and ecological connectivity, local-scale assessments examine individual fields or habitat patches, providing insights into detailed species interactions and community dynamics (Swan et al., 2021). Habitat size, connectivity, and compositional heterogeneity are pivotal in shaping arthropod communities and ecosystem functions at both scales (Dunning et al., 1992; Wu and Qi, 2000).

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Understanding these dynamics is essential for effectively enhancing biodiversity and managing its potential drawbacks. By analysing landscape heterogeneity, this study informs Community-Based Conservation strategies within the broader context of pest management. This study aims to investigate the influence of landscape heterogeneity on arthropod diversity by addressing three key objectives. It seeks to 1. quantify how variations in landscape diversity affect arthropod abundance and species richness across different habitats, 2. evaluate the role of habitat size in shaping these attributes, and 3. analyse how habitat types at various spatial scales influence arthropod abundance. By exploring these aspects, the study aims to provide insights into the relationship between landscape composition and arthropod diversity, contributing to better management of agroecosystems to support biodiversity and ecosystem services.

2.2. Materials and methods

2.2.1. Study area

The study was conducted in the Tshipise area within the Vhembe District, Limpopo Province, South Africa (Figure 2.1). This region features the Musina Mopane Bushveld (Mucina and Rutherford, 2006), dominated by savannah, grassland, and forest biomes (Department of Environmental Affairs et al., 2014). The climate features an annual rainfall of 400-600 mm, with temperatures ranging from 15°C in winter to 35°C in summer (South African Weather Services, 2023). The area includes citrus orchards adjacent to the Nzhelele River, comprising diverse habitats. We collected data from five citrus orchards, namely, Doreen (DB), Nzhelele Valley Estate (NVE), Hayoma Estate (HE), Alicedale Estate (AD), Maswiri Boerdery (MS), and Maremani Nature Reserve (NR). The DB and MS study areas consisted of two separate orchards that were 1.5 km away from each other. All the study areas were at least 5 km apart to ensure spatial independence. We selected orchards based on the diversity of habitats they encompassed, ensuring the presence of citrus cropland of varying sizes and ages, water sources, and patches of natural habitat.

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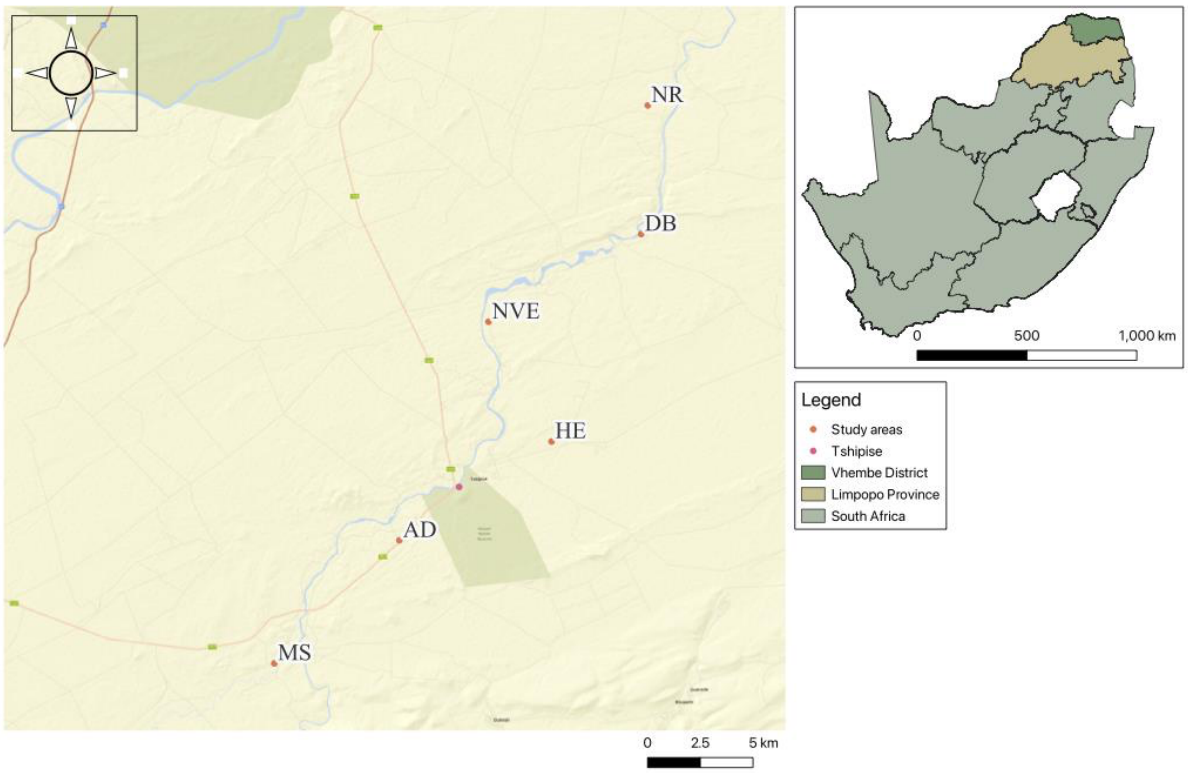


Figure 2.1: The five citrus study areas: DB (-22.501680, 30.248721), NVE (-22.538475, 30.182068), HE (-22.590684, 30.210313), AD (-22.631208, 30.140695), and MS (-22.686619, 30.074106) and the Maremani Nature Reserve NR (-22.425019, 30.221862) are shown on the map of the Tshipise agricultural area, in the Vhembe district, Limpopo, South Africa—imagery: ESRI (2024).

Orchard management

The study area had similar layouts and designs, with standard tree spacing of 6-7 meters between rows and 3-4 meters between individual trees. However, AD stood out with its windbreaks of the common bamboo, *Bambusa vulgaris* Schrad. ex J.C.Wendl (Poaceae), and the whistling pine, *Casuarina equisetifolia* L. (Casuarinaceae). The orchards primarily used drip (AD only) and sprinkler irrigation systems. Soil moisture sensors and evaporation data were used to create irrigation schedules that met the trees' water needs. Orchards HE and MS did not use these advanced irrigation practices and irrigated weekly. Most orchards integrated fertigation into their irrigation systems to optimise tree nutrient delivery. At the time of the study, orchard DB had an abandoned section for at least two years, while orchard AD used an Integrated Pest Management (IPM) approach for pest control. Chemical controls were only used when pest populations reached Economic Injury levels (EIL). All orchards followed an annual pruning schedule. Ground cover crops were present in four orchards, except for AD. Additionally, using recommended scouting devices, these orchards were under surveillance for

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insect pests, including *Thaumatotibia leucotreta* (Meyrick) (Lepidoptera: Tortricidae, *Ectomyelois ceratoniae* (Zeller) (Lepidoptera: Pyralidae), and Tephritidae spp. Lastly, orchards HE and MS had been neglected before the establishment of this study, and new proper orchard management had recently been implemented.

Maremani Nature Reserve Management

The Maremani Nature Reserve constitutes 40,000 ha of tropical savannah in northernmost South Africa (https://www.maremani.com/). The Nature Reserve is a crucial conservation area dedicated to preserving biodiversity and promoting sustainable land use practices. The reserve covers various ecosystems, including savannahs, wetlands, and riverine forests, which are vital in conserving multiple plant and animal species. The primary focus of the reserve's management is to protect and restore these essential ecosystems, ensuring the ecological health of the reserve's varied habitats to support its diverse wildlife populations. Therefore, this reserve is shaped mainly by the conserved animals in the absence of anthropogenic activities.

The sampling sites.

The sampling sites were categorised based on the landscape's habitat types, which included crop, woodland, and riparian zones. Study trees were randomly chosen within each category to ensure a representative sample across the landscape. In September 2023, we sampled 33 points across the study areas: orchard interior (number of sampling points (n) = 10), orchard edge (n = 12), woodland (n = 5), and riparian (n = 6). In January 2024, we sampled 29 points across the study areas Orchard Interior (n = 9), Orchard Edge (n = 11), Woodland (n = 4), and Riparian (n = 5) (Figure 2.1) to capture seasonal variations in arthropod diversity. To maintain spatial consistency, the same sampling sites and study trees surveyed in September were revisited in January, ensuring that observed differences reflected seasonal changes rather than spatial variation. Sampling in September corresponds with early spring, when arthropod activity increases with blooming citrus, while January demonstrates the peak of summer, providing insights into the arthropod community during warmer conditions and fruit development. Our study examined how land fragments influence arthropod diversity within a 300-meter radius around each study area (Figure 2.2).

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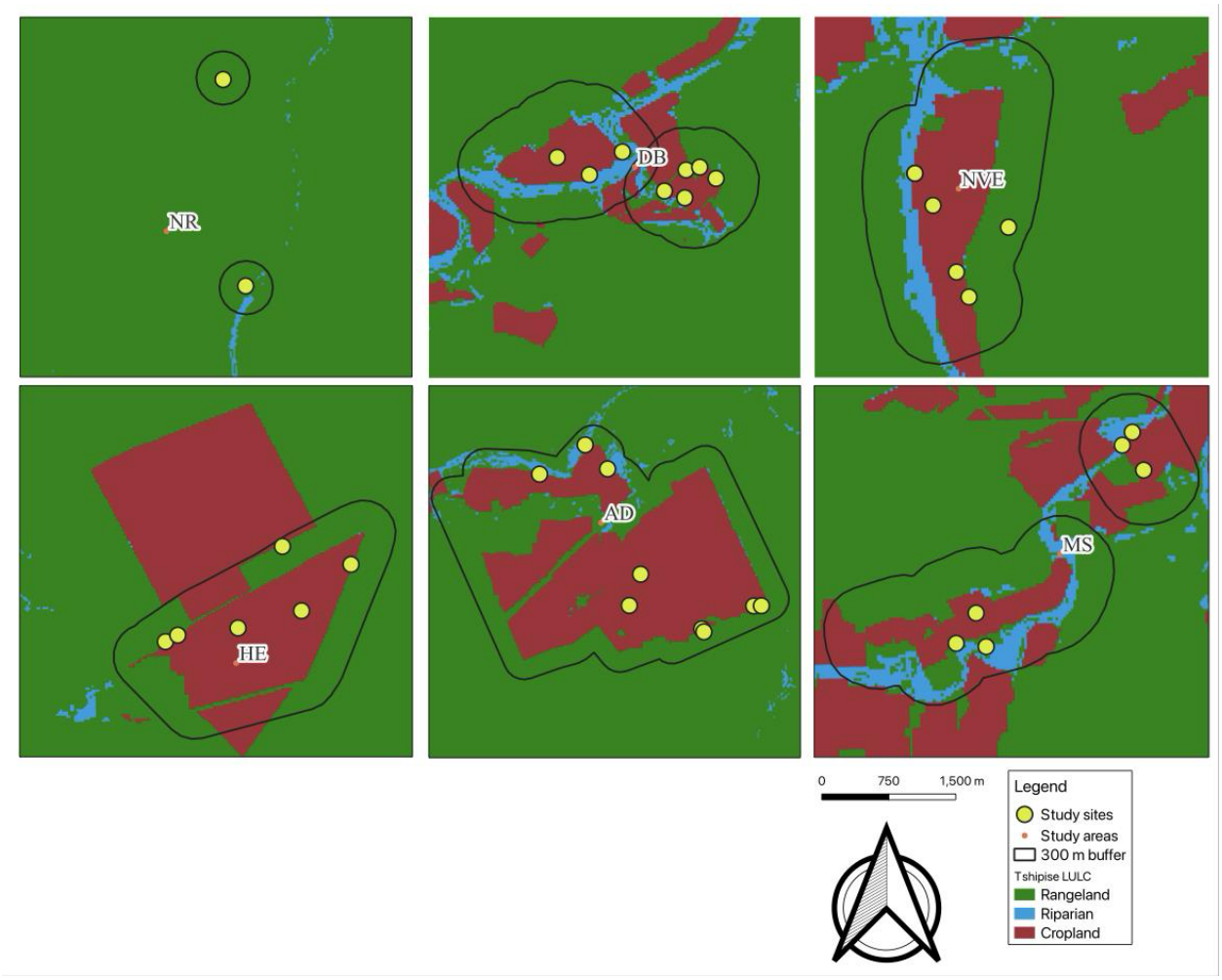


Figure 2.2: A 300-m radius LULC map showing the nature reserve's surroundings and the five studied citrus orchards shown here with 100-m buffered study sites.

2.2.2. Study design

This study examined how landscape composition and spatial configuration influence arthropod diversity at different scales. At the first scale, we looked at the landscape-scale structure (composition and configuration)—that is, at each area scale. We applied a 300-meter buffer around each farm (Stotter, 2009) and extracted various landscape metrics. Landscape diversity metrics (*viz.*, Shannon diversity index, Shannon evenness index, and Simpson diversity index) describe the landscape composition. At the same time, we specifically examined patch size and shape metrics to describe the spatial arrangement (*i.e.,* largest patch index).

At the second scale, we investigated how local-scale composition affects arthropod diversity—that is, at each sampling site by buffering each sampling site with a 100-meter radius and extracting land cover percentages to capture fine-scale habitat features, such as woodland, riparian zone, and cropland. This allowed us to assess large-scale landscape and localised

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effects on arthropod diversity. Through a quantitative research approach, we evaluated the impact of landscape structure on arthropod diversity. The landscape variables describing the structure were derived from the Geographic Information System (GIS) and remote sensing data obtained through computer-automated imagery from the South African Department of Forestry and Fisheries (DFFE).

2.2.3. Plants and arthropods

The study sampled arboreal insects inhabiting trees within citrus orchards and the surrounding natural habitats. Arboreal arthropods are a group of insects characterised by intricate community structures, various feeding traits, and substantial taxonomic diversity and have been identified as particularly vulnerable to the impacts of agricultural intensification (Santos et al., 2007). Although the study generally focused on arboreal insects, it was also our desire to encounter the diverse insect species (~20) that have been identified as critical pests in citrus orchards (see Chapter 1; Urbaneja et al., 2020), including *Thaumatotibia leucotreta* and *Ectomyelois ceratoniae* (Grout and Moore, 2015). Citrus orchards in this region are bordered by woodland and riparian zones, creating a mosaic of habitats. In the citrus orchards, we sampled arthropods on three citrus tree species: *Citrus sinensis (L.)* Osbeck, *C. limon* (L.) Osbeck, and *C. paradisi* Macfad (Rutaceae). These tree species were considered the representative of all commercialised *Citrus* spp. Despite a high diversity of common arthropods in these *Citrus* spp, these plants recruit similar suites of insect pest species (Niu et al., 2021; Liu et al., 2023). In the natural habitats, sampling was conducted on trees such as the umbrella thorn *Vachellia tortilis* (Forssk.) Galasso and Banfi (Fabaceae), the leadwood *Combretum imberbe* Wawra (Combretaceae), the mopane *Colophospermum mopane* J.Léonard (Fabaceae), and the ana tree *Faidherbia albida* (Fabaceae). These tree species were dominant in this area, contributing the largest biomass perceived to support high diversity and abundance of arthropods.

2.2.4. Arthropod sampling

The fogging technique (Adis et al., 1997) was used to sample insects in tree canopies at each site. This method, commonly employed in entomological research, entails spraying a fine mist of insecticide containing Dyna-fog™ ULV solution (Adis et al., 1997). A commercial portable 1.2L VectorFog thermal fog machine equipped with a small fuel tank was used to disperse a hot cloud of ultra-low volume droplets of the Dyna-fog™ ULV solution (active ingredients:

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deltamethrin (10 g/L), pyrethroid (6 g/L), and piperonyl butoxide (50 g/L)) in a hydrocarbon mixture derived from petroleum oil (Adis et al., 1997) at a ratio of 1:3. Pyrethrum was chosen for its biodegradability and suitability for sensitive habitats (Hauser and Riede, 2015).

Arthropods were sampled from two adjacent tree canopies within each habitat type (Figure 2.3A & B). Before fogging, shrub plants beneath and around the selected study trees were cleared to prevent overlapping of sampling focus between these plants and to make space for the collection sheets (9 x 6 m). Fogging commenced 2 to 3 minutes after clearing the understory cover. Durable plastic sheets were laid on the ground under the sampled trees at each study site. Fogging lasted 5 minutes (Adis., 1997), and the sheets were left for 30 minutes to collect insects (Figure 2.3C). After 20 minutes, branches were shaken to release trapped or stuck arthropods (Schoeman, 2020). Sampling was conducted at dawn or during calm, sunny conditions to ensure the chemicals reached the necessary heights of the study trees.

Trees were selected using stratified random sampling to ensure coverage of different habitat types, including cropland (interior and edge), woodland, and riparian zones. Each sampling site was spaced at least 50 meters apart, and sampling occurred 10 meters from habitat edges to minimise edge effects. Arthropods were collected by hand, using putters and forceps.
Collected arthropods were immediately placed in a solution of propylene glycol and 70% ethanol (1:50 ratio; Figure 2.3D) to prevent species from drying out and transported to the University of Venda's Entomology laboratory in the Biological Sciences Department for identification, which was done to the order level due to the limited insect taxonomy expertise guided by Picker et al., (2014). Despite this limitation, insect pests were identified at the species level, guided by several reports on their taxonomy and field occurrence (see Tables 1.3 and 1.4). Identifying these insect pests was critical to understanding their role in citrus fruit production, which we explored further in Chapter 3. Some insect pests were only identified during preliminary evaluations of the insect's impact on the experimental citrus fruits in Chapter 3.

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Figure 2.3: Sampling methods: **A.** Two adjacent citrus trees with sheets laid on the ground. **B.** Two adjacent non-crop habitat trees. **C.** Collection process. **D.** Placing arthropods immediately into preservation mixture.

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After the identification process, the diversity and abundance of insect orders were established. Arthropods were further classified into five groups considered agriculturally crucial in the citrus orchards: (1) herbivore insects (including significant pests); (2) insect predators; (3) insect parasitoids; (4) insect pollinators; and (5) other "secondary" functional groups, including decomposers, anthophilous species, and uncommon species (fewer than five individuals at a site, regardless of habitat cover type), found in literature, e.g., Grout and Moore, 2015. To aid the grouping of these arthropods, feeding mouthparts and other body features such as oviposition posteriors were also employed to characterise these insects; the diagnostic features were adapted from the book Insect Mouthparts (form, function, development, and performance) (Krenn, 2019). Arthropods were returned to their fixing solution at the end of this analysis and shelved as voucher specimens in a reference collection.

2.2.4. Quantifying landscape heterogeneity

a. Landscape (area-scale) and local (site-scale) composition heterogeneity

We used the South African National Land Cover (SANLC) 2022 dataset, derived from 20-meter multi-seasonal Sentinel 2 satellite imagery, to extract land cover classes for both landscape scale (area scale) and local scale (site scale) (Figures 2.1 and 2.2). The imagery, covering the period from January 1, 2022, to December 31, 2022, represents the entire temporal range of available Sentinel 2 imagery. The SANLC 2022 dataset is based on the new gazetted land-cover classification standard (SANS 19144-2) and includes 73 classes of information. We cross-referenced the dataset with Google Earth imagery in QGIS. We used the SERVAL plugin (Pasiok, 2023) v 3.32.0 to correct for any difference in the land cover classes that were no longer accurate by the time of the study. Subsequently, we reclassified SANLC classes into three significant classes relevant to the study: woodland, riparian, and cropland (Table 2.1).

We used a 300-meter buffer around each farm for the landscape-scale analysis to calculate landscape composition. This distance was chosen based on the findings of Stotter (2009), which indicate that 200 - 400 meters from the orchard represent the maximum distance at which male *T. leucotreta i*s abundant. The classes (woodland, riparian, and cropland) were used to estimate landscape diversity metrics (*viz*., Shannon diversity, Shannon equitability, and Simpson diversity indexes). The diversity metrics were used to describe the composition at a landscape scale. We buffered each sampling site with a 100-meter radius at the local scale and extracted

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the percentages of the three classified land cover types (woodland, riparian, and cropland; Appendix 2.1) for further analysis.

Table 2.1: The land use land cover type classification based on the 2022 South African National Land-Cover Classes.

Land-cover classes	National land-cover classes 2022
Woodland	Contiguous Indigenous Forest, contiguous low thicket, dense forest and Woodland, open Woodland, open and sparse plantation, temporary unplanted plantations, sparsely wooded grassland, natural grassland, fallow land, old fields, herbaceous wetlands,
Riparian	Natural rivers, artificial dams, contiguous and dense plantations
Cropland	Cultivated commercial permanent orchards, cultivated annual crops

b. Quantifying landscape (area-scale) spatial configuration

In addition to landscape composition metrics, spatial configuration metrics were calculated exclusively at the landscape scale (within a 300-meter radius) to characterise the patch size of landscape classes, including woodland, riparian, and cropland. Since habitat area and heterogeneity are often highly correlated (e.g., Öckinger et al., 2010), these metrics were specifically chosen to provide a clearer understanding of patch size independent of compositional heterogeneity. Among these, the largest patch index (Cushman and McGarigal, 2019) was assessed to quantify the dominance of the largest patch within each land cover type to capture the influence of dominant patches on ecological patterns and processes.

The three subsets of landscape variables were calculated and are described in Table 2.2, with their measurement units (https://fragstats.org/index.php). We used the Landscape Ecology Statistics (LecoS) v3.0.1 plugin (Jung, 2012), a Python-based tool modelled after FRAGSTATS (McGarigal and Marks, 1995) to analyse 20-meter resolution raster land cover data. All geospatial information analyses were performed using QGIS 3.38 (QGIS Development Team, 2024).

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2.2.5. Statistical analysis

All statistical analyses were conducted using R version 4.3.1 (R Development Core Team, 2023). This analysis compared order richness, species richness, and abundance to landscape diversity, spatial configuration, and local scale habitat proportions (orchard interior, edge, riparian, and woodland). The fogging process was standardised at each sampling site to ensure uniform sampling effort. As a result, there was no need for effort correction. We calculated order richness as the count of observed orders at each site. Species richness was determined by counting the times an order was detected at each site.

Additionally, abundance was estimated as the total count of individuals for each order-site combination. We subsequently tested various biologically plausible hypotheses regarding the influence of landscape-scale and local-scale heterogeneity on arthropod diversity (Table 2.2). Additionally, we proposed plausible effects of various landscape variables on arthropod diversity (Table 2.3).

a. Landscape-scale analysis

We investigated the influence of landscape diversity (viz., Shannon diversity, Shannon evenness, and Simpson diversity indexes) on order richness, species richness, and arthropod abundance. The high correlation among the various landscape cover types also extended to the landscape diversity indices (Table S2.1). To address this, we performed a Principal Component Analysis (PCA) to minimise redundancy. The advantage of using PCA is that the axes (PC1 and PC2) are orthogonal (uncorrelated), allowing for independent interpretation of the variation in arthropod abundance. This created three main components representing the main patterns in the landscape diversity data (Table S2.2). The first two components explained 99% of the variation in landscape diversity and were retained for further modelling (Figure S2.1). PC1 represented the main axis of variation, with all the diversity metrics contributing equally (DIV_SH = 0.582, DIV_EV = 0.576, DIV_SI = 0.574). This suggested that PC1 has balanced contributions, as their loadings are similar and positive. PC2, DIV_SI has a robust positive loading (0.759), while DIV_EV has a strong negative loading (-0.640). DIV_SH has a smaller, slightly negative contribution. This suggested that PC2 captured a contrast between Simpson diversity (positive) and Shannon equitability (negative). Secondly, we examined the effects of the dominance of the largest contiguous habitat patch, which helped understand habitat fragmentation and how larger patches emphasising cropland affected the diversity of arthropods through connectivity, movement, and resource availability.

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b. Local-scale analysis

At the local scale, we assessed how habitat proportions (viz., woodland, riparian, and cropland) influence arthropod species richness, order richness, and abundance. Due to the high correlation in land cover types (Table. S2.1), we performed a PCA, generating three principal components for habitat cover type (Table. S2.3). The first two components explained 99% of the variation in land cover and were retained for further modelling (Figure S2.2). PC1 represented the main axis of variation, with woodland contributing a robust negative effect (-0.67) and cropland a strong positive effect (0.72), while the riparian zone had a minor influence (-0.122). This axis contrasts crop-dominated (positively) and woodland-dominated areas (negatively), with riparian zones playing a smaller role, reflecting an inverse relationship between crop-dominated and woodland-dominated areas. PC2, the secondary axis, showed a substantial negative contribution from the riparian zone (-0.898), a moderate positive contribution from woodland (+0.386), and a weak positive contribution from cropland (0.209). This dimension captures the contrast between riparian (strong negative load) and woodland areas (moderately positive). And crops have a smaller influence. This dimension captures the differences between riparian and woodland areas.

For both scales (i.e., landscape scale and local scale), we fitted Generalised Linear Mixed Effects Models (GLMM) with farms included as a random effect (Bates et al., 2015). Separate models were created for arthropod species richness, order richness, and abundance. Each model tested the effects of PC1 only, PC2 only, and PC1 + PC2 on species richness, order richness, and abundance. The models were contrasted with a null model and ranked based on the Akaike Information Criterion corrected for small samples (AICc) (Burnham and Anderson, 2002). Models within Δ 2 AICc were regarded as having equal support (Burnham and Anderson, 2002, and the model with the lowest AICc was retained for further inference. Model fit was evaluated by plotting residuals against fitted values and using QQ plots to check for the normality of residuals (Hartig, 2023, Figures S2.3 and 2.4). A likelihood ratio test was applied to assess the significance of variables (Felsenstein, 1981; Huelsenbeck and Crandall, 1997). A generalised linear latent variable model (GLLVM) was also applied for both constrained and unconstrained ordination, utilising the gllvm package (Niku et al., 2019), with model performance evaluated based on AIC values.

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Table 2.2: Description of landscape structural metrics

	Factors	Metric	Description	Abbr.	Unit (range)
Landscape Diversity Metrics	Landscape diversity	Shannon diversity Index	This metric quantifies a landscape's diversity of patch types, such as land cover classes. It considers the number of distinct patch types (richness) and their relative abundances (evenness).	DIV_SH	(≥ 0; ∞)
		Shannon evenness	Measures how equally distributed the different patch types are within the landscape. It describes whether one patch type dominates or if all patch types are represented in relatively equal proportions.	DIV_EV	(0;1)
		Simpson index	Measures the probability that two randomly selected patches will belong to different patch types. It emphasises dominance by giving more weight to the most abundant patch types.	DIV_SI	(0;1)
Composition Metrics	Habitat availability	Landcover	The physical material on the earth's surface, such as crops and woodland.		%(≥ 0)
Configuration Metrics	Patch size and shape	Largest patch index	The metric quantifies the dominance of the largest patch within a landscape	LPI	% (0;100)

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Table 2.3: Prediction of the landscape metrics and their influence on arthropod diversity

Hypothesis	Metrics	Prediction
Landscape diversity	DIV_SH DIV_EV DIV_SI	A mix of natural habitats and croplands in diverse landscapes increases arthropod abundance, order richness, and species richness.
Spatial configuration	LPI	Larger, dominant, and more simple habitat patches support greater arthropod abundance and richness.
Habitat cover type	Woodland Riparian zone Cropland	Habitat type across spatial scales strongly influences arthropod abundance, with local natural habitats having a more substantial positive impact than croplands.
Proximity of natural habitats	Woodland Riparian Orchard Edge Orchard Interior	Natural habitats close to citrus orchards enhance arthropod diversity by facilitating movement and boosting biodiversity, more specifically, warm and humid conditions facilitate the abundance.

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2.3. Results

2.3.1. Arboreal arthropod diversity in a landscape context

The fogging survey revealed a diverse community across various habitats with a total abundance of 34,991 individuals, representing 21 orders (Table 2.4). On average, the woodland contributed 33.53% of the total abundance and riparian zones (31.92%). The Orchard edge and interior showed comparatively lower contributions of 17.95% and 16.60%, respectively.

Arthropod orders display distinct patterns in their distribution across habitat types. Hemiptera contributes the highest proportions, with 59.61% in Riparian-Woodland habitats (Hereafter, remnant natural vegetation (RNV)) and 61.33% in Orchard Edge-Interior habitats (hereafter, cropland). Hymenoptera accounts for 52.79% of RNV habitats and 45.76% of cropland habitats. Coleoptera provides 50.45% of RNV habitats but only 19.85% of cropland habitats. Diptera shows contrasting percentages, contributing 7.91% in RNV habitats and 35.33% in cropland habitats. Araneae adds 11.69% in RNV habitats and 26.35% in cropland habitats.

Across the habitat groups, RNVs harbour more arthropod predators (Coleoptera and Araneae) and parasitoids (Hymenoptera) than Cropland habitats. Cropland habitats, however, contain higher proportions of insect pest species (Table 2.5), particularly Hemiptera and Diptera. Beneficial insects, including pollinators and predators, thrived in semi-natural habitats, while monoculture orchards exhibit limited support for these functional groups.

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Table 2.4: Summary Results on the Arthropod Abundance, Functional Traits, and Distribution Across Landscape Scales.

Arthropod Order	Total Abundance	Feeding Traits[1]	Riparian-dominate	Woodland-dominated	Cropland Edge	Cropland Interior
			$n = 6$	$n = 5$	$n = 12$	$n = 10$
Hemiptera	10561	H, Pr	2502	2265	3246	2548
Hymenoptera	8701	Pr, Pa, Po	2311	1926	3001	1463
Coleoptera	5958	H, Pr,	2309	1756	1123	770
Diptera	3839	H, Pa, Po	251	369	1382	1837
Araneae	3406	Pr	372	544	1397	1093
Orthoptera	1476	S	346	300	479	351
Acari	386	H	302	62	20	2
Blattodea	337	S	249	44	28	16
Mantodea	80	Pr	18	25	19	18
Neuroptera	66	Pr	6	2	34	24
Odonata	44	S	0	0	35	7
Phasmatodea	30	S	13	4	9	4
Solifugae	24	Pr	11	8	6	0
Pseudoscorpion	20	Pr	10	9	0	1
Dermaptera	17	Pr	0	8	1	8
Isopoda	17	S	11	5	1	0
Lepidoptera	15	H	0	0	0	15
Thysanoptera	6	H	6	0	0	0
Scorpiones	4	Pr	3	0	1	0
Isoptera	3	S	0	0	1	2
Chilopoda	1	S	0	0	0	1
Σ =	34991		8719	7327	10783	8160

[1] Insect functions are grouped as H = Herbivore (Leaf, stem, bark, fruit); Pr = Predator; Pa = parasitoids; Po = pollinator; S = secondary group (decomposer, anthophilous, and uncommon).

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Table 2.5: List of identified insect pest species emerging from the overall sampled arthropod across the study landscape scale.

Order	Family	Scientific Name	Feeds on [1]
Hemiptera	Monophlebidae	*Icerya purchase* Maskell	L, Tw, Br
	Pseudococcidae	*Ferrisia virgata* Cockerell	L, Fr, Tw
	Pseudococcidae	*Planococcus citri* Risso	L, Fr, Tw
	Diaspididae	*Aonidiella aurantii* Maskell	L. Fr, Br
	Pentatomidae	*Antestiopsis thunergii* Gmelin	F, Fr
	Pentatomidae	*Nezara viridula* Linnaeus	Fr
	Flatidae	*Decipha spp*. nymphs	L, Fr
	Fulgoroidea	*Empoasca distinguenda* ***Paoli***	L, Fr
	Deltocephalinae	*Penthimiola bella* Stål	L, Fr
	Triozidae	*Trioza erytreae* ***Del Guercio***	L, V
Coleoptera	Curculionidae	*Pantomorus cervinus* Boheman	L, Fr
	Chrysomelidae	*Colasposoma fulgidum* Bouche	L, F, Fr
	Chrysomelidae	*Cassida circumdata* Herst	L
	Anthribidae	*Araecerus fasciculatus* De Geer	Fr
Diptera	Tephritidae	*Bactrocera invadens* Drew, Tsuruta & White	Fr
		Ceratitis capitata Wiedemann	Fr
		Ceratitis rosa Karsch s. l.	Fr
	Drosophilidae	*Drosophila melanogaster* Lindsley	Fr
Lepidoptera	Pyralidae	*Endotricha sp.*	F, Fr
Thysanoptera	Thripidae	*Scirtothrips aurantii* Faure	L, Fr

[1.] Plant parts: L = Leaves. Tw = twigs. Br = Branches. F = Flowers. Fr = Fruits.

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2.3.2. The influence of landscape diversity (Shannon diversity, Shannon equitability, and Simpson diversity indices) on order richness, species richness, and arthropod abundance.

We found no evidence that landscape diversity indices influenced order richness, with the most parsimonious model being the null model (Appendix 2.2).

The null model was also most parsimonious for species richness, but the model with PC2 fell within 0.22 AICc units of the null model. A likelihood ratio test confirmed that adding PC2 significantly improved model fit (Chi = 5.37, df = 1, p = 0.020), thus retaining PC2 in the model. PC2 positively affected species richness (B = 1.53, p = 0.006), with species richness increasing from lower to higher PC2 values (Figure 2.3A). Negative loadings for DIV_EV (-0.64) and positive loadings for DIV_SI (0.75) in PC2 indicate species richness increases in sites with high DIV_SI and low DIV_EV.

For arthropod abundance, PC1 emerged as the most parsimonious model (Appendix 2.2), though the null model was within 0.21 delta AICc units. The likelihood ratio test suggested that adding PC1 significantly improved model fit (Chi = 5.81, df = 1, p = 0.01). PC1 significantly positively affected arthropod abundance (B = 0.27, p = 0.003; Figure 2.3B), suggesting that as landscape diversity (represented by high positive loadings across all three diversity indices) increases, arthropod abundance also increases.

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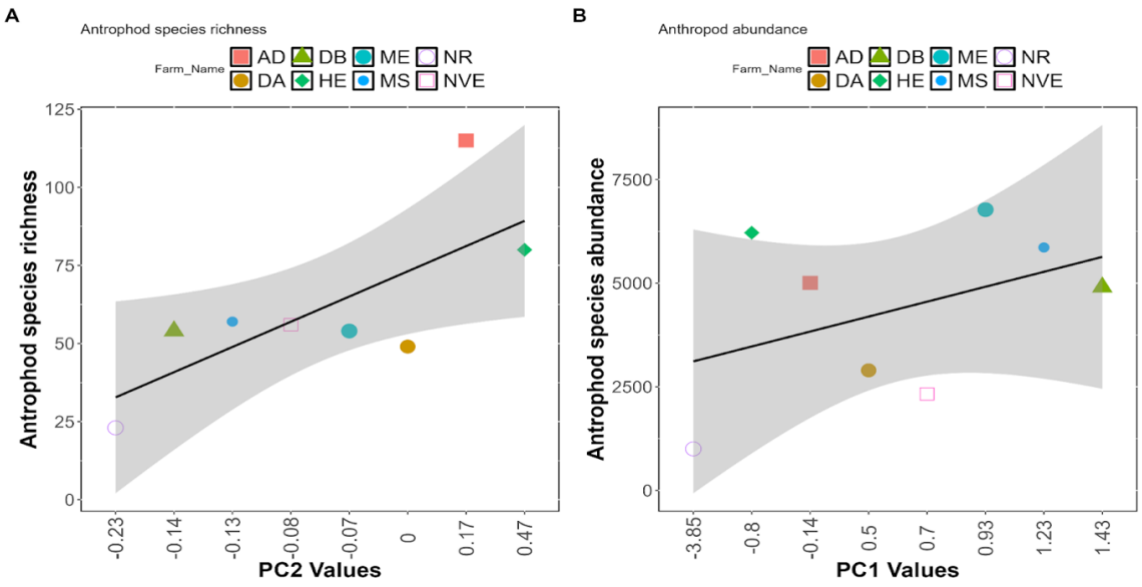


Figure 2.3: Relationship between principal components of landscape diversity and arthropod metrics.. (A) Species richness increased with higher values of PC2, which reflects a gradient from high variability in evenness (DIV_EV) to high Simpson diversity (DIV_SI). (B) Arthropod abundance increased significantly with PC1, which captures overall landscape diversity based on positive loadings from all three indices: Shannon (DIV_SH), Simpson (DIV_SI), and Evenness (DIV_EV).

2.3.2. The effects of spatial configuration (largest patch index) on arthropod abundance, order richness, and species richness

Our results showed no significant impact of any Largest Patch Index (LPI) on arthropod order richness (Appendix 2.3). However, we observed that LPI for cropland significantly and positively affected species richness ($B = 0.025$, $p = 0.0003$; Figure 2.4A), indicating that larger cropland patches support higher species richness. Riparian and woodland LPIs did not significantly affect species richness, suggesting consistency in species richness across varying LPI scores for these habitat types.

For arthropod abundance, woodland LPI was the most parsimonious model (Appendix 2.3), with abundance decreasing significantly as woodland LPI increased ($B = -0.023$, $p < 0.001$; Figure 2.4 B).

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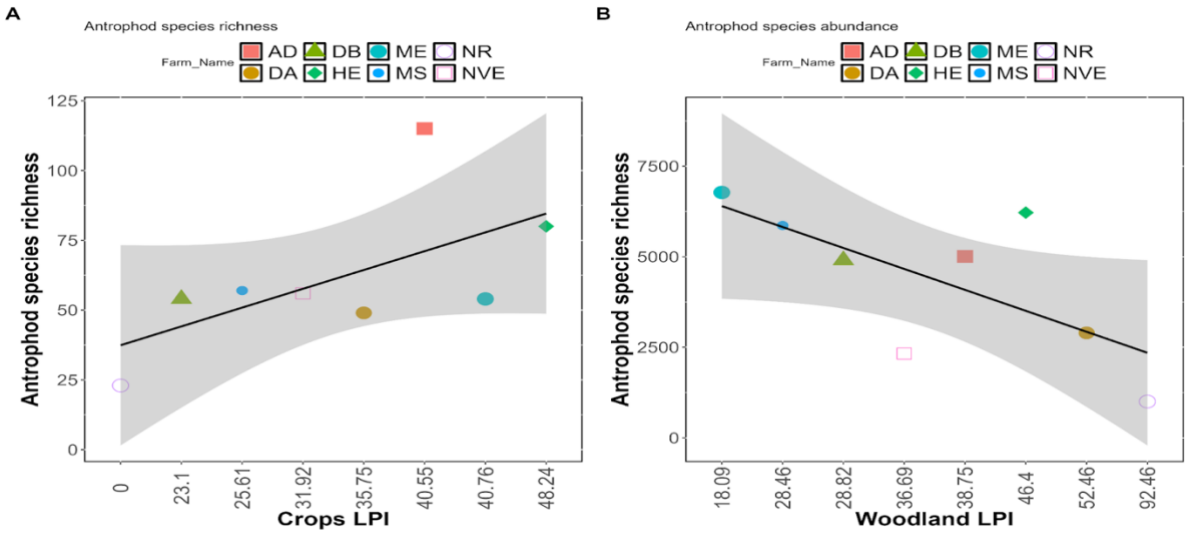


Figure 2.4: Largest Patch Index of the habitat types and their relationship with arthropod species richness**.** (A) Species richness increased significantly with higher cropland LPI, indicating that landscapes with larger, contiguous cropland patches support greater arthropod species richness. Riparian and woodland LPIs had no significant effect on species richness. (B) Arthropod abundance declined significantly with increasing woodland LPI, suggesting that larger woodland patches are associated with lower arthropod abundance in this context. Error bars represent ± standard error.

2.3.3. The influence of habitat cover (woodland, riparian, and cropland) on arthropod richness, order richness, and abundance at the local scale

Order richness did not respond significantly to the tested variables (Appendix 2.4). For species richness at the sampling site scale, PC2 provided the most parsimonious model (Appendix 2.4), although the model with both PC1 and PC2 was within 2 AICc units. Adding PC1 did not significantly improve model fit (LRT; Chi = 0.83, p = 0.359), so we retained only PC2. PC2 negatively impacted species richness (B = -0.14, p = 0.006; Figure 2.5A), with richness higher at sites dominated by riparian and edge landscapes, although PC2 explained only 18% of species richness variance (R^2m), which increased to 40% (R^2c) when accounting for random effects. Arthropod abundance declined with both higher PC2 (B = 0.034, p < 0.001; Figure 2.5B) and PC1 values (B = -0.02, p < 0.001; Figure 2.5C). PC2's strong negative loading for riparian areas (-0.892) and positive loading for woodland (0.427) suggest abundance decreases in sites transitioning from riparian to woodland-dominated landscapes (Figure 2.5B).

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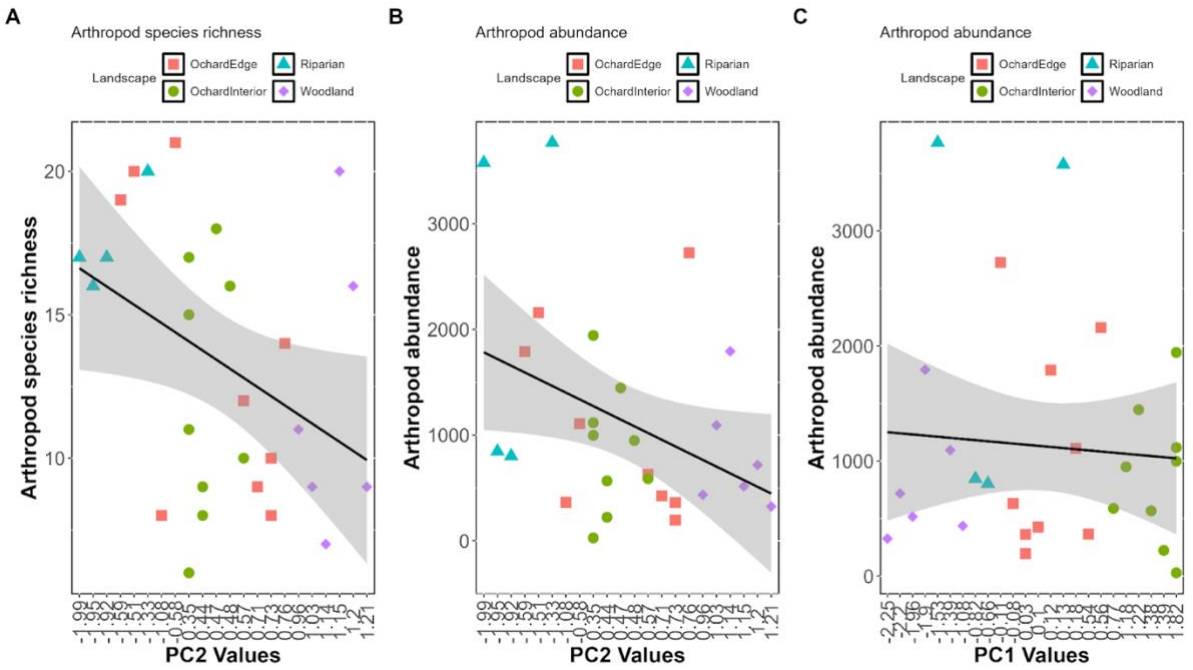


Figure 2.5: Generalised linear mixed model of arthropod richness and abundance across different habitat types. (A) Species richness was significantly negatively associated with PC2, which reflects a gradient from riparian and edge-dominated to woodland-dominated landscapes. Richness was higher at sampling sites dominated by riparian and edge habitats. (B) Arthropod abundance declined significantly with increasing PC2 values, indicating lower abundance in woodland-dominated landscapes compared to riparian areas. (C) Arthropod abundance also declined with higher PC1 values, which broadly represent gradients of habitat composition and configuration. Error bars represent ± standard error.

The community composition model, which included landscapes, showed the lowest AIC at 2853.27, compared to 3061.68 for the unconstrained models. Order composition remained consistent across landscapes (Figure 2.6), though edge landscapes displayed slightly more significant variation in composition.

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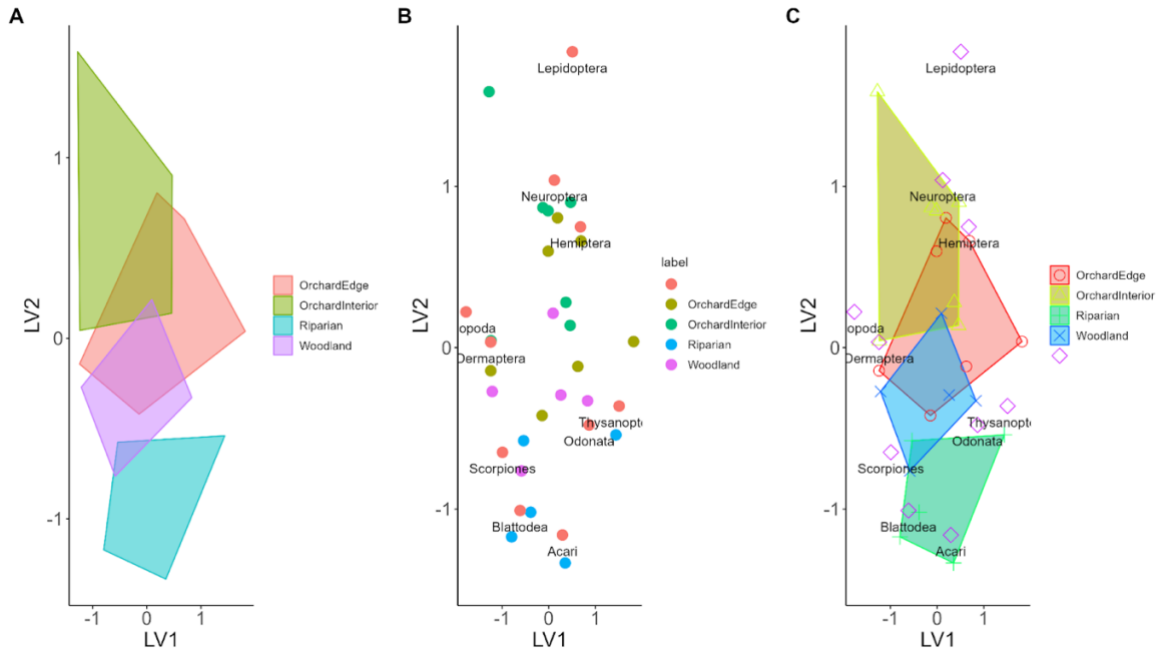


Figure 2. 6: Bayesian ordination of order-level community composition across the eight study areas.

2.4. Discussion

This study examined how landscape composition and spatial configuration within a broader landscape context influence arthropod richness and abundance. We aimed to understand the impact of landscape diversity and spatial arrangement on arthropod communities, providing insights into the ecological dynamics of agricultural landscapes. Our findings reveal significant variations in arthropod diversity and distribution across different habitat types and spatial scales within the citrus agroecosystem. The findings were consistent with previous studies suggesting that arthropod diversity is strongly influenced by the diversity of habitat types rather than being uniformly distributed across the landscape. This supports the growing body of literature emphasising the role of maintaining natural habitats to enhance biodiversity (Benton et al., 2003; Tscharntke et al., 2005; Bianchi et al., 2006; Fahrig et al., 2011).

2.4.1. Influence of landscape diversity and spatial configuration on order richness, species richness, and arthropod abundance

The results indicate that increased compositional heterogeneity, quantified by various diversity indices, significantly enhances arthropod richness and abundance. This suggests that diverse habitats provide multiple resources and niches that support larger populations. This finding aligns with existing ecological theories that suggest greater biodiversity within a habitat can

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lead to more stable and productive ecosystems (Tilman et al., 2014; O'Brien et al., 2017). Specifically, the increase in arthropod diversity observed in our study suggests that heterogeneous environments provide a wider array of niches and resources, which can support a greater variety of species. The relationship between compositional heterogeneity and arthropod diversity has important implications for ecosystem functioning, particularly in agricultural systems (O'Brien et al., 2017). Diverse arthropod communities often include beneficial species such as pollinators and natural pest predators, which are crucial in maintaining crop health and productivity (Gurr et al., 2016). By fostering environments with high compositional heterogeneity, farmers can enhance the presence of these beneficial organisms, potentially reducing the need for chemical pest control measures. This aligns with CBC principles, emphasising sustainable practices that leverage natural ecological processes. Our findings corroborate previous studies that have documented similar trends. For instance, Cardinale et al. (2012) found that increased plant diversity led to higher herbivore diversity, supporting a more complex food web. Haddad et al. (2011) also demonstrated that landscapes with greater compositional heterogeneity supported more diverse insect communities and exhibited greater resilience to pest outbreaks. These studies reinforce that promoting biodiversity through habitat complexity can be a crucial strategy for sustainable agriculture.

Regarding spatial configuration (largest patch index), the study found that the dominance of the large cropland positively influenced species richness, with a higher cropland index associated with increased richness. There can be several reasons for this result. First, the cropping areas in the study area were always located near the Nzhelele River. Thus, by mere proximity, we could expect that larger farms near the rivers will host more species. Our findings, consistent with those of Tscharntke et al. (2016) and Bianchi et al. (2006), show that spatial configuration significantly affects species richness and community composition. The positive correlation between cropland patch size and species richness likely reflects proximity to the Nzhelele River, which facilitates biodiversity through resource availability and connectivity (Fahrig et al., 2011).

Secondly, this result likely reflects the proliferation of pest species promoted by homogeneous cropland landscapes, consistent with the findings of Sirami et al. (2019) and Tscharntke et al. (2016), who demonstrated a positive association between landscape homogeneity and pest dominance.. The dominance of pests from orders such as Hemiptera, Lepidoptera, and Diptera—like mealybugs, weevils, leafhoppers, leaf miners, and fruit flies—highlights a

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critical vulnerability in monoculture systems (Newson, 2020). These pests thrive in homogeneous landscapes where their natural enemies may be less effective due to reduced habitat complexity. In a recent study, Gaigher et al. (2024) showed that the area and configuration of semi-natural habitats and vineyard landscapes significantly influence arthropod diversity in vineyards across South Africa and Austria. Increased vegetation cover in vineyard inter-rows consistently enhanced arthropod populations, while the spatial arrangement of landscape elements was as important as their total area. Different arthropod taxa, such as spiders, beetles, and bees, responded uniquely to landscape configurations, highlighting the need for tailored conservation strategies.

This study demonstrates that riparian and woodland dominance (quantified using LPI) has no significant impact on species richness or abundance. The lack of significant influence from riparian and woodland patch dominance on species richness reflects the unique semi-arid conditions (Mathivha et al., 2020) and resource limitations of the northern region of South Africa. These conditions are characterised by increased drought frequency and severity that have resulted in a 10% decline in soil moisture across most semi-arid areas of South Africa (Hermans & McLeman, 2021; Mudau et al., 2022) and elevated soil salinity due to high temperatures (Ramamurthy and Pardyjak, 2011). These conditions have favoured woody cover, which is more resilient to extreme temperatures than grasses and other herbaceous species (Ward et al., 2014), limiting the availability of diverse habitats and resources to support higher species diversity. Given that the cropland consistently sits near the Nzhelele River and benefits from irrigation, we expect these irrigated crops to host a greater species diversity than drier woodland areas. The irrigation likely provides a more favourable environment for various taxa, enhancing species richness in agricultural systems.

2.4.2. Influence of habitat types (woodland, riparian, and cropland) on arthropod diversity at the local scale

At the local scale, the results showed variations in how arthropod communities respond to habitat proportions. We found no significant effects of the measured landscape variables on arthropod order richness. This lack of correlation suggests that factors other than landscape composition may drive the richness of arthropod orders in this study area. In contrast, species richness showed a significant negative correlation with the surrounding natural habitats, particularly along the gradient from riparian-dominated to woodland-dominated areas, demonstrating the distinct ecological conditions of these habitats. Riparian zones support

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higher richness (Sabo et al., 2005) due to their proximity to water resources, which provide essential moisture, nutrients, and continuous structural connectivity. These favourable conditions create a cooler, humid microclimate that sustains diverse arthropod populations (Pusey and Arthington, 2003).

Similarly, Bennett et al., (2014) found that riparian zones support higher richness due to their proximity to water resources, which provide essential moisture, nutrients, and structural connectivity. Examining 24 landscapes with varying tree cover (60% to <2%), the study revealed that riparian sites consistently maintained greater species richness than woodlands, benefiting from cooler, humid microclimates, fertile soils, and reliable food resources. Conversely, woodland habitats in semi-arid regions present harsher environmental conditions. These areas are often sparsely distributed, with drier and hotter microclimates, limited resources, and reduced structural connectivity. Bennett et al. (2014) also observed that as landscape tree cover declined, species assemblages in non-riparian sites became increasingly homogenised, while riparian zones maintained stable and diverse compositions. Furthermore, in highly modified landscapes, riparian vegetation became disproportionately crucial for biodiversity, contributing a larger share of unique species not found elsewhere. These findings align with research emphasising the role of microclimatic conditions and resource availability in shaping biodiversity patterns in semi-arid landscapes.

Our results also indicate that arthropod abundance declines with increasing values of riparian-dominated to woodland-dominated and woodland-cropland gradients. This pattern aligns with studies on biodiversity, highlighting the challenging environmental conditions that limit species persistence. The decline reflects potential ecological stressors, including limited water resources and microclimate variations characteristic of arid ecosystems. The environmental implications extend beyond simple landscape metrics. Pryke and Samways (2012) emphasise that arthropod communities in arid regions represent complex adaptive systems influenced by multiple environmental factors. The results challenge conventional biodiversity models, suggesting that local-scale factors play a crucial role in determining species distribution and abundance. Our results on community composition support this. Arthropod community composition identified landscape as an influential factor, indicating that landscape context meaningfully contributes to composition. This finding points to the potential for underlying ecological processes that maintain order composition despite changes in habitat structure. We noted that edge landscapes displayed slightly more significant composition variation than other

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landscape types. The observed pattern suggests that individual spillover occurs from remnant vegetation into the orchard. In agricultural landscapes, spatial arrangements, including edge length, habitat size, and the connectivity of semi-natural habitats, strongly influence species distribution and diversity (Marja et al., 2022; Schirmel et al., 2016; Tscharntke et al., 2012). The significant differences in species richness between remnant natural vegetation, field edges, and field interiors likely result from edge effects. Edges often support higher biodiversity due to spillover from adjacent habitats and the presence of species adapted to edge environments (Ries et al., 2017). Field edges play a critical role in agricultural landscapes by facilitating spillover and acting as keystone features. Their proximity to semi-natural vegetation, which remains stable and less disturbed by crop management, enhances their ecological importance (Gallé et al., 2020).

2.5. Conclusion

This study examined the influence of landscape diversity, spatial configuration, and habitat cover on arthropod richness, order richness, and abundance at the local scale. Results showed that higher compositional heterogeneity increased arthropod abundance, likely due to diverse resources and niches. Simpson diversity positively correlated with species richness, while Shannon equitability negatively impacted it. Large cropland patches boosted species richness but favoured pests, whereas riparian and edge habitats supported higher richness than woodland areas. Landscape structure strongly shaped arthropod abundance and community composition, with edge habitats introducing variability and enhancing biodiversity.

Guided by the hypothesis that compositional and spatial heterogeneity shapes arthropod communities, the study used diversity indices and spatial metrics to assess these effects. The results revealed significant relationships between landscape heterogeneity and arthropod abundance, highlighting the complex interplay of dominant species, habitat types, and landscape structure. For instance, cropland patches increased richness but also pest abundance, while riparian and edge habitats emerged as biodiversity hotspots. Woodland areas, by contrast, exhibited lower abundance and richness, likely due to resource limitations. The findings emphasise the importance of landscape heterogeneity in promoting arthropod abundance and richness, highlighting the value of diverse habitat mosaics in agroecosystems. Riparian and edge habitats were identified as crucial biodiversity reservoirs, while the positive effects of large cropland patches on richness underscore the need to integrate semi-natural habitats. A “Single Large and Several Small” (SLASS) approach (Kruess & Tscharntke, 2000), combining

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larger natural areas with smaller patches, could enhance biodiversity and ecosystem services. Managing woodland-dominated areas to mitigate resource limitations is critical.

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2.6. Appendices data

Appendix 2.1: Landcover percentages

Farm Name	Site_ID	Landscape	Woodland%	Riparian%	Crops%
AD	Alice_DryEdge1	Orchard Edge	41.18	0	58.82
	Alice_DryEdge2	Orchard Edge	25	0	75
	Alice_In1	Orchard Interior	0	0	100
	Alice_In2	Orchard Interior	0	0	100
	Alice_Riparian1	Riparian	35.29	61.18	3.53
	Alice_Riparian2	Riparian	38.1	61.9	0
	Alice_WetEdge1	Orchard Edge	6.02	26.51	67.47
	Alice_WetEdge2	Orchard Edge	9.3	17.44	73.26
	Alice_Wood1	Woodland	98.81	0	1.19
	Alice_Wood2	Woodland	91.57	0	8.43
DA	D_Aband_Edge1	Orchard Edge	44.05	0	55.95
	D_Aband_Edge2	Orchard Edge	44.19	3.49	52.33
	D_Aband_In1	Orchard Interior	25.88	0	74.12
	D_Aband_In2	Orchard Interior	10.59	0	89.41
	D_Aband_Wood	Woodland	78.82	0	21.18
DB	Doreen_Edge	Orchard Edge	1.18	41.18	57.65
	Doreen_In	Orchard Interior	0	0	100

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	Doreen_Riparian	Riparian	21.69	54.22	24.1
ME	Evert_Edge	Orchard Edge	9.41	44.71	45.88
	Evert_In	Orchard Interior	14.63	0	85.37
	Evert_Riparian	Riparian	3.57	52.38	44.05
HE	Hayoma_Edge1	Orchard Edge	47.5	0	52.5
	Hayoma_Edge2	Orchard Edge	42.35	0	57.65
	Hayoma_In1	Orchard Interior	0	0	100
	Hayoma_In2	Orchard Interior	0	0	100
	Hayoma_Wood1	Woodland	71.25	0	28.75
	Hayoma_Wood2	Woodland	92.94	0	7.06
MS	Maswiri_Edge	Orchard Edge	22.35	24.71	52.94
	Maswiri_In	Orchard Interior	15.66	0	84.34
	Maswiri_Riparian	Riparian	48.81	46.43	4.76
NVE	RB_Edge1	Orchard Edge	7.59	32.91	59.49
	RB_Edge2	Orchard Edge	44.05	0	55.95
	RB_In1	Orchard Interior	0	0	100
	RB_In2	Orchard Interior	10.71	0	89.29
	RB_Riparian	Riparian	24.69	55.56	19.75
	RB_Wood	Woodland	100	0	0
NR	Reserve_Riparian	Riparian	81.18	18.82	0
	Reserve_Wood	Woodland	100	0	0

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Appendix 2.2: Order richness, species richness, and abundance in response to Shannon diversity, Shannon equitability, and Simpson diversity indices and their interactions were included as covariates. The AIC difference (ΔAIC) between the best, second-best, and null models is also provided. The null model accounted for random effects.

Response	Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
Order Richness	Null	2	43.56	0	0.89	0.89	-18.58
	PC2	3	48.99	5.44	0.06	0.94	-18.5
	PC1	3	49.13	5.57	0.05	1	-18.56
	PC1_PC2	4	58.3	14.74	0	1	-18.48
Species Richness	Null	2	79.74	0	0.46	0.46	-36.67
	PC2	3	79.96	0.22	0.41	0.88	-33.98
	PC1	3	83.22	3.49	0.08	0.96	-35.61
	PC1_PC2	4	84.51	4.77	0.04	1	-31.59
Abundance	Null	2	153.01	0.21	0.42	0.88	-73.3
	PC2	3	156.59	3.79	0.07	0.95	-72.29
	PC1	3	152.79	0	0.46	0.46	-70.4
	PC1_PC2	4	157.16	4.37	0.05	1	-67.91

Appendix 2.3: Order and species richness in response to the largest patch Index.

Response	LPI	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
Order Richness	Null	2	43.56	0	0.84	0.84	-18.58
	Woodland	3	49.1	5.55	0.05	0.9	-18.55
	Riparian	3	49.1	5.55	0.05	0.95	-18.55
	Cropland	3	49.13	5.58	0.05	1	-18.57
Species Richness	Null	2	79.74	0	0.16	0.92	-36.67
	Woodland	3	81.89	5.2	0.06	0.97	-34.95
	Riparian	3	83.24	6.55	0.03	1	-35.62
	Cropland	3	76.69	0	0.75	0.75	-32.35

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Appendix 2.4: Order richness, species richness, and abundance in response to landcover percentages.

Response	Model	K	AICc	ΔAICc	AICc. Wt	Cum.Wt	LL
Order Richness	Null	2	128.63	0	0.55	0.55	-62.07
	PC1	3	130.81	2.19	0.19	0.94	-61.91
	PC2	3	130.66	2.04	0.2	0.75	-61.83
	PC1_PC2	4	132.97	4.34	0.06	1	-61.62
Species Richness	Null	2	164.81	4.6	0.07	0.97	-80.16
	PC1	3	166.38	6.18	0.03	1	-79.69
	PC2	3	160.2	0	0.65	0.65	-76.6
	PC1_PC2	4	162.1	1.9	0.25	0.9	-76.18
Abundance	Null	2	12152.77	3061.68	0	1	-6074.15
	PC1	3	11944.36	2853.27	0	1	-5968.68
	PC2	3	9105.5	14.4	0	1	-4549.25
	PC1_PC2	4	9091.09	0	1	1	-4540.68

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2.8. Supplementary Data

Table S2.1: Correlation of land cover type (woodland, riparian, and cropland)

	Woodland	Riparian	Cropland
Woodland	1.000	-0.220	-0.798
Riparian	-0.220	1.000	-0.412
Cropland	-0.798	-0.412	1.000

Table S2.2: The Principal Component Analysis for DIV_SH, DIV_EV, and DIV_SI for PC1, PC2, and PC3.

	SD	DIV_SH	DIV_EV	DIV_SI
PC1	1.717	0.582	0.576	0.574
PC2	0.224	-0.115	-0.640	0.759
PC3	0.018	0.805	-0.508	-0.307

Table S2.3: The Principal Component Analysis for Woodland, Riparian, and Crops for PC1, PC2, and PC3.

	SD	Woodland	Riparian	Crops
PC1	1.339314 *e* + 00	-0.676	-0.122	0.727
PC2	1.098288 *e* + 00	0.386	-0.898	0.209
PC3	6.153603 *e* - 16	0.627	0.422	0.654

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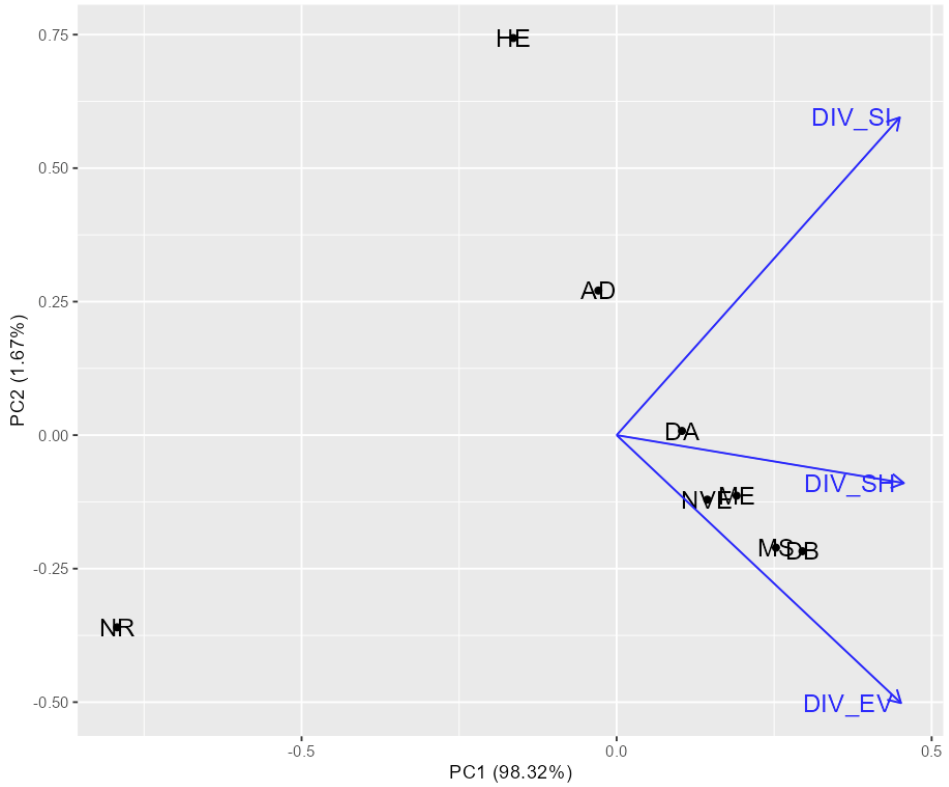


Figure S2.1: A PCA was generated for landscape diversity indices.

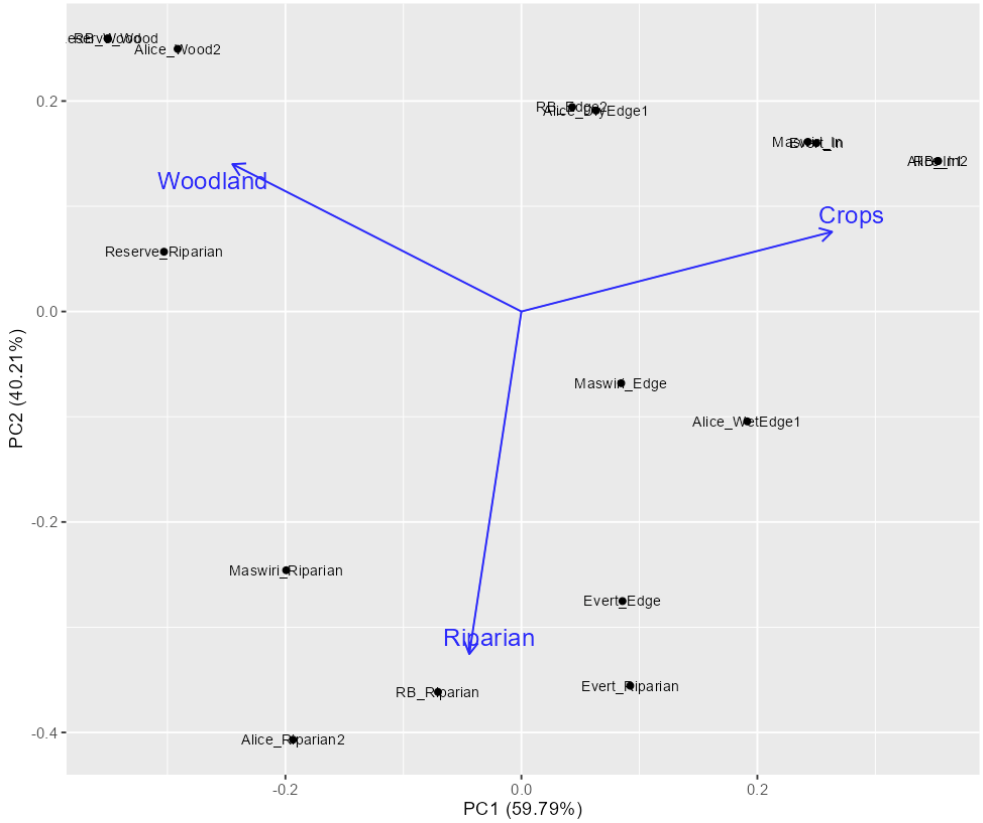


Figure S2.2: A PCA was generated for habitat cover type.

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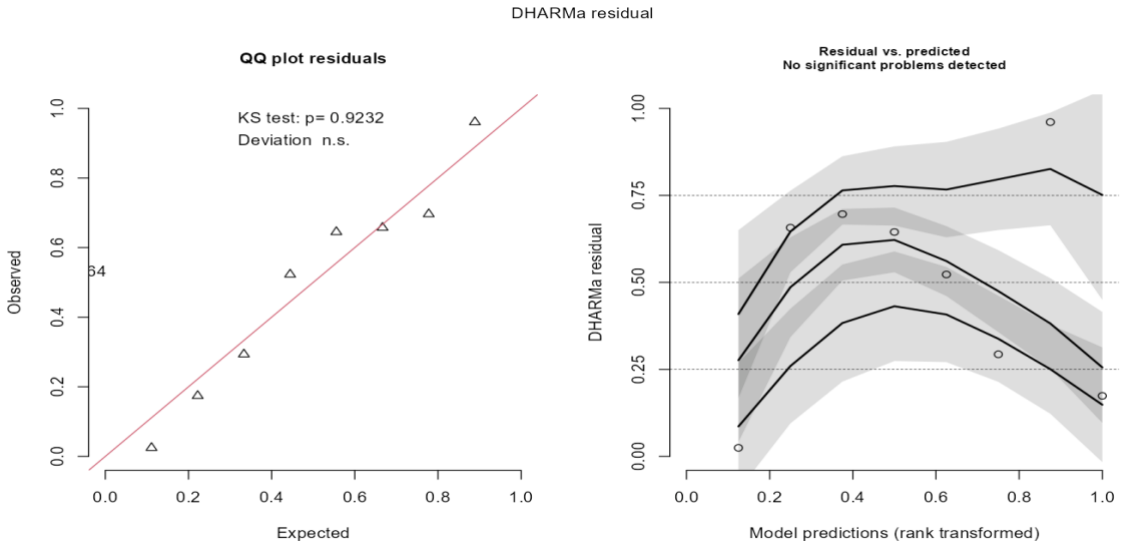


Figure S2.3: Parsimonious model checking on arthropod richness ~ PC2

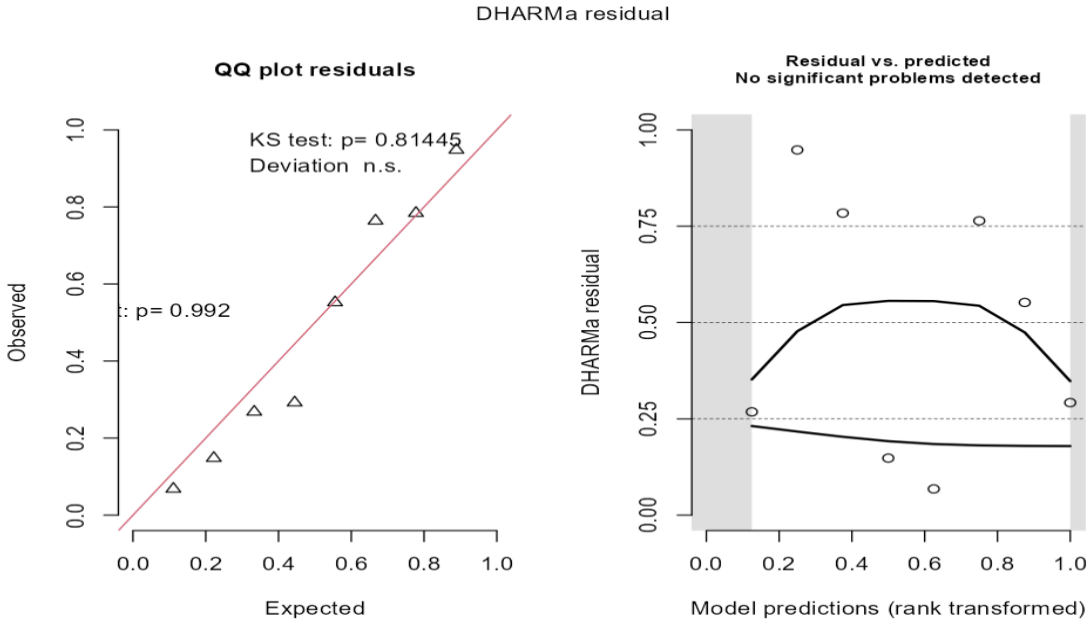


Figure S2.4: Parsimonious model checking on arthropod abundance ~ PC1

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CHAPTER THREE

INSECTIVOROUS VOLANT VERTEBRATES AND SPATIOTEMPORAL DYNAMICS OF INSECT COMMUNITIES IN AGRICULTURAL LANDSCAPES

Abstract

Modern agriculture faces the critical challenge of balancing productivity with environmental sustainability. This balance is crucial for meeting current food demands, safeguarding ecosystem health, ensuring long-term resource availability, and promoting resilience in agricultural landscapes. Citrus crops, however, are particularly vulnerable to pest pressures from economically significant species such as the *Thaumatotibia leucotreta*. Traditionally, synthetic pesticides have been used to control these pests. Still, this reliance has resulted in various ecological and economic drawbacks, including pesticide resistance, harm to non-target species, and reduced ecosystem services. These challenges highlight the urgent need for sustainable, ecologically based pest management strategies. We explored how spatiotemporal variations influence nocturnal flying insect diversity in agroecosystems and how insectivorous vertebrates, such as bats and birds, influence crop damage. The study aims to reduce reliance on chemical pesticides in agroecosystems by integrating these natural predators into pest management strategies. Field surveys were conducted to compare crop and noncrop habitats and examine the influence of landscape composition on insect diversity. Predator exclusion cages were constructed to quantify the role of bats and birds in pest suppression and crop damage reduction. We found that insect abundance was the highest in noncrop habitats and significantly lower in croplands. FCM populations fluctuated spatially, with annual environmental and management conditions, while predator exclusion treatments demonstrated that insectivorous birds and bats contribute to pest suppression. However, their effects varied spatially within croplands, with reduced crop damage observed at the orchard edges. This highlights the critical role of heterogeneity within orchards in maintaining biodiversity and enhancing natural pest control. These findings emphasise the importance of integrating semi-natural habitats into agricultural landscapes to support biodiversity, promote ecosystem services, and improve crop yield. This study provides valuable insights into the landscape context factors affecting insect diversity and pest management, offering guidance for achieving sustainable crop production.

Keywords: landscape heterogeneity; ecological intensification; integrated pest management; *Thaumatotibia leucotreta*

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3.1. Introduction

Modern agriculture faces the critical challenge of balancing productivity with environmental sustainability. Central to this challenge is managing the complex interactions between insect pests, their natural enemies, and the surrounding landscape (Rusch et al., 2010). In perennial cropping systems like citrus farming, uncontrolled insect pests can cause significant economic losses by damaging fruits and rendering them unsuitable for trade, especially those established in Chapter 2 (Table 2.5) and some outlined in Chapter 1 (Table 1.1) cause direct damage to citrus plants, rendering their fruits unsuitable for trading, mainly export. *Thaumatotibia leucotreta* Meyrick (Tortricidae) is an iconic example. As this insect is a significant phytosanitary pest, false codling moth (FCM) poses severe economic and ecological challenges in South African citrus production (Schwartz, 1981; Newton, 1998). FCM is highly polyphagous, with a host range exceeding 70 plant species across 40 families, including cultivated and wild species (van de Vossenberg, 2023). Despite its broad host range, FCM exhibits varying levels of infestation among plant species and varieties, influenced by host characteristics and environmental conditions (Moore et al., 2017). In South Africa, citrus species (*Citrus* spp.) are among the most preferred hosts, representing a significant concern for the citrus industry (Newton, 1998). Moreover, FCM's host preference may shift with climatic conditions, affecting infestation patterns (Love et al., 2014). Notably, FCM is a nocturnal species, with adults exhibiting peak activity after dusk, which limits the effectiveness of visual scouting methods during the day. However, its reliance on sex pheromones for mate location has enabled the development of highly effective pheromone-based monitoring systems. Pheromone and light traps are increasingly employed as integrated pest management (IPM) tools to track adult male activity and phenology, providing early warning and guiding control strategies (Moore, 2002; Moore & Hattingh, 2012).

Pesticides remain the dominant method for pest control in citrus farming. However, over-reliance on chemical pesticides harms non-target organisms, disrupts ecosystem services, and undermines ecological sustainability (Bianchi et al., 2006; Tscharntke et al., 2016). Moreover, no single control measure currently suppresses FCM populations satisfactorily (Moore, 2017). Therefore, a multidisciplinary approach integrating various strategies is necessary for effective and sustainable management (Moore and Hattingh, 2012). Sustainable alternatives, such as ecological intensification, enhance ecosystem services over chemical inputs. While most citrus pests in South Africa are native, their natural enemies—including specific and generalist

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parasitoids and predators—often face challenges such as habitat loss and insufficient breeding sites. Despite these limitations, volant vertebrates like bats and birds play crucial roles in biological pest control. Bats and birds provide continuous pest control by targeting pests at different times. Bats, active at night, feed on pests such as FCM and fruit flies, while birds, active during the day, target multiple pest life stages. Studies across crops—including rice (Puig-Montserrat et al., 2015), maize (Maine and Boyles, 2015) and pecans (Braun de Torrez et al., 2019)—demonstrate the significant pest control benefits of these predators. Orchards near natural habitats often host higher predator abundance and diversity, reducing pest damage and minimising pesticide reliance (Boesing et al., 2017; Weier et al., 2018).

Monoculture landscapes exacerbate pest outbreaks by reducing habitat diversity and disrupting predator-prey dynamics. The absence of natural and semi-natural habitats limits predator populations, increasing pest pressure, crop damage, and pesticide use (Haddad et al., 2009; Karp et al., 2018). In contrast, semi-natural habitats provide refuges and alternative prey, enhancing natural pest control and promoting ecosystem resilience (Bianchi et al., 2006; Gurr et al., 2017). However, rapid pest recolonisation in monocultures often undermines natural control efforts (Tscharntke et al., 2012). Integrating bats and birds into integrated pest management (IPM) strategies can mitigate these challenges by leveraging their adaptability to heterogeneous landscapes and their role as vital ecosystem service providers. Effective and sustainable management strategies require an in-depth understanding of the factors influencing FCM population dynamics, including climatic conditions, host availability, and landscape context. Warmer temperatures and rainfall variability accelerate FCM life cycles, often synchronising pest activity with citrus phenology (Boardman et al., 2012). Landscape composition and the spatial arrangement of orchards further shape pest pressure, highlighting the need for a multiscale approach to FCM management that considers spatial and temporal variations.

In South Africa, particularly in Limpopo, pioneering research by Taylor has laid the groundwork for understanding bats' role in agricultural pest control. Molecular diet analysis was used to demonstrate that bats feeding in macadamia orchards consume significant numbers of crop pests, including moths and stinkbugs (Weier et al., 2019). Building on this, Swartz et al. (2022) showed that bat activity is highest along orchard edges and near natural vegetation, underscoring the importance of landscape context. More recently, Howard’s work in apple orchards has sought to quantify the economic value of bats as pest regulators. Collectively,

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these studies emphasise that insectivorous bats can contribute meaningfully to reducing pest pressure in high-value crops across Limpopo. However, little is known about their role in citrus systems, despite evidence that bats feed on key citrus pests such as *T. leucotreta* and fruit flies. Incorporating this knowledge into citrus-focused research will help bridge a critical gap and expand the applicability of ecological intensification strategies in subtropical agroecosystems.

This study aims to evaluate the role of insectivorous bats and birds in pest control in South African citrus agroecosystems and to explore how landscape compositional heterogeneity influences pest management outcomes. Specifically, it: 1. Examine habitat factors influencing nocturnal flying insect abundance and richness in citrus orchards and surrounding landscapes. 2. Describe the spatial and temporal distribution of the FCM in citrus orchards throughout the growing season, assessing how FCM populations vary between the orchard interior and edges. 3. Evaluate the effect of landscape context on pest damage, comparing the condition of fruits from orchard edges near natural habitats to those from the orchard interior. 4. Quantify the impact of insectivorous bats and birds on pest damage by excluding these predators from a subset of citrus trees.

3.2. Materials And Methods

3.2.1. Study areas and sites

All study areas were in the Tshipise (22.5314 ^{0}S, 30.6756 ^{0}E) region, on the northern foothills of the Soutpansberg Mountain range along the Nzhelele floodplain (Figure 3.1). We conducted arthropod sampling in four study areas, which included Marimane Nature Reserve (NR) and three orchards with different management intensities, namely Maswiri Boerdery (MS, which had two isolated orchards, and for this study, we treated the orchards separately), Alicedale Estate (AD), and Nzhelele Valley Estate (NVE). Arthropods were sampled across 17 sites, representing three habitat types: (i) cropland (interior, n = 4; edge, n = 5), (ii) woodland (n = 3), and (iii) riparian zone (n = 5). All study sites were fixed for the duration of the study. The study area at the Soutpansberg mountain range is part of the UNESCO Vhembe Biosphere Reserve. It is vital for animal diversity in South Africa, as it is a national hotspot for bat richness and harbours about 75% of the country's bird species (Clark et al., 2011).

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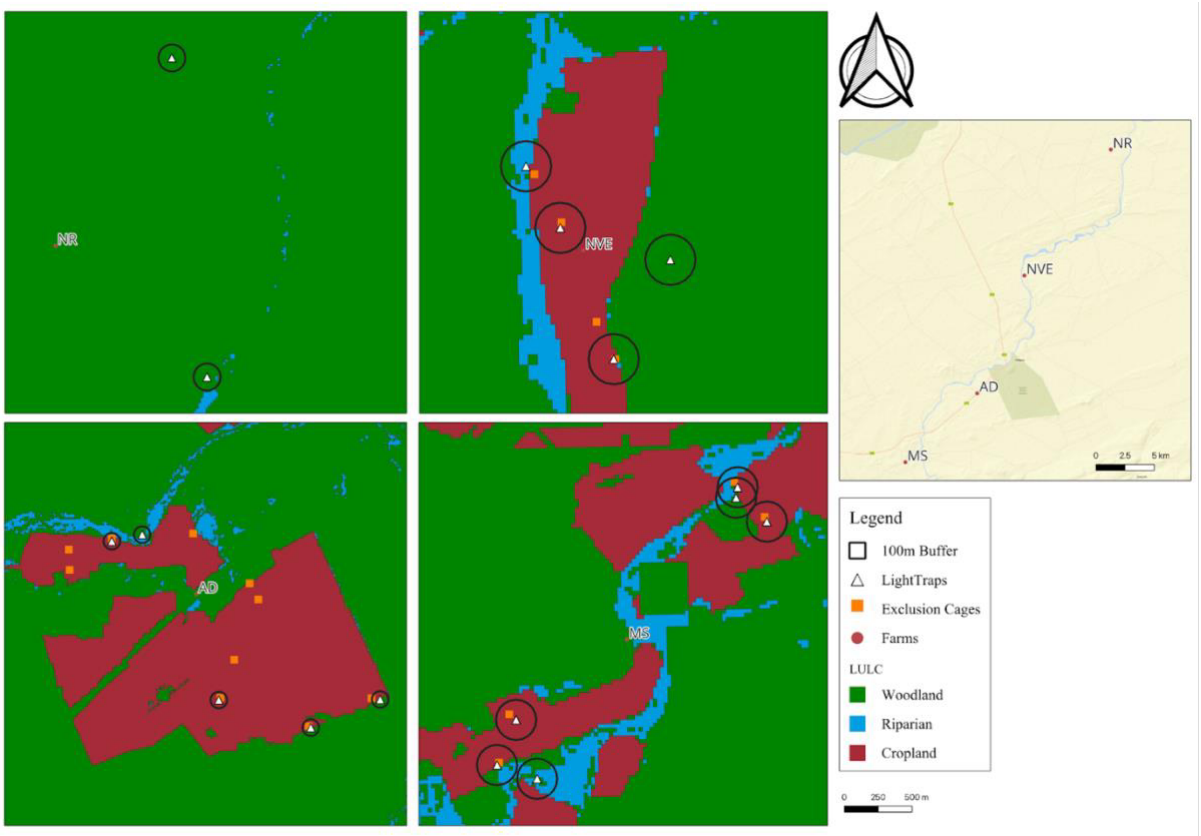


Figure 3.1: Map of study sites in the Tshipise Area along the Nzhelele Floodplain, including selected conventional orchards and Maremani Nature Reserve for exclosure treatments and data collection. The Maremani Nature Reserve NR (-22.425019, 30.221862); NVE (-22.538475, 30.182068), AD (-22.631208, 30.140695), and MS (-22.686619, 30.074106).

3.2.2. Study design

This study formed part of a more extensive study led by Citrus Research International (CRI), investigating the effect of flying vertebrates on insect pest populations inflicting damage on citrus. However, the present study focused only on arthropod, not vertebrate sampling. Nocturnal flying insects were sampled from October 2023 to July 2024, with bimonthly visits designed to capture seasonal variations across four study areas. We distributed sample sites within each orchard to address its landscape context, covering remnant natural vegetation, the edge, and areas over 50 meters into the orchard interior. The overall orchard size determined the distance of the interior sites. The orchard edge and interior included a treatment and control sampling unit. Treatment consisted of two citrus trees enclosed by a cage, excluding arboreal vertebrate taxa (birds, bats, and vervet monkeys) but allowing invertebrates access. Two trees adjacent to the exclusion cages served as control sites, and we sampled insects using light traps at the same sites where we installed the exclusion cages. Each light trap was positioned in the

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tree canopy at least 2 m above the ground and within 20 meters of the enclosure treatments to prevent interference with insects inside the cages. The traps were at least 50 meters apart to prevent the lights from interfering with each other (Horvath et al., 2016). Additionally, we conducted stratified random sampling in surrounding natural areas, including riparian zones and woodland, to ensure representative habitat coverage while minimising risks of theft and destruction.

3.2.3. Arthropod sampling

Nocturnal flying insects were collected using custom-designed LED UV light traps (Appendix 3.1; Figure 3.3E), deployed bimonthly from October 2023 to July 2024 to capture temporal variations. The UV LED light emits wavelengths between 395 nm and 405 nm (https://www.entosphinx.cz), which are effective wavelengths for trapping light-attracted insects, including lepidopterans (Balamurugan and Kandasamy, 2021; Brehm et al., 2021; Knight et al., 2023). The traps were custom-made and consisted of 2 mm-thick white polystyrene cylinders (55 cm in height and 25 cm in width) with open sides to facilitate insect entry, attached to a funnel cone with a 5 cm opening that directed insects into a 5-litre plastic container. A 10W ultraviolet (UV) LED light strip (BioQuip Products, Inc., Rancho Dominguez, CA) was attached to an aluminium wire at the top of each trap to attract flying invertebrates. The lights were powered by a 12V battery and set on a timer to activate at sunset for three hours on three consecutive nights every two months (Appendix 3.1). UV light traps are a standard method for general insect surveys (Schauff, 2005), allowing for the capture of insects without damage, thereby facilitating accurate identification. After each sampling session, we sealed the traps and transported them to the laboratory. We euthanised the insects by placing a cotton pad soaked in ethyl acetate inside each trap prior to deployment and left overnight to ensure all captured insects were killed in situ. Subsequently, we transferred the insects to labelled glass vials containing a preservative mixture of 70% ethanol and propylene glycol. Lepidoptera species were placed in glassine envelopes and frozen for later identification. We identified all insects to the order level using relevant literature, such as Picker et al. (2012). After identification, we assessed the diversity and abundance of insect orders. Arthropods were further classified into five groups considered agriculturally crucial in the citrus orchards: (1) herbivore insects (including significant pests); (2) insect predators; (3) insect parasitoids; (4) insect pollinators; and (5) other “secondary” functional groups, including

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decomposers, anthophilous species, and uncommon species (fewer than five individuals at a site, regardless of habitat cover type), found in literature.

3.2.4. *Thaumatotibia leucotreta* in Alicedale citrus orchard

Thaumatotibia leucotreta was only sampled in one study area (AD), covering ~800 ha of citrus crops, as this site provided the complete dataset on FCM and various citrus trees required for this study. To investigate the spatial and temporal distribution of FCM abundance within the citrus orchard, we used a synthetic pheromone-based trapping system that utilises a yellow delta trap with Chempac sticky pads baited with Lorelei® pheromone dispensers (species-specific FCM): https://insectscience.co.za/product/f-c-m-pherolure/ over time to monitor male FCM distribution within the orchard. Each dispenser contains 0.1 ml per ampule of (E)-7-dodecyl acetate/(E)-8-dodecyl acetate/(Z)-8-dodecyl acetate, produced by Hendrik Hofmeyr from Citrus Research International (CRI). Each X-Mate dispenser covers an average area of 250 m^2. We suspended the traps approximately 1.5 m above ground level to optimise pheromone dispersal within each orchard block (Moore, 2002).

Within Orchard AD, traps were deployed in every orchard block, with one trap randomly placed per block to ensure unbiased sampling of male FCM activity across the production area. Traps were not placed in surrounding natural vegetation, as the focus of this study was limited to FCM activity within the citrus production matrix. Monitoring was conducted weekly on the same day for three consecutive years, from January 2022 to September 2024. Each year, we stopped tracking at the end of the all-fruit harvest, i.e., on the 37th week of the year. The sampling period spanned both the wet season (approximately weeks 1–16 and 35–37) and the dry season (approximately weeks 17–34), corresponding to the regional climatic pattern in the Limpopo Province. This allowed for a comprehensive assessment of FCM phenology and activity across contrasting seasonal conditions.

We determined the spatial distribution of FCM by digitising the orchard (AD) using heads-up digitising from Google satellite imagery in QGIS. Additionally, we created inward buffers from the orchard edge at ten scales, ranging from 100 m to identify the blocks within each scale.
The citrus cultivars differentiated the orchard, with 286,311 actual tree counts and 291 blocks, the smallest covering 0.46 ha and the largest covering 12.69 ha. The oldest trees are from 1984, with the youngest trees from 2020.

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Orchard AD has a variety of citrus cultivars (Figure 3.2), which include *Citrus limon (viz.*, Eureka); *C. paradisi* (*viz.,* Star Ruby); *C. reticulata (*viz.*,* Leandri, RHM, Tamborr, Nova, Orri, and Nardocott LS); and *C. sinensis (viz.,* Delta, Turkey, Bennies, Jassie, Kobus du Toit, Valencia and Midknight). This range of cultivars enabled the determination of FCM presence at different times of the year. The orchard's various cultivars mature in different periods (see Table 3.1). Infestation levels vary among citrus varieties: *Citrus limon* are rarely infested, *Citrus sinensis* cultivars have low susceptibility, mid-season cultivars exhibit moderate susceptibility, and Navel oranges are highly susceptible (Grout and Moore, 2015).

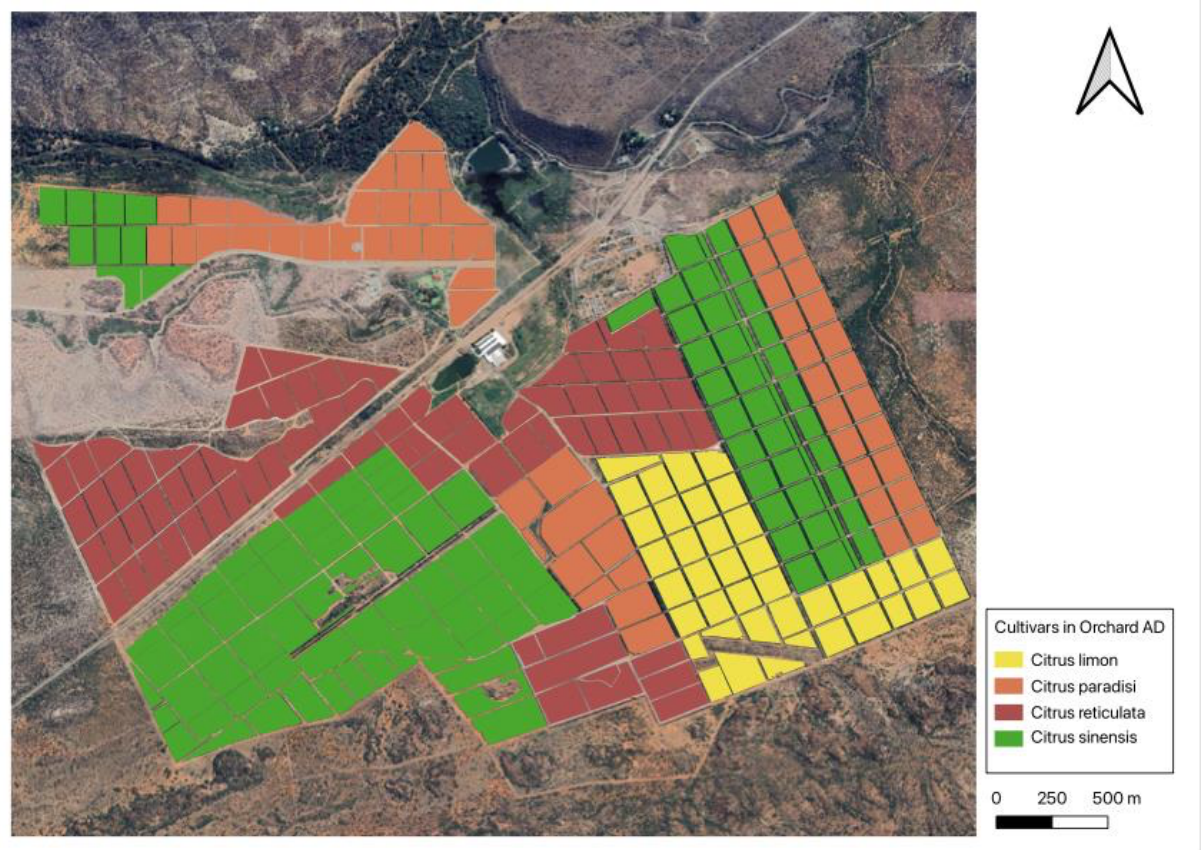


Figure 3.2: A digitised orchard AD map showing the four citrus cultivars.

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Table 3.1: Maturity of citrus cultivars in Orchard AD across the year.

Cultivar	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Citrus limon												
Citrus paradisi												
Citrus reticulata												
Citrus sinensis												

3.2.5. Vertebrate exclusion plots

After the first round of arboreal arthropod survey in Chapter 2 highlighted a diverse range of insect pests in the study orchards and their potential impact on citrus crops, we aimed to investigate the role of insectivorous flying vertebrates in biocontrol within a landscape context, emphasising their contributions to pest regulation, biodiversity, and ecosystem services. To achieve this, we established two experimental treatments within each orchard to assess the impact of flying vertebrate predation on crop yield: volant vertebrate exclusion and control (no exclusion) (Figure 3.3A & B). Exclosure plots were created using rectangular cages constructed from wooden frames and covered with structured agricultural nylon mesh. We selected mesh sizes that excluded birds, bats, and monkeys while allowing the insects in (Figure 3.3C & D). We customised cages due to variations in tree sizes and spacing, to accommodate two trees, with the most oversized measuring 7 x 5 x 5 m (Figure 3.3F) covered with a nylon mesh (1 x 1 cm) (Bouarakia et al., 2023). This mesh size allowed a free flow of arthropods in and out of the cages. These cages remained in place and were maintained throughout the growing season, enabling the comparison of crop yield between exclusion and control treatments. We replicated the experimental setup across four orchards, with 18 sampling points randomly stratified across orchard interiors (n = 8) and edges (n = 10), where exclusion cages were placed in three orchards at a local scale.

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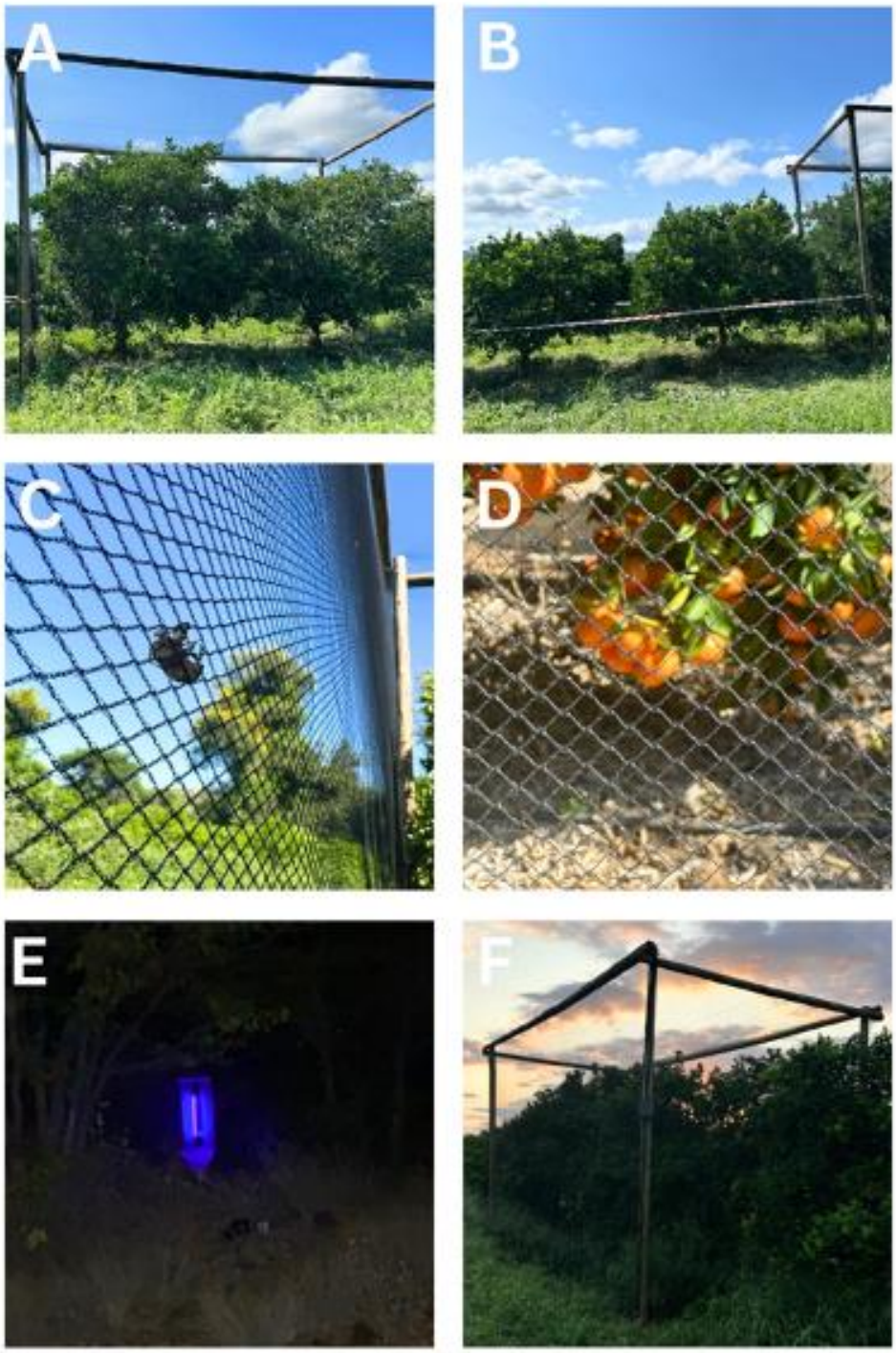


Figure 3.3: Study design and equipment overview: *A.* Exclusion cages used to exclude bats and birds from two trees. *B.* Control treatment with two adjacent trees left open without exclosure. *C.* Nylon mesh with a size sufficient to exclude bats, birds, and very large insects. *D.* An alternative size of nylon mesh for comparison. *E.* Custom-designed LED UV light traps used for nocturnal arthropod sampling. The cage height covers the trees. *F.* Customised cages in orchards.

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3.2.6. Identifying the cause of fruit damage

We inspected citrus fruits biweekly throughout the growing season, adjusting the schedule based on adverse weather conditions and periods of heightened pest activity. At each site, we evaluated four focal trees per treatment—two exclusion-caged trees and two adjacent uncaged control trees—resulting in a total of 48 trees distributed across two orchards (NVE and AD). Fruit inspections could not be conducted in orchards ME and MS, as fruits had already been harvested prior to the scheduled damage assessment. All fruits on each sampled tree were inspected individually for signs of insect damage. Insect damage was assessed per pest species, with damage recorded based on pest-specific symptoms (e.g., frass and larval presence for *T. leucotreta*, honeydew and sooty mould for mealybugs). Assessments focused solely on citrus fruits, as these are the economically significant plant organs in citrus production. Each fruit was evaluated for pest-specific damage symptoms, and incidence was quantified as the proportion of damaged fruits relative to the total number examined. During each inspection, each fruit was carefully evaluated for visible signs of damage, including blemishes, discolouration, punctures, scabbing, rotting spots, sunken areas indicative of internal damage, and deformities or abnormal growth patterns. For fruits showing internal damage or tunnelling, we performed dissections to identify fruit-piercing insects, noting the presence of larvae, frass, head capsules, and live or dead insects. Additionally, we documented damage caused by abiotic factors, such as hail and intense winds, which resulted in scarring and abrasions. Inspections were also conducted at harvest across all sampled blocks to evaluate cumulative seasonal damage.

These inspections explicitly focused on primary pestiferous insects directly affecting citrus fruits (Table 3.2). We prioritised these pests because of their significant economic impact and widespread prevalence in citrus-growing regions. These pests render fruits unmarketable for local and international markets by directly reducing fruit quality and yield.

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Table 3.2: Primary pests of the citrus fruit.

Order	Family	Scientific name	Common name	Damage indicator
Lepidoptera	Tortricidae	*Thaumatotibia leucotreta*	False codling moth	Entry holes on fruit, internal discoloration, frass around holes, early fruit drop.
	Pyralidae	*Ectomyelois ceratoniae*	Carob moth	Entry holes, pulp damage, secondary infections, premature rotting of fruit.
	Noctuidae	*Helicoverpa armigera*	Bollworm	Surface punctures and scars, exposed pulp, increased susceptibility to decay.
Diptera	Tephritidae	*Ceratitis capitata*	Mediterranean fruit fly	Punctures from egg-laying, soft sunken areas, larval feeding zones, premature fruit drop, fermentation smell.
		Ceratitis rosa	Natal fruit fly	Like Mediterranean fruit fly: punctures, internal decay, soft spots, early fruit drop.
		Bactrocera dorsalis	Oriental fruit fly	Entry punctures, internal fruit breakdown, mushy texture, sour smell from decay.
Thysanoptera	Thripidae	*Scirtothrips aurantii*	Citrus thrips	Silvery or bronzed scars on fruit surface, especially at stem end, cosmetic damage only.
Hemiptera	Diaspididae	*Aonidiella aurantii*	Red scale	Small reddish-brown or grey circular scales, discoloration or blemishes around scales, reduced market value.
	Pseudococcidae	*Planococcus citri*	Citrus mealybug	Waxy white deposits, sticky honeydew, black sooty mould, distorted fruit development in severe cases.

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3.2.7. Statistical analysis

We treated farm management and sampling sites as random factors in the Generalized Linear Mixed Model (GLMM) to account for variability among the studied farms and sampling sites. Additionally, we used a Generalized Linear Model (GLM) to analyse the effects of the studied years (2024), local scale, and their interaction on insect damage in the Full and Control exclusion treatments separately, using orchard as a blocking factor. We conducted all statistical analyses in R Studio version 4.4.1 (2024).

a. Quantifying site (local scale) composition heterogeneity

We explored how landscape composition affects arthropod abundance and diversity by extracting the relevant land cover classes at the local scale (i.e., sampling site). We first analysed different habitat types and generated various landscape composition metrics (Fahrig et al., 2011). Then, we used imagery data from the South African National Land Cover (2022, South African Department of Forestry, Fisheries, and the Environment (DFFE), https://egis.environment.gov.za/data_egis/data_download/current) to quantify land cover land use (LULC) proportions (Table 3.3). We cross-referenced the dataset with Google Earth and reclassified SANLC into the correct classes.

We classified land cover into cropland, woodland, and riparian categories and estimated the percentage of each site's landscape composition. To assess site composition, we buffered each sampling point with 100 meters and used a zonal histogram in QGIS to calculate the proportions of each land cover class per sampling site. Because the landscape compositions were highly correlated, we performed a Principal Component Analysis (PCA) to minimise redundancy. PCA provided the advantage of orthogonal (uncorrelated) axes, allowing us to interpret the variation in arthropod abundance independently analysis produced three main components representing the dominant patterns in landscape composition. We excluded the nature reserve from this analysis to avoid skewing the results, as its homogeneity and lack of compositional variation could distort landscape metrics and reduce the robustness of ecological interpretations that depend on heterogeneity. The first two components explained 99% of the variation in landscape diversity, and we retained them for further modelling (Appendix 3.4).

PC1 represented the main axis of variation (SD = 1.33), with woodland contributing a robust negative effect (- 0.67) and cropland having a strong positive effect (+0.72), while the riparian

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zone had a minor influence (- 0.122). This axis contrasts crop-dominated (positively) and woodland-dominated areas (negatively), with riparian zones playing a minor role, reflecting an inverse relationship between crop-dominated and woodland-dominated areas. PC2, the secondary axis (SD = +1.09), showed a substantial negative contribution from the riparian zone (- 0.898), a moderate positive contribution from woodland (+0.386), and a weak positive contribution from cropland (0.209). This dimension captures the contrast between riparian (substantial negative load) and woodland areas (moderately positive), and crops have a minor influence.

We collected atmospheric data from a local weather station in the orchard (Alicedale Estate) and used air temperature and precipitation as weather predictors. To assess landscape composition, we selected variables listed in Table 3.3, following the framework of Dunning et al. (1992). At each sample site, we directly measured predictors such as nocturnal flying insects, FCM, and categorical habitat type (Table 3.4).

Table 3.3: The land use land cover type classification is based on the National Land-Cover Classes 2022.

Land-cover classes	National land-cover classes 2022
Woodland	Contiguous Indigenous Forest, contiguous low thicket, dense forest and Woodland, open Woodland, open and sparse plantations, temporary unplanted plantations, sparsely wooded grassland, natural grasslands, fallow land, old fields, herbaceous wetlands,
Riparian	Natural rivers, artificial dams, contiguous and dense plantations
Cropland	Cultivated commercial permanent orchards, cultivated annual crops

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Table 3.4: Classes of predictors and predictors used to explain the probability of crop damage and species richness across the landscape.

Predictor class	Predictor	Units(range)	Prediction
Insect Pest	FCM		We expect FCM spatial distribution to increase with distance from natural habitats into the orchard interior, as croplands offer favourable conditions for feeding and reproduction.
Composition heterogeneity	Cropland	% (≥ 0)	We predict that increased crop cover will cause more crop damage because simplified and homogeneous cropland favours pest proliferation.
	Natural habitats	% (≥ 0)	The proportion of rangeland and riparian zones within the landscape scale may support natural enemies and reduce pest colonisation.
Atmospheric conditions	Air temperature	°C (≥ 0)	We expect higher temperatures to increase the activity and reproduction rates of FCM and other pests under warmer conditions, potentially resulting in more significant crop damage.
	Precipitation	mm (≥ 0)	We expect higher precipitation levels to increase FCM activity by creating more humid conditions.
Local scale	Orchard interior		We expect crop damage to be higher in the orchard interior because reduced access to natural predators allows pests to thrive.
	Orchard edge		We expect crop damage to be lower at the orchard edge because proximity to natural habitat may support higher predator activity.
Treatment	Exclusion		We predict exclusion treatments will increase crop damage because volant vertebrates contribute to pest control.
	Control		Control treatments (with predator access) are expected to have less crop damage due to insectivorous birds and bats' natural suppression of pests.

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b. Nocturnal flying insects' abundance and diversity

We determined order richness by counting the number of arthropod orders observed at each site and calculated species richness by counting the occurrences of each order at each site. We estimated abundance by counting the total number of individuals for each order at each site. We developed several biologically plausible models to explore the influence of local compositional heterogeneity and seasonality on arthropod richness and abundance. The models tested the effects of PC1 only, PC2 only, Season only, PC1 + PC2, PC1 + Season, and PC2 + Season and their interactions on species richness, order richness, and abundance. We compared all models to a null model and ranked them using the Akaike Information Criterion (AIC) corrected for small sample sizes (AICc; Burnham and Anderson, 2002). We considered models with $\Delta AICc \leq 2$ to have similar support (Burnham and Anderson, 2002) and selected the model with the lowest AICc for further analysis. In cases of model uncertainty, we assessed variable importance using the likelihood ratio test (LRT) and AICc weights (Burnham and Anderson, 2002).

c. Spatial distribution of FCM over the growing season

We only had long-term (2022-2024) FCM monitoring data for Alicedale Estate (Figure 3.2). For FCM spatial and temporal distribution, we were interested in two main questions. Does landscape composition affect FCM abundance? To test this hypothesis, we developed three models. First, FCM abundance is affected by distance from the edge; second, it is affected by year; third, year*distance from the edge interaction, contrasted to a null model.

Second, which combination of variables best explained FCM abundance in the second modelling scenario? This question aimed to identify the most influential factors contributing to variation in FCM populations across time and space. We tested the effect of weekly temperature, rainfall, year, distance to the edge, and citrus growing season as the main effects. The year was coded as categorical since we wanted to know the effect of year on FCM. We check for multicollinearity using the Variance Inflation Factor (Thompson, 2017). FCM models had high dispersion due to excessive zeros; therefore, we fitted a negative binomial mixed-effect model using the glmmTMB R package (Brooks et al., 2017). Sampling sites were considered a random effect to capture site-specific influence. We compared all models to a null model. Additionally, we identified the best-fitting GLMM by selecting the model with the lowest AIC while including all additional models within 2 ΔAIC of the best-fitting model.

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d. Quantifying the probability of crop damage

The effects of the exclusion of bats and birds, as well as landscape context (edge or interior), on the probability of insect damage to the citrus fruit were analysed using generalised linear mixed effect models (GLMM; Stroup, 2012) with binomial error structure and a log link function. The sampling site was added as a random effect to account for repeated sampling at the same sites over time (Zuur et al., 2009). We evaluated model fit, and if under- or overdispersion was detected, we fitted a quasi-binomial model (McCullagh and Nelder, 1989). We tested four models: i) insect damage is affected by exclusion treatments (complete exclosure and control), ii) affected by local scale (orchard interior and edge), iii) their interaction (context * treatments) or iv) only as main effects (context + treatments). We fitted two modelling scenarios, first with all insect damage, and secondly, focusing on the 2023/24 FCM damages. We contrasted all models with a null model and selected the best-fitting Generalised Linear Mixed Models (GLMM) based on the lowest AIC. We also considered additional models within 2ΔAIC of the best-fitting model. To validate the models, we plotted deviance residuals against fitted values and examined residuals relative to predictor variables to identify patterns. We used Tukey's post-hoc test (Tukey, 1977) to compare multiple means by exclusion treatment. Finally, we conducted the statistical analysis and created data visualisations using the R packages "multcomp" (Hothorn et al., 2008; 2016), "ggplot2" (Wickham, 2009), "lme4" (Bates et al., 2015), and "MuMIn" (Barton, 2020; 2024).

3.3. Results

3.3.1. Nocturnal flying insect abundance and richness

Over 45 light-trap hours at each sampling site from October 2023 to July 2024, we collected 47,989 arthropods across all land uses (Table 3.5). In terms of raw abundance, the riparian zone exhibited the highest abundance, with 45.76% of the total, followed by woodland with 19.8%, and the edge with 18.45%. Cropland edge and interior habitats provide smaller contributions, at 18.45% and 16.00%, respectively.

Coleoptera, which dominates overall abundance (56.05%), account for 50.83% of riparian zones and 20.85% in woodlands, while cropland edge and interior habitats add 15.27% and 13.05%, respectively. Lepidoptera, comprising 13.89% of the total abundance, with riparian zones hosting 33.31%, woodlands 23.32%, and cropland edge and interior habitats contributing

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28.60% and 14.78%, respectively. Hymenoptera, known for their diverse roles in pollination and parasitism, achieve 50.79% of their abundance in riparian zones, while cropland edge and interior habitats support 31.92%. Hemiptera, which include both herbivorous and predatory species, show an even distribution, with riparian zones holding 28.40%, woodlands 32.91%, and croplands contributing a combined 30.53%.

Riparian and woodland habitats (natural vegetation) sustain more significant numbers of beneficial arthropods, such as predators (e.g., Coleoptera and Neuroptera). In contrast, cropland habitats support higher proportions of pest species, such as Hemiptera and Diptera, but provide limited resources for beneficial arthropods. These patterns highlight the critical role of natural habitats in maintaining biodiversity and supporting ecosystem services like pest control and pollination.

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Table 3.5: The abundance of most dominated arthropods at different seasons within the 17 sites.

Order	Abundance	Functional Traits[1]	Abundance at the landscape scale			
			Riparian-dominated	Woodland-dominated	Cropland Edge	Cropland Interior
			n = 5	*n* = 3	*n* = 5	*n* = 4
Coleoptera	26894	H, Pr	14116	4565	4165	4048
Lepidoptera	6669	H	2221	1555	1907	986
Hemiptera	6525	H, Pr	1853	2148	1317	1207
Hymenoptera	3594	Pr, Pa, Po	1825	622	629	518
Diptera	2250	H, Pa, Po	832	426	592	400
Isoptera	825	S	534	3	38	250
Odonata	660	S	309	86	127	138
Dermaptera	176	Pr	85	29	30	32
Plecoptera	93	S	36	5	10	42
Neuroptera	88	Pr	25	16	19	28
Orthoptera	84	S	68	7	2	7
Blattodea	67	S	25	32	8	2
Mantodea	33	Pr	20	0	6	7
Mecoptera	17	Pr, Pa	4	3	1	9
Araneae	10	P	4	2	2	2
Embioptera	3	S	0	3	0	0
Phasmatodea	1	S	1	0	0	0
Σ =	47 989		21 958	9502	8853	7676

[1] H = Herbivore (Leaf, stem, bark, Fruit, minor pest, major pest). Pr = Predator, Pa = Parasitoids, Po = Pollinator, S = Secondary group (decomposer, anthophilous, and uncommon).

Arthropods were monitored bimonthly from October 2023 to July 2024 across various land uses, totalling 15 days at each sampling site (Table 3.6). In October 2023, the arthropod community was relatively small, totalling 7,353 individuals. January 2024 marked a peak in abundance at 25,300 individuals, primarily due to a surge in Coleoptera (17,306), with notable increases in Hemiptera (3,797) and Lepidoptera (2,829). Hymenoptera (933) and Dermaptera

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(171) also became more pronounced. Abundance declined significantly in March 2024 (6,340), remained moderate in May 2024 (5,950), and reached a low in July 2024 (3,146).

Table 3.6: The abundance of the most dominant arthropods at different seasons within the 33 sites.

	Arthropod abundance monthly				
Order	Oct-23	Jan-24	Mar-24	May-24	Jul-24
Araneae	0	1	3	1	5
Blattodea	6	41	5	9	6
Coleoptera	5461	17306	2888	979	260
Dermaptera	0	171	5	0	0
Diptera	27	56	29	736	1402
Embioptera	0	0	0	0	3
Hemiptera	273	3797	1006	1297	152
Hymenoptera	205	933	1546	658	252
Isoptera	825	0	0	0	0
Lepidoptera	546	2829	552	1768	974
Mantodea	3	11	18	1	0
Mecoptera	0	2	1	10	4
Neuroptera	0	7	25	31	25
Odonata	7	8	144	448	53
Orthoptera	0	65	13	5	1
Phasmatodea	0	0	0	0	1
Plecoptera	0	73	5	7	8
Σ =	7353	25300	6340	5950	3146

Our analysis showed that seasonality significantly influenced species richness (Appendix 3.2), with richness being lower in the wet than the dry season ($B = -0.59$; $p < 0.001$; Figure 3.3:A). No other variable on its own or in interaction had support in affecting arthropod species richness (Appendix 3.2). Order richness models fitted with mixed effect models showed poor fit; we, therefore, fitted a negative binomial mixed effect model. There was great model uncertainty regarding factors affecting arthropod order richness (Appendix 3.2). PC1 fell

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within Δ2 AICc units of the null model (Appendix 3.2). We, therefore, used the AICcWeights of models with < 4 AICc units to select the most crucial variable. Thus, we retained PC1 for further inference as it had the highest combined AICc weight (0.46). Arthropod order richness decreased as PC1 scores increased, showing a negative effect of PC1 on order richness (Figure 3.3:B).

Arthropod abundance data showed overdispersion, so we fitted a negative binomial model. Multimodel inference remained uncertain, with the top three models falling within Δ2 AICc units (Appendix 3.3). The top three models included PC1 and season as main or interaction effects (Table S2). Starting with the Season model, we found that adding PC1 improved model fit (LRT; chisq = 3.58, p = 0.05). Subsequently, we found that adding an interaction term does not improve model fit (chisq = 0.59, p = 0.46) and, therefore, retained the PC1 + Season for further analysis. PC1 had a negative effect (B = -0.16, p = 0.04; Figure 3.3:D) on arthropod abundance, where abundance declined, moving from natural habitats to orchards (Figure 3.3:D). The wet season had a positive effect (B = 1.124, p < 0.00; Figure 3.4:C), with a substantial increase in abundance from dry to wet season.

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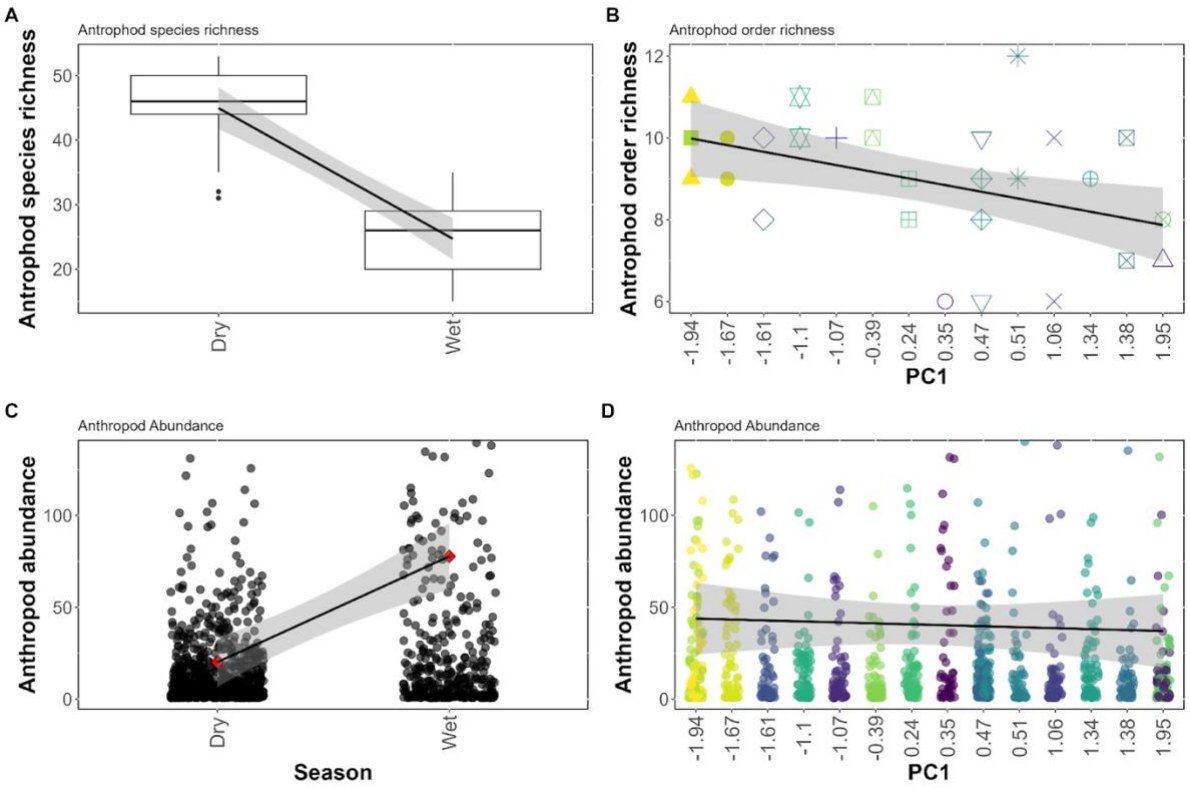


Figure 3.4: Effects of season and PC1 in arthropod species richness and abundance in Citrus orchards and natural habitats. A. Comparison of arthropod species richness between wet and dry seasons. B. Negative relationship between arthropod order richness and PC1 scores. C. Arthropod abundance increases from dry to wet season. D. Negative impact of PC1 scores on arthropod abundance across landscape types.

3.3.2. Spatiotemporal abundance of FCM

In testing the effect of distance from Edge and year, we found support that the FromEgde*Year model had the highest support (AICcWt = 0.69; Appendix 3.4). LRT suggested that the FromEdge interaction term significantly improved the model's fit with the year-only model (chisq = 7.64, p = 0.05). Generally, there was a difference in mean annual trap counts per year, with the lowest mean trap count in 2024 (0.02; sd = 0.20; Figure 3.4) and the highest in 2022 (0.15; sd = 0.66; Figure 3.4). Similarly, over three years, FCM abundance slightly increased (B = 0.04) with distance away from the edge, but only marginally significant (p = 0.05; Figure 3.4).

However, the interaction between distance from the edge and year showed that from 2022, the effect of distance from the edge weakens (2023 vs 2022; B = -0.0008; p = 0.04; Figure 3.5;

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2024 vs 2022; B = -0.0008, p = 0.012). In 2024, distance from the edge had almost no impact on FCM mean trap abundance (Figure 3.5)

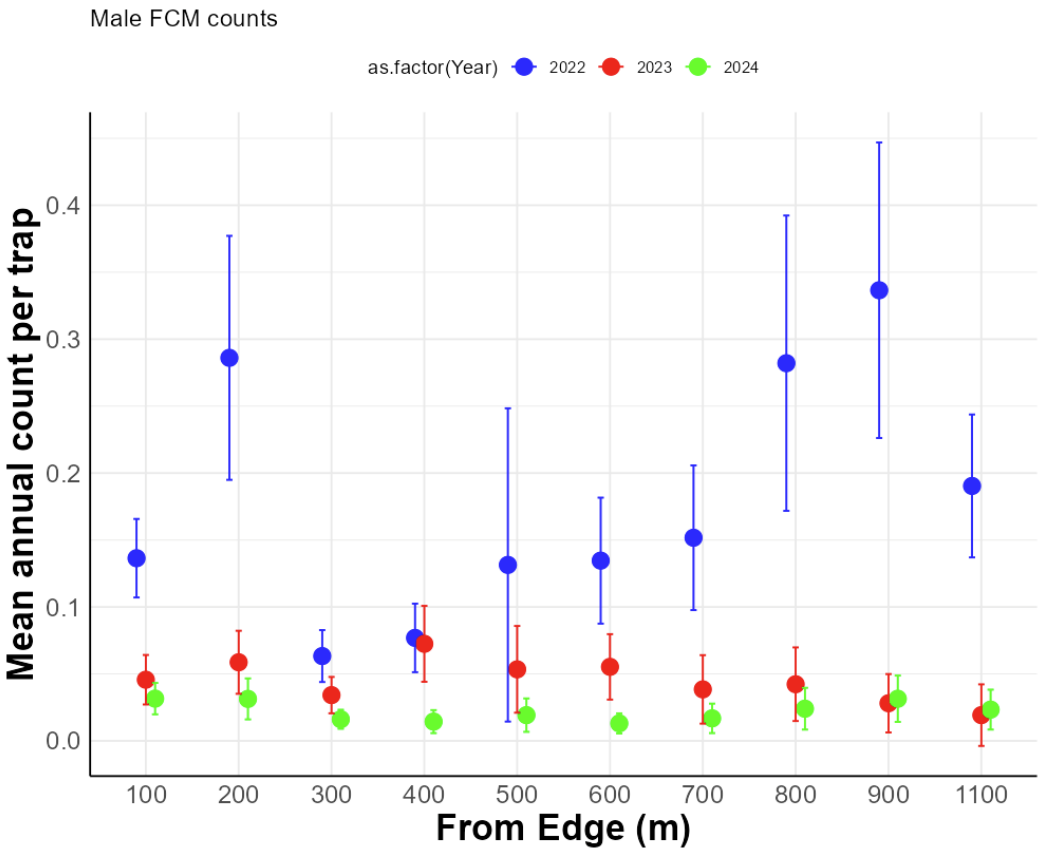


Figure 3.5: Interaction of edge distance and year on False codling moth (FCM) abundance, showing annual variability and the influence of proximity to semi-natural habitat edges. Bars represent mean FCM abundance (± standard error) per sampling point at varying distances from the edge across multiple years. The interaction highlights how both temporal variation and spatial position influence pest pressure in citrus orchards.

To evaluate the effect of all variables on FCM counts, we used the 'dredge' function in the MuMin R package (Barton, 2023). This approach generated all possible models using the variables Rain, Temperature, Season, Citrus Growing Season, and Distance from Edge. We only evaluated the main effects. Variable inflation was low for all values, and we retained all variables. We found that all variables contributed to some extent to FCM counts (Appendix 3.5), and we, therefore, fitted a final model with all the variables as main effects. Season, Citrus growing season, and temperature all significantly affected FCM counts (Figure 3.6:A), while rainfall and distance from the edge had marginal effects (Figure 3.6:B)

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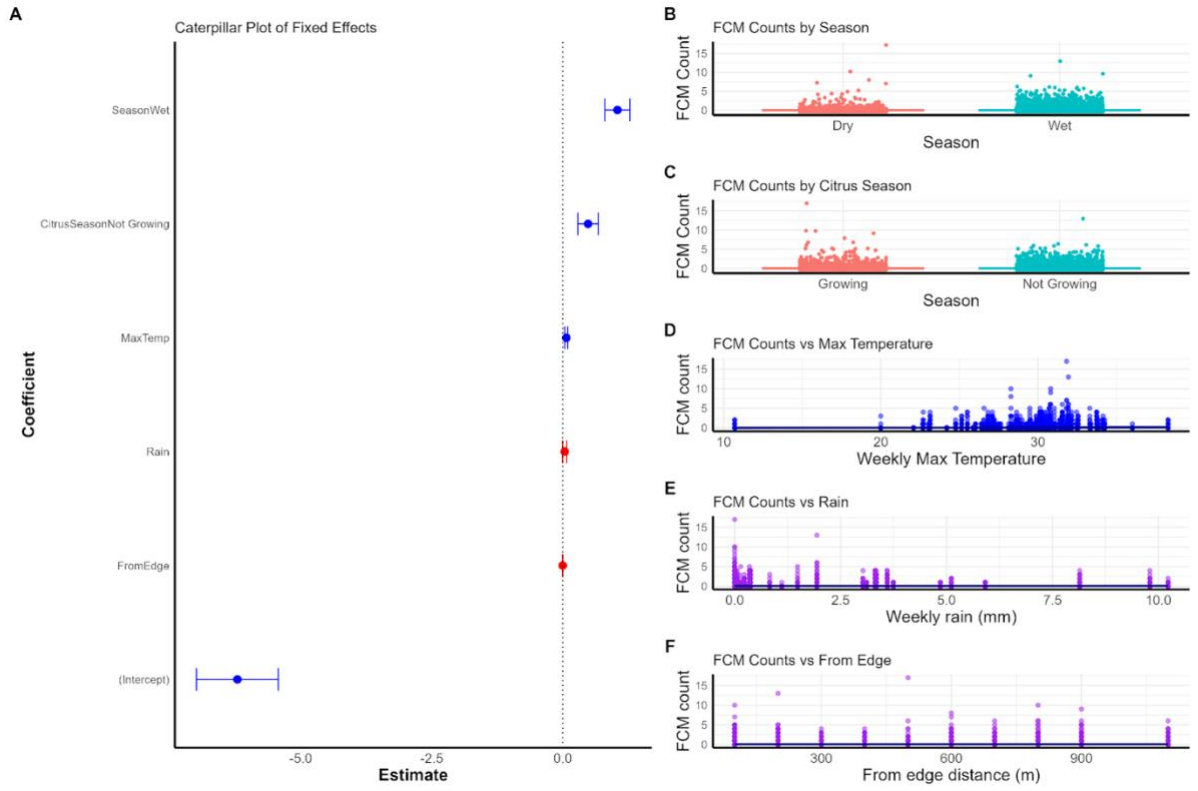


Figure 3.6: Impact of environmental and spatial variables on False codling moth (FCM) counts. (A) Significant predictors of FCM abundance included season, citrus growing season, and temperature, indicating strong temporal and climatic influences on FCM population dynamics. (B) Rainfall and distance from the orchard edge showed marginal effects on FCM counts, suggesting a weaker or context-dependent influence of these variables.

Using a heatmap algorithm in QGIS, we conducted kernel density estimation (KDE) to analyse the spatial distribution of FCM within the orchard and the surrounding landscape. We applied a kernel radius of 250 meters to estimate density. KDE calculated the density at each block by summing the influence of nearby blocks based on their distance, using a uniform kernel function that assigns equal weight to all blocks within the radius. The method generated a continuous density surface, with higher density values in areas near blocks with higher concentrations of FCM and lower values in regions with fewer or no nearby blocks. Dark red areas on the heatmap represent blocks with the highest FCM concentrations; lighter red areas indicate regions with fewer FCM; and white areas show regions with little to no FCM presence.

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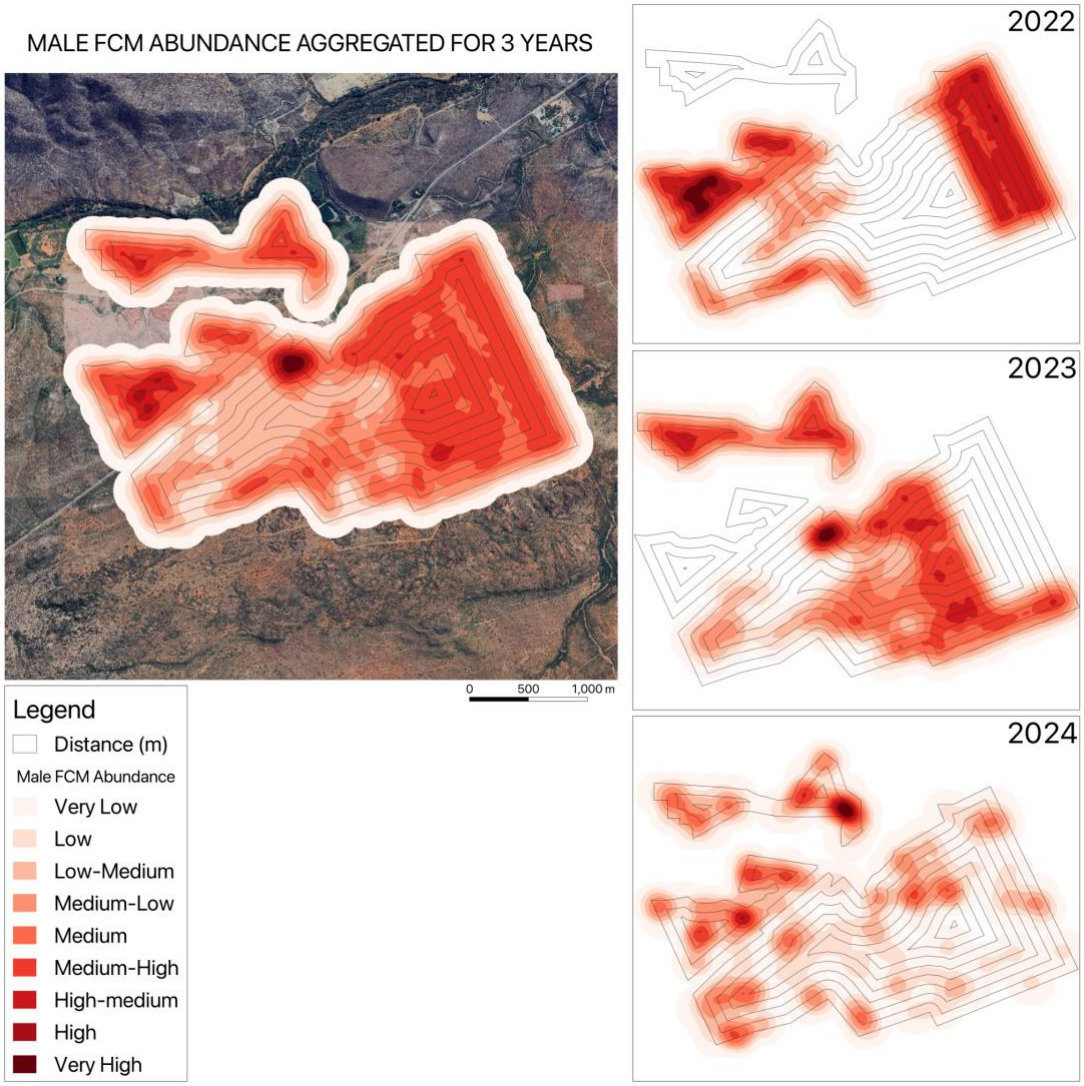


Figure 3.7. Kernel density estimation heatmap showing the concentration of FCM per block within Citrus Orchard AD from January 2022 to September 2024.

3.3.3. Local scale dynamics and the role of exclusion cages

Over a combined 21 sampling days (from January 5th to September 10th, 2024) of orchard sanitation and harvest, we sampled 42,007 citrus fruits, focusing specifically on insect-caused damage. Of the total fruits inspected, 36,050 (85.82%) were undamaged, while 5,957 (14.18%) showed damage from pest insects. Among the damaged fruits (Table 3.7), 2.77% showed signs of infestation, such as frass, tunnelling, head capsules, or the presence of larvae (Figure 3.8:A to I); specifically, 1.16% were affected by either the FCM or carob moth and 1.23% were infested by fruit flies.

We observed that 10.71% of the damaged fruits had signs of mealybugs, such as sooty mould, honeydew, and deformations (Figure 3.8: J, K, N). Phytosanitary pests impacted 13.1% of fruits

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during the 2023/24 growing season. Production pests, particularly red scale, accounted for 81.27% of the damage observed (Figure 3.8:M). Cosmetic pests contributed to 5.64% of the overall damage, with 3% attributed to thrips and 2.63% to bollworms (Figure 3.8:L and O, respectively)

Table 3.7: Insect Damage on Citrus Fruits: Pest Categories and Occurrence Rates

Pest category	Insect pest	Occurrence	Occurrence percentage (%)
Phytosanitary	FCM/Carob moth	69	1.16
	Fruit fly	73	1.23
	Mealybug	638	10.71
Production	Redscale	4,841	81.27
Cosmetic	Thrips	179	3
	Bollworm	157	2.63
	∑ =	5957	100

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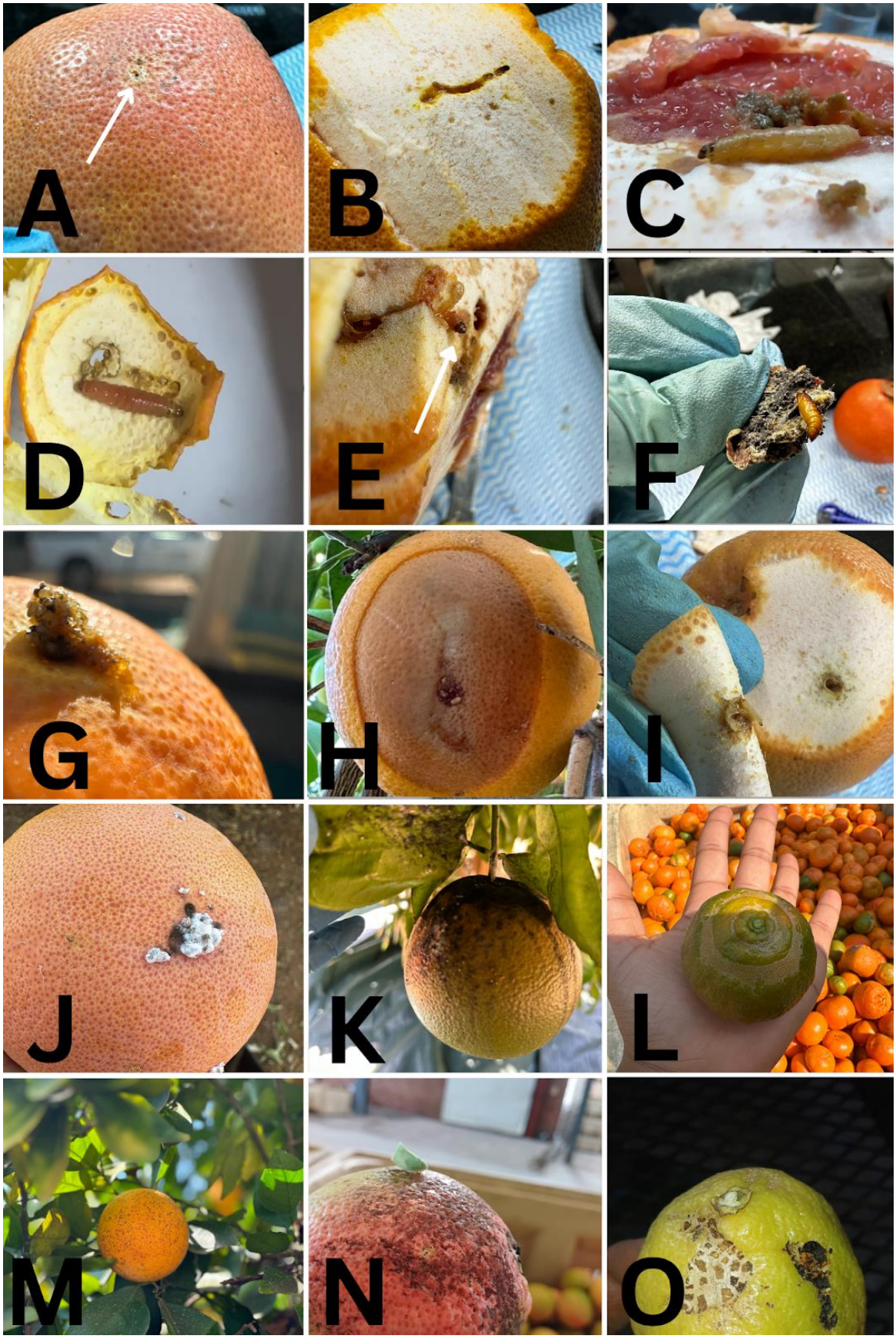


Figure 3.8: Fruit damage by the primary pests of citrus crops. A–I: Internal fruit damage due to infestation. A. Entry hole and frass on rind — *Thaumatotibia leucotreta* (False codling moth, FCM) B. Larval tunnelling into

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pulp — FCM or carob moth (*Ectomyelois ceratoniae*) C-F. Pupal casing and larval remains — FCM/ Carob moth G. Blackened exit hole and frass. H. Internal fruit breakdown and bacterial rot following fruit fly damage. I. Multiple oviposition scars from infestation. J–N: External damage due to sap-sucking insects. J. Sticky honeydew secretion on fruit surface — Mealybugs (*Planococcus citri*). K. Sooty mould developing on honeydew — Mealybug association. L. Silvering and scarring of fruit skin — Citrus thrips (*Scirtothrips aurantii*). M. Red scale (*Aonidiella aurantii*) infestation, visible as red-brown spots on rind. N. Deformed fruit with uneven growth — Chronic mealybug feeding damage. O: Chewing damage on the rind surface. O. Feeding lesion and rind boring — Bollworm species (*Helicoverpa armigera*).

At the local scale and the exclusion treatment (Table 3.8), the edge landscape demonstrated the highest percentage of undamaged fruits, with 88.48%. In contrast, the interior landscape had 81.59% undamaged fruits, the lowest percentage across all landscapes.

In the exclusion treatment, the control exhibited the lowest damaged fruit percentage at 13.89%. The treatment displayed a damaged fruit percentage of 16.05%, placing it between the control and random groups. Fruits exposed to the random treatment experienced a higher damage rate, with 16.68% classified as damaged.

Table 3.8: Effect of local scale and exclusion treatments on fruit damage rates in edge and interior citrus landscapes

Landscape	Design	Average Not Damaged	Average Damaged	Not Damaged %	Damaged %
Orchard Interior	Treatment	479.69	118.69	80.16	19.84
	Control	689.55	141.18	83.01	16.99
Orchard Edge	Treatment	563.47	78.71	87.74	12.26
	Control	790.31	95.5	89.22	10.78

Effect of exclusion cages and landscape context on total insect and FCM damage

Although excluding bats and birds at the edge landscapes had a lower probability of insect damage (43%) compared to the interior (56%), this result was not significant ($p = 0.318$; Figure 3.8:A). However, the landscape context modulated this effect, as multimodel inference identified the interaction model as having the most substantial support (Appendix 3.6). At the edge sites, the treatments had a lower probability of insect damage (8.2% vs. 9.6%; Figure 3.8:A). This result was significant ($p = 0.002$); it translated to a medium effect size of 0.5 (Cohen's d). In contrast, at interior sites, treatment sites showed a significantly higher

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probability of insect damage (19% vs. 15%; p < 0.001; Figure 3.8:A), with a moderate to large effect size of 0.77 (Cohen's d).

The base probability of FCM damage was low (mean = 0.065%, SD = 0.75). We found support for the fact that only the landscape context affected FCM damage probability (Appendix 3.7). Although the Design + Landscape model fell within 2.27 AICc units, the LRT suggested that adding landscape to the design did not improve model fit (chisq = 0.049, p = 0.82). FCM damage probability was lower in the treatment (0.04%, SE 0.035; Figure 3.8:B) than in the control (0.06%, SE 0.06; Figure 3.8:B).

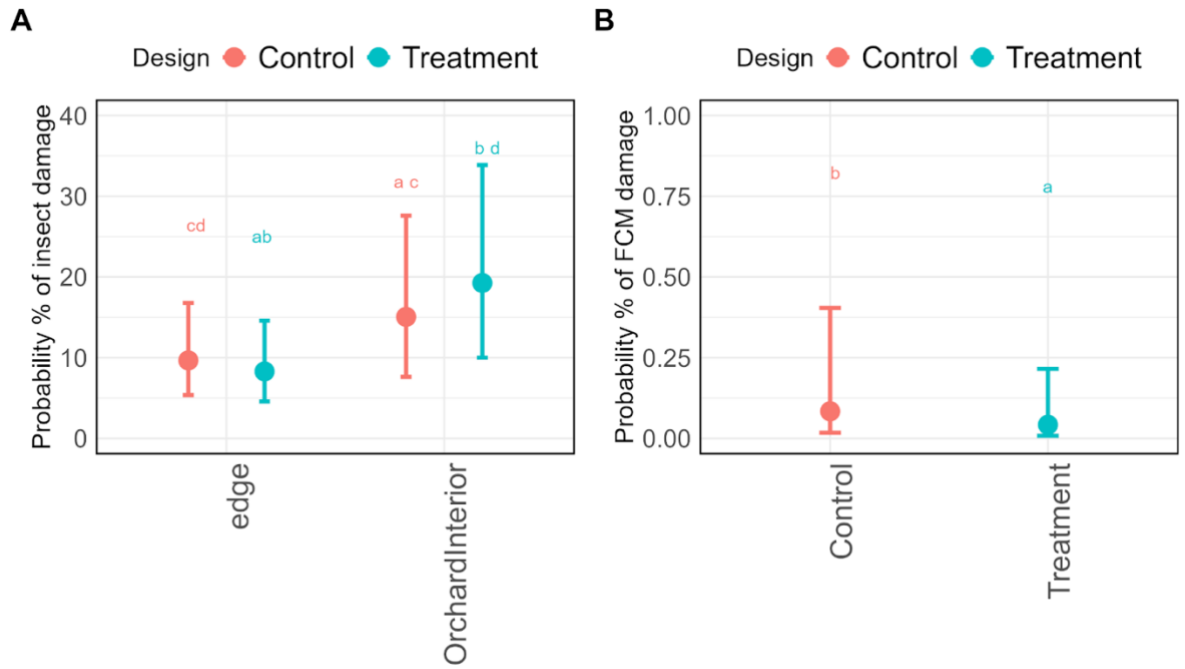


Figure 3.9: Influence of landscape context and treatment on probability of insect damage and False codling moth (FCM) damage in edge and interior sites. (A) Insect damage probability varied by landscape and treatment, with significantly lower damage in treated edge sites (8.2% vs. 9.6%, $p = 0.002$) and higher damage in treated interior sites (19% vs. 15%, $p < 0.001$). (B) FCM damage was low overall and unaffected by treatment. Landscape context was the only significant predictor (see Appendices 3.6 and 3.7). Error bars represent SE.

3.4. Discussion

This study investigated how spatial and temporal variations and insectivorous birds and bats affect the richness and abundance of nocturnal flying insects in citrus agroecosystems, focusing on their role in crop damage. We observed substantial differences across habitat types, with the highest abundance in noncrop habitats and notably lower abundance in cropland. These findings align with prior research indicating that non-crop habitats can serve as biodiversity

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refuges, providing resources and ecological stability that support diverse arthropod communities (Holland et al., 2004; Bianchi et al., 2006). The findings highlight the roles of habitat heterogeneity and seasonality in shaping arthropod communities within agroecosystems. They support the view that diverse landscapes incorporating natural habitat features, such as woodlands and riparian zones, can enhance biodiversity and provide ecosystem services beneficial for pest management (Landis et al., 2000; Tscharntke et al., 2005). We observed a significant effect of exclusion cages in the orchard interiors, underscoring the importance of insectivorous vertebrates in pest suppression within agricultural landscapes. Numerous studies have documented the valuable role of birds and bats in regulating pest populations, particularly within crop fields where pest density can be high (Karp et al., 2013; Maas et al., 2015).

3.4.1. The spatiotemporal variations of nocturnal flying insects

The temporal effects had the most substantial influence on arthropod species richness, with significantly lower richness in the wet season (the hottest and most humid time of year) than in the dry season (typically sunny and cool). Contrary to the richness, arthropod abundance increased in the wet season. This result contrasts with much of the existing literature from tropical and subtropical regions (e.g., Sousa et al., 2021), where both species richness and abundance are typically higher in the wet season due to favourable environmental conditions such as increased food availability, humidity, and vegetation growth (Novotny et al., 2006; Basset et al., 2015). However, heavily managed agricultural landscapes often show reduced richness but increased abundance during the wet season, as resource homogenisation and the dominance of a few opportunistic species suppress diversity (Perfecto and Vandermeer, 2010; Tylianakis et al., 2007). The findings may also reflect the influence of agricultural intensification, where monoculture crops and wet season farming practices such as pesticide application promote pest species while limiting the niches available to specialist arthropods (Tscharntke et al., 2005). The discrepancy between richness and abundance suggests that high arthropod numbers during the wet season do not necessarily indicate ecological balance, as reduced diversity may impair critical ecosystem services such as pest control (Tylianakis et al., 2007). Maintaining landscape heterogeneity and adopting biodiversity-friendly practices in agricultural systems is crucial for ensuring ecological stability and resilience (Tscharntke et al., 2012). Effective management practices in agricultural landscapes should consider these seasonal dynamics; promoting habitat diversity and resource availability during wet and dry

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seasons could enhance arthropod diversity and ecosystem resilience, ultimately benefiting farm productivity and sustainability.

Spatially, the negative association of arthropod richness and abundance highlights the impact of landscape simplification, where the transition from natural habitats to agricultural orchards likely reduces niche diversity, limiting the establishment of specialist species and favouring a more homogenised community dominated by fewer species. Insect diversity decreased when moving from natural habitats towards orchard interiors, consistent with literature suggesting that landscape homogenisation and loss of semi-natural habitats reduce arthropod diversity in favour of pest-dominant communities (Duflot et al., 2017; Landis, 2017). For example, Galloway et al., (2021) found that natural vegetation adjacent to citrus orchards strongly influenced the predator complex within both habitats. Their findings indicate that moving from natural habitats to orchard interiors reduces niche diversity, limits the establishment of specialist species, and promotes a more homogenised community dominated by fewer species. The findings imply that habitats with higher structural complexity support higher arthropod richness and abundance, likely due to diverse habitats and resources favouring arthropod diversity. This result supports the "habitat complexity hypothesis" (Diamond, 1969; Kohn, 1968; MacArthur, 1965; Paine & Vadas, 1969; Pianka, 1969; Rosenzweig & Winakur, 1969), which posits that complex habitats sustain greater biodiversity due to the availability of diverse resources and niches. The results highlight the critical role of natural habitat preservation in supporting biodiversity in agroecosystems.

3.4.2. The spatiotemporal variations of FCM

FCM trap counts varied significantly over the three-year study period. Abundance peaked in 2022 and declined sharply by 2024, reflecting substantial fluctuations in FCM population dynamics. This reduction in later years is likely due to several factors. First, improved pest management practices may have contributed to this decline. As a key phytosanitary pest in South Africa, maintaining FCM populations close to zero is essential. Additionally, Daiber (1980) highlighted the critical role of environmental factors in shaping FCM lifecycle dynamics.

Climatic conditions also likely influenced the observed decline in FCM populations. South Africa experienced a transition toward drier conditions starting in 2022, driven by the El Niño phenomenon, as highlighted in the *National State of Water Report 2023*. El Niño conditions,

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characterised by higher temperatures, create unfavourable microclimates for FCM reproduction and survival in the northern regions of South Africa (Newton 1998; Moore 2012; Moore & Hattingh 2012). Predictions of below-normal rainfall during critical months likely exacerbated these conditions, imposing significant stress on FCM populations. Warmer and drier conditions negatively limited FCM abundance as the eggs are sensitive to periods of low humidity (Gendall, 2007). These climatic factors underscore the importance of adapting pest management strategies to changing environmental conditions.

FCM abundance varies regionally across South African citrus production areas, influenced by climate and host availability (Grout and Moore, 2015). For instance, the Limpopo Province consistently reported lower FCM abundance (Moore, 2022) due to less favourable climatic conditions, reducing pest pressure on citrus crops. Warmer and drier conditions in northern areas explain the consistently lower FCM abundance in regions like Limpopo. In the Tshipise area, this trend aligns with the limited availability of cultivated host plants for FCM, which may further suppress its populations. These regional differences highlight the need for adaptive pest management strategies that address microclimatic variations and landscape-specific challenges.

Stotter (2009) demonstrated that FCM does not migrate into citrus orchards from surrounding vegetation. Instead, citrus orchards serve as reservoirs for FCM populations, which then disperse into adjacent habitats. The current study supports this finding, as spatial trends revealed an initial increase in FCM abundance with distance from the orchard edge into the interior. This pattern may indicate that interior orchard areas provide more stable conditions for FCM, potentially due to fewer natural enemies than edge areas. These findings emphasise the importance of considering landscape context when developing FCM control strategies, as the *National State of Water Report 2023 highlighted*. Enhancing pest management in citrus production systems requires addressing local-scale dynamics and landscape-scale microclimatic differences.

Although FCM is a highly polyphagous pest with the potential to infest a wide range of fruit crops, the Tshipise area is currently dominated by citrus production, with limited or no cultivation of alternative FCM host crops such as maize, guava, cotton, or pecans. Therefore, in this context, intra-orchard and inter-orchard movement of FCM is more likely to occur within the citrus production matrix itself. This limits the likelihood of external crop reservoirs but underscores the importance of coordinated area-wide management among citrus growers to prevent reinfestation from unmanaged blocks or abandoned orchards. Nonetheless, future

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research could investigate whether native or ornamental plant species in adjacent semi-natural habitats may also serve as incidental reservoirs for FCM or other citrus pests in the region.

The results show that *Citrus reticulata*, highly susceptible to FCM (Love et al., 2014), supports higher pest densities, revealing a weakness in current management strategies. The absence of natural or semi-natural habitats further amplifies the reliance on citrus varieties, which is crucial in sustaining FCM populations. *Citrus sinensis*, particularly Late Valencia, can act as a seasonal bridge for FCM (Moore, 2022), reaching maturity as FCM abundance rises in this region. This alignment enables the pest to persist and reproduce between seasons. These findings emphasise the need for pest control strategies focusing on citrus variety management and interrupting the seasonal cycle that allows FCM populations to thrive. The spatial arrangement of *Citrus reticulata* creates microclimatic conditions that favour the proliferation of the FCM. A nearby water source contributes to increased humidity in a warm environment, favouring FCM development. Additionally, the proximity of *Citrus sinensis*, known to be susceptible to FCM, poses a risk as it can act as a reservoir for FCM populations, allowing them to survive and potentially spread into subsequent growing seasons, facilitating their survival and potential spread into subsequent growing seasons. This configuration places mandarins at a heightened risk of FCM infestation yearly.

The results show that seasonality, citrus growing season, and temperature significantly affected FCM abundance. We observe high abundance in the wet season. However, temperature was more of an influencing factor than precipitation. Temporal effects on FCM abundance highlight the importance of climatic and phenological factors in pest dynamics. These findings are consistent with studies in subtropical citrus systems, where pest abundance is typically highest during warmer growing seasons when fruit availability peaks. For instance, Moore et al. (2014) showed that FCM populations often peak during warmer seasons due to accelerated insect life cycles at higher temperatures. Elevated temperatures can accelerate FCM life cycles while synchronising pest activity with fruit development, which increases the risk of economic damage. Citrus phenology significantly influences FCM abundance as the larvae rely on fruit as a host, with pest abundance rising during fruiting periods (Grout and Moore, 2015). Citrus phenology is equally influential, as FCM relies on citrus fruit availability for oviposition and larval development; thus, pest counts rise with citrus phenological stages that provide necessary resources. The longer the fruit stays on the tree, the more it attracts FCM. The marginally

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significant effect of distance from the edge to the interior and rainfall suggests that these factors may modulate pest dynamics and do not independently drive FCM abundance in this context.

3.4.3. Determining drivers of fruit damage probability

Our results demonstrate that edge landscapes exhibited a lower probability of insect damage than interior landscapes when we excluded insectivorous bats and birds from predation, although this difference was statistically insignificant. However, the proximity to the remnant natural vegetation significantly modulated the effects, reducing the likelihood of insect damage at edge sites when used. At interior sites, excluding vertebrate predators led to a significant increase in the probability of insect damage. These findings align with studies by Tscharntke et al. (2016) and Karp et al. (2018), highlighting semi-natural habitats' role in enhancing biological control through increased predator activity and diversity at habitat edges. Similarly, Williams-Guillén et al. (2008) and Maas et al. (2016) observed that insectivorous birds and bats are more active in edge habitats due to higher habitat connectivity and resource availability. In South Africa, studies such as those by Boyles et al. (2011) and Taylor et al. (2018) have demonstrated the significant role of bats and birds in pest suppression, particularly in agricultural landscapes. Bouarakia et al. (2023) showed that bats and birds significantly reduced pest damage in South African macadamia orchards, with greater suppression observed near natural vegetation, supporting the notion that landscape heterogeneity enhances predator activity.

Similarly, Khavheli (2024) demonstrated higher bat activity in the Tshipise citrus orchards near natural habitats, which correlated with reduced pest outbreaks, including consumption of key pests like FCM and carob moth. Bats are highly effective in controlling nocturnal pests like moths and beetles, while birds are known to reduce diurnal pest populations. The increased insect damage within exclusion cages in interior sites mirrors findings by Rogers et al. (2020), who reported greater pest activity and crop damage in simplified agricultural landscapes following predator exclusion. Predation services by bats and birds tend to decline towards the interior of the orchard, compared to the natural edges (Milligan et al., 2016). The activity of these predators in agricultural landscapes is supported by structural landscape features, landscape heterogeneity and natural vegetation (Kalda et al., 2015; Boesing et al., 2017; Weier et al., 2021). These results suggest that enhanced predator activity near edges provides a degree of pest suppression even under restricted access.

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In contrast, reduced predator activity within orchard interiors highlights the increased vulnerability of monoculture systems to pest outbreaks. Khavheli (2024) conducted acoustic monitoring of bat activity across citrus orchards and found significantly higher activity levels at habitat edges compared to interior zones. The strong support for the interaction model underscores the spatial heterogeneity in predator-mediated pest suppression. It emphasises the importance of maintaining semi-natural habitats and enhancing landscape complexity to optimise ecosystem services in agricultural systems.

Our findings further indicate that the baseline probability of FCM damage was low. However, landscape context emerged as the sole significant predictor of FCM damage, with edge habitats experiencing reduced damage compared to interior sites. These results align with studies by Bouarakia et al. (2023) and Khavheli (2024), who demonstrated the influence of semi-natural habitats in enhancing pest suppression by supporting predators such as bats and birds. In contrast, Moore and Kirkman (2008) reported that FCM often disperses to adjacent vegetation for refuge, which might mitigate control efforts. The reduced FCM damage near edges likely results from higher predator activity in semi-natural habitats, which serve as refuges and feeding grounds for insectivorous vertebrates, corroborating findings by Taylor et al. (2018).

Conversely, more significant damage in orchard interiors reflects limited predator access and reduced landscape heterogeneity, consistent with Malan et al. (2018), who highlighted the vulnerability of monocultures to pest outbreaks. For example, in 2024, Orchard AD experienced its lowest recorded abundance of FCM. Within the same orchard, *Citrus reticulata* (var. Tambor) exhibited the highest infestation levels among all observed citrus varieties (Personal communication). These findings suggest that, despite overall reduced FCM populations, certain citrus varieties may remain disproportionately vulnerable to infestations, potentially due to their phenological characteristics or other host-specific traits. These findings underscore the critical interplay between temporal variability and spatial landscape factors in influencing FCM damage, advocating for adaptive, landscape-scale management practices that integrate natural habitat conservation to enhance biological control and reduce reliance on chemical interventions in agroecosystems.

3.5. Conclusion

This study investigated the spatiotemporal dynamics of nocturnal flying insects, FCM abundance, and fruit damage in citrus orchards within an agricultural landscape matrix.

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Seasonal effects strongly influenced arthropod richness and abundance, with reduced richness but higher abundance during the wet season. Initially, FCM abundance was higher in orchard interiors than at edges, but this trend declined over time, likely due to improved pest management and unfavourable climatic conditions. These findings highlight the importance of landscape complexity, seasonality, and predator activity in shaping pest dynamics and crop damage, informing agroecosystem management.

This study revealed complex interactions based on the hypothesis that landscape heterogeneity, seasonality, and predator exclusion influence arthropod diversity, pest abundance, and crop damage. Agricultural intensification and resource homogenisation prevented arthropod diversity and abundance from consistently increasing in the wet season. Effective management and natural habitats supported FCM abundance, which declined over time. Predator exclusion experiments confirmed the role of semi-natural habitats in reducing pest damage near edges while leaving interiors vulnerable. The results highlight the critical role of semi-natural habitats in biological pest control and the seasonal mismatch between arthropod richness and abundance in managed landscapes. FCM reductions highlight the combined effects of climate, crop phenology, and pest management, providing practical insights for control strategies. These findings stress the need for adaptive management that integrates habitat conservation and promotes landscape complexity.

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3.6. Appendices Data

Appendix 3.1: Custom-designed light trap for capturing nocturnal insects: 1. Aluminium Ring: Supports and holds the UV LED light strip in place. 2. 10W Ultraviolet (UV) LED Light Strip: Attracts nocturnal insects to the trap. 3. Polyethylene cylinder: A 2 mm thick white cylindrical structure measuring 55 cm in height and 25 cm in width, with open sides to allow insect entry. 4. Funnel with 5 cm opening: Guides insects into the 5-litre plastic collection container. 5. 5 Litre plastic container: Collects and stores captured insects. 6. Cotton pad soaked in ethyl acetate: euthanises insects inside the trap for subsequent identification. 7. 12V Battery: Powers the UV light strip. 8. Timer: Automatically activates the light trap at sunset for three hours.



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Appendix 3.2: Factors influencing nocturnal flying insect richness model selection.

Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
PC1	3	943.58	0	0.46	0.46	-468.74
PC1INTSeason	5	944.83	1.25	0.25	0.7	-467.28
PC1_PC2	4	945.49	1.91	0.18	0.88	-468.66
Null	2	947.5	3.92	0.06	0.95	-471.72
PC2	3	949.35	5.77	0.03	0.97	-471.62
Season	3	949.41	5.83	0.02	1	-471.65
PC2INTSeason	5	953.1	9.52	0	1	-471.42

Appendix 3.3: Factors influencing nocturnal flying insect abundance model selection.

Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
PC1ANDSeason	5	10069.14	0	0.41	0.41	-5029.54
PC1INTSeason	6	10070.63	1.49	0.19	0.6	-5029.28
Season	4	10070.71	1.57	0.19	0.79	-5031.34
PC2INTSeason	6	10071.3	2.16	0.14	0.93	-5029.61
PC2ANDSeason	5	10072.58	3.44	0.07	1	-5031.26
PC1	4	10265.97	196.83	0	1	-5128.97
Null	3	10266	196.86	0	1	-5129.99
PC1_PC2	5	10267.53	198.39	0	1	-5128.74
PC2	4	10267.6	198.47	0	1	-5129.79

Appendix 3.4: Factors influencing FCM abundance model selection.

Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
FromEdgeINTYear	8	9250.6	0	0.69	0.69	-4617.3
Year	5	9252.24	1.64	0.31	1	-4621.12
Null	3	9605.81	355.21	0	1	-4799.9
FromEdge	4	9607.57	356.97	0	1	-4799.79

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Appendix 3.5: The effect of exclusion cages and landscape context on total insect model selection

Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
Season	3	232.57	0	0.75	0.75	-112.89
PC1INTSeaon	5	235.24	2.67	0.2	0.94	-111.55
PC2INTSeason	5	237.66	5.08	0.06	1	-112.76
Null	2	331.56	98.99	0	1	-163.59
PC1	3	331.58	99	0	1	-162.39
PC2	3	333.8	101.22	0	1	-163.5
PC1_PC2	4	333.94	101.37	0	1	-162.28

Appendix 3.6: Probability of crop damage by landscape context and design model selection

Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
Null	2	697.8	58.4	0	1	-346.79
Design	3	690.49	51.09	0	1	-342.02
Landscape	3	697.81	58.41	0	1	-345.68
DesignANDLandscape	4	690.64	51.24	0	1	-340.93
DesignINTLandscape	5	639.4	0	1	1	-314.11

Appendix 3.7: FCM base probability model selection

Model	K	AICc	ΔAICc	AICc. Wt	Cum. Wt	LL
Design	3	112.66	0	0.55	0.55	-53.1
DesignANDLandscape	4	114.93	2.27	0.18	0.73	-53.08
Null	2	115.09	2.42	0.16	0.89	-55.43
Landscape	3	117.25	4.59	0.06	0.95	-55.4
DesignINTLandscape	5	117.34	4.67	0.05	1	-53.08

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3.8. Supplementary Data

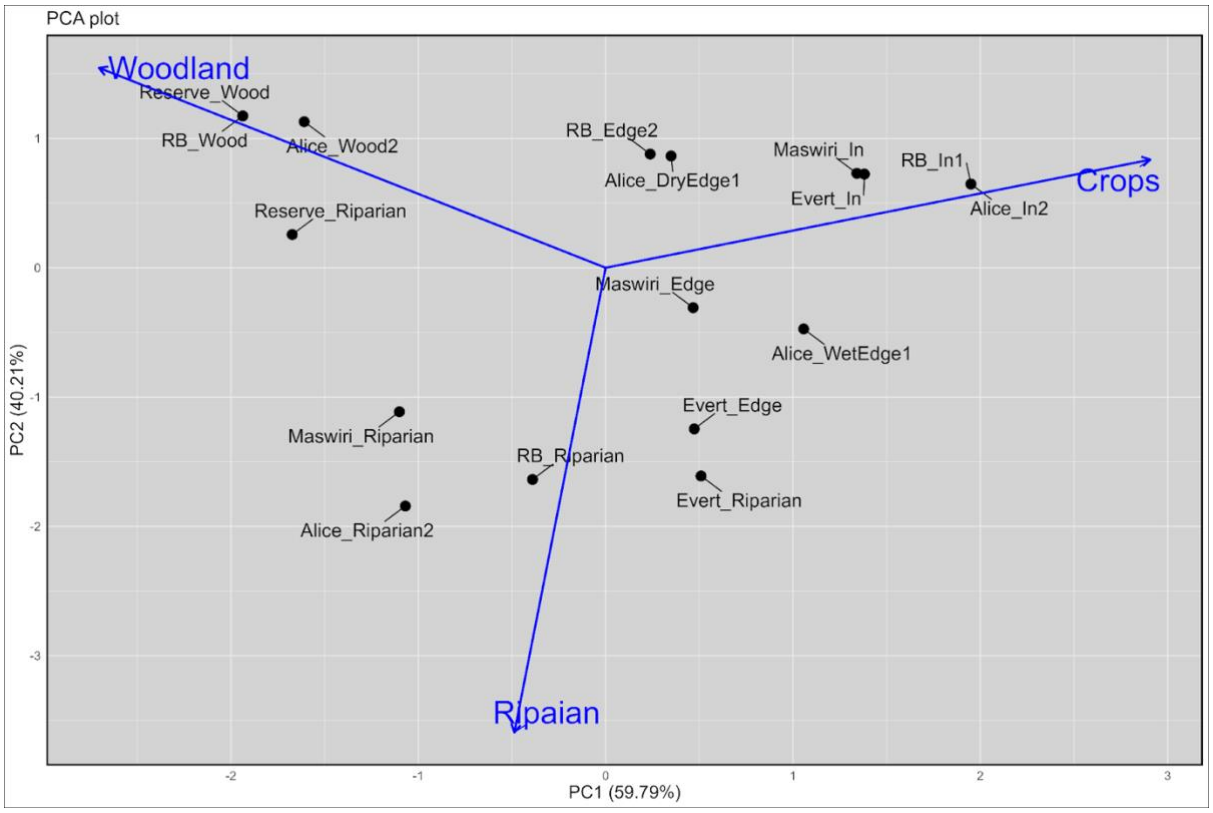


Figure S3.1: Principal Component Analysis for Landscape composition per site

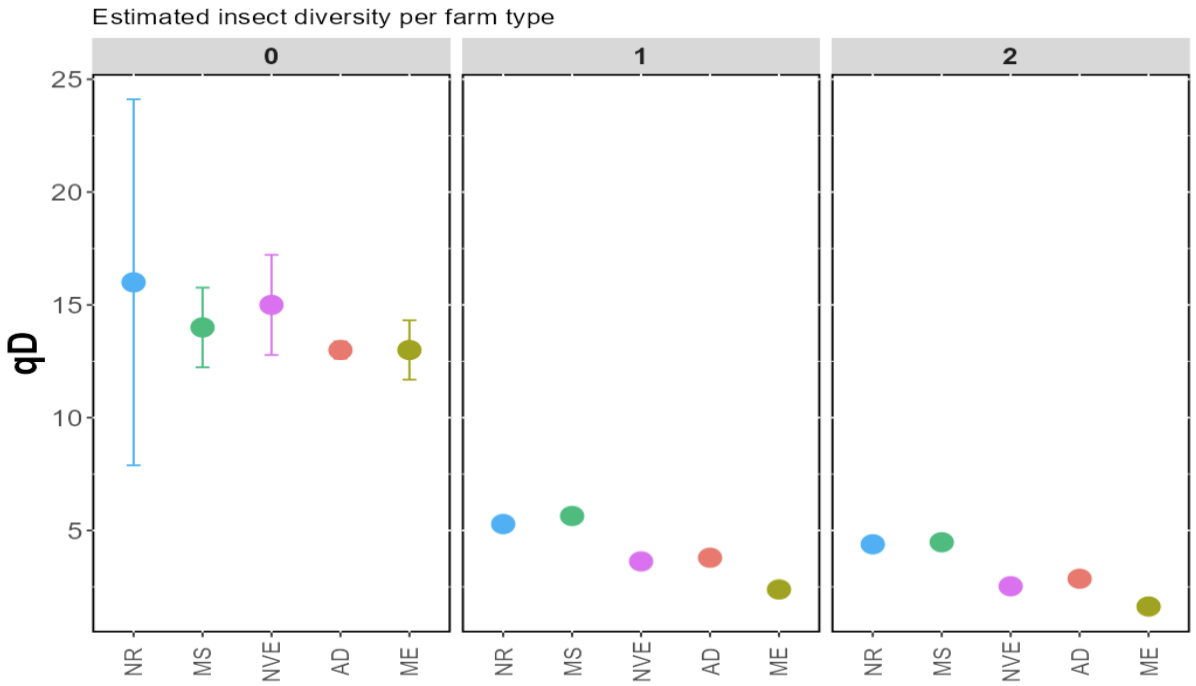


Figure S3.2: Estimated insect diversity per farm type

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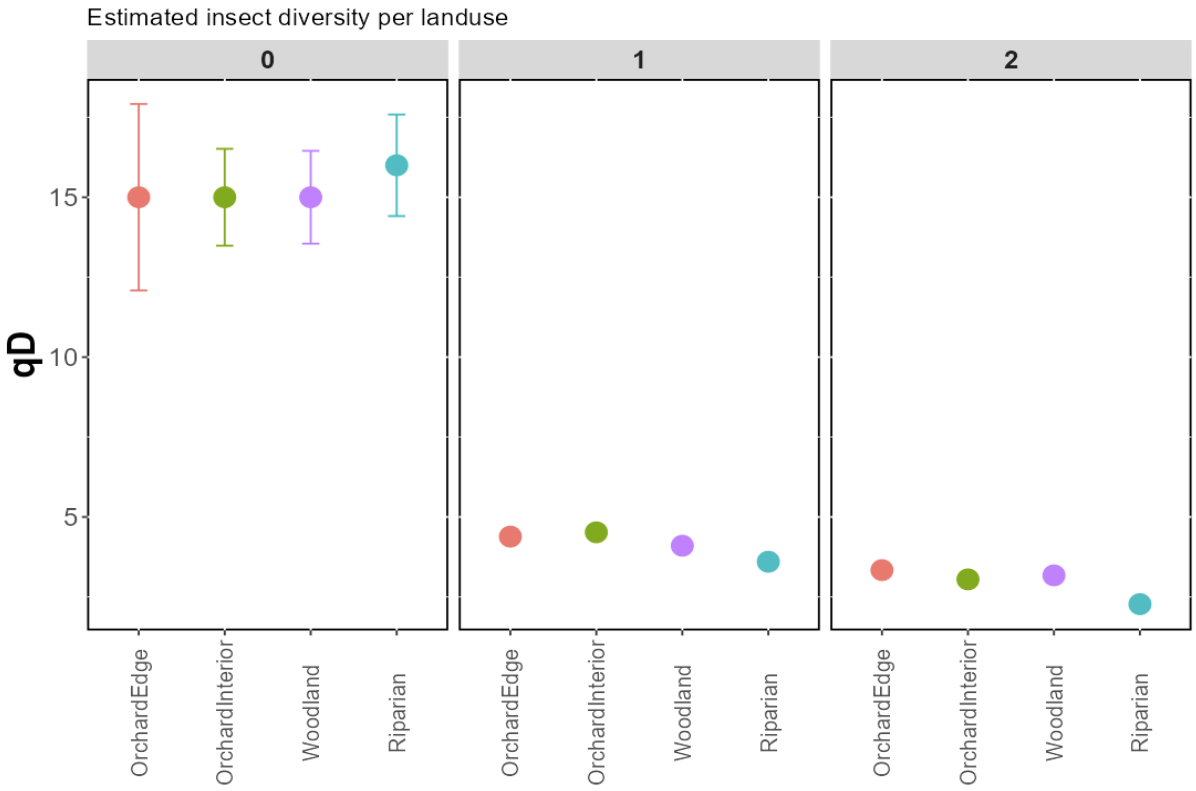


Figure S3.4: Estimated insect diversity per land use

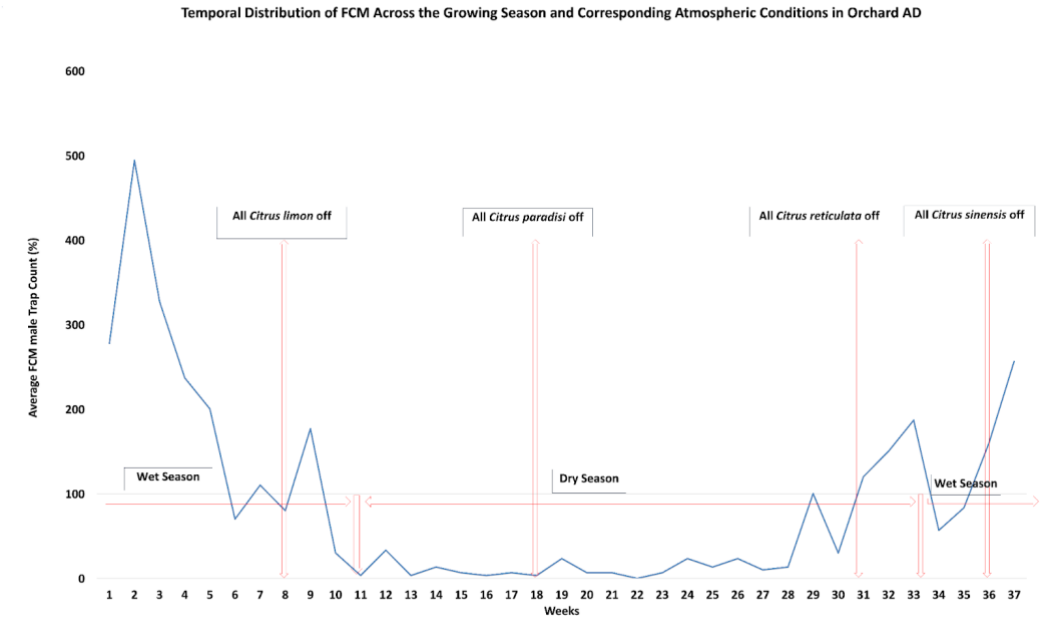


Figure S3.4: Temporal distribution of FCM across the growing season with maturation of citrus cultivars. "Weeks" refer to consecutive calendar weeks starting from the beginning of the citrus growing season (Week 1 = first week of January). The timeline includes key cultivar maturation stages and transitions between wet and dry seasons.

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CHAPTER FOUR
SYNTHESIS AND RECOMMENDATIONS

4.1. Synthesis

This thesis explored how citrus landscape structure influences arthropod diversity and IPM strategies in citrus agroecosystems, specifically within a subtropical developing region. The study emphasises ecological intensification alternatives to conventional intensification practices, advocating for ecosystem services and functioning to maintain or enhance agricultural yields (Bommarco et al., 2013). The study begins by addressing the broader issue of landscape homogeneity and fragmentation, which, though aimed at meeting global food demands (FAO et al., 2017; Hunter et al., 2017), has contributed to significant biodiversity loss. This loss includes declines in beneficial arthropods, such as predators and pollinators, which are essential for natural pest control and crop pollination, followed by examining insectivorous volant vertebrates' role in citrus orchards' biocontrol services. The findings show that landscape structure impacts biodiversity and ecosystem functioning, aligning with the growing body of research (Benton et al., 2003; Tscharntke et al., 2005; Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Fahrig et al., 2011; Bianchi et al., 2013; Fahrig et al., 2015). Much of the existing evidence originates from developed countries with extensively transformed landscapes. However, this thesis identifies a significant gap in research about developing countries and tropical regions, where the interactions between landscape heterogeneity, biodiversity, and ecosystem services remain underexplored (Suárez-Castro et al., 2022). This study examined the role of landscape structure on arthropod assemblages in South African citrus orchards, a significant agricultural sector, focusing on the Tshipise, Limpopo region, where citrus orchards vary in intensification and size. The study's novelty lies in its dual focus: exploring the effects of landscape structure and context on arthropod diversity for investigating IPM strategies, particularly CBC and the role of insectivorous volant vertebrates in controlling citrus pests, with more emphasis on *Thaumatotibia leucotreta* (FCM), a major pest of citrus.

Chapter two addressed the relationship between landscape context and arthropod diversity, considering species abundance, richness, and functional traits. The results show that less fragmented orchards support higher species abundance, aligning with the broader landscape ecology literature emphasising the importance of habitat continuity for biodiversity (Hanski, 1999; Fenberg and Rivadeneira, 2019). The findings suggest that orchard management practices that reduce habitat diversity fragmentation could reduce arthropod diversity and

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ecosystem services. It is crucial to adopt a landscape perspective when managing agricultural systems to conserve biodiversity and ensure the provision of ecosystem services effectively, as highlighted by Tscharntke et al. (2007). Strategically enhancing landscape heterogeneity while considering the size and connectivity of different habitat patches may be a promising approach to support robust and functionally diverse arthropod communities that can contribute to effective biological pest control (Jeanneret et al., 2021).

In chapter three, the thesis shifted focus to the role of insectivorous vertebrates, particularly bats and birds, in biocontrol. While the effect of volant vertebrates on citrus pests was significant, the study suggests that their role may be seasonally dependent, with bat activity increasing in response to prey availability during the wet season (Weier et al., 2018). The correlation between increased bat and FCM activity with rising temperatures raises important questions about whether temperature directly influences predator-prey dynamics. Further research is needed to determine whether temperature-driven increases in bat activity effectively regulate FCM populations. The findings further demonstrated that landscape heterogeneity, particularly the balance between natural habitats and cropland, is a crucial driver of arthropod assemblages and pest proliferation. Furthermore, as insectivorous vertebrates, bats and birds provide vital biocontrol services and reduce the reliance on chemical interventions (Taylor et al., 2017; Weier et al., 2018). While this study was limited to a specific geographic region, the insights gained have broader implications for developing sustainable integrated pest management approaches in perennial cropping systems, thereby underscoring the practical relevance of the research.

The findings from chapters two and three, which focus on arboreal arthropods and nocturnal flying insects, respectively (Table 4.1), collectively provide complementary insights into the distribution, functional roles, and habitat preferences of arthropods in citrus agroecosystems. These findings underscore the critical ecological importance of preserving natural and semi-natural habitats within these systems. Riparian and woodland habitats consistently support the highest abundances of both arboreal (49.83% and 41.88%, respectively) and nocturnal arthropods (45.76% and 19.81%, respectively), providing critical refuges for beneficial arthropods, such as predators (Coleoptera, Araneae). Cropland habitats, particularly edges, exhibit higher proportions of nocturnal flying pests like Hemiptera and Diptera while supporting fewer arboreal species, underscoring their susceptibility to pest outbreaks.

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Arboreal arthropods and nocturnal flying insects differ in mobility, habitat use, and community composition but overlap in ecological roles. Arboreal arthropods include non-flying taxa like spiders (Araneae), mites (Acari), and pseudoscorpions, which rely on vegetation for survival. In contrast, highly mobile taxa such as moths (Lepidoptera), beetles (Coleoptera), and flies (Diptera) dominate nocturnal flying insect communities. Arboreal habitats also support ground-associated taxa like woodlice (Isopoda) and stick insects (Phasmatodea), which flying communities rarely include. Both groups share taxa like Hemiptera, Coleoptera, and Hymenoptera, which actively contribute to pest control, pollination, and nutrient cycling. Predatory arthropods, such as spiders and mantises, find counterparts in nocturnal flying beetles. Herbivorous taxa like Hemiptera demonstrate their ecological versatility by thriving in both groups. Hymenoptera play essential roles in pollination and parasitism across both communities. These similarities illustrate a continuum of environmental function, where taxonomic groups and functional roles overlap. Despite differences in activity patterns and habitat use, both communities actively support ecosystem health and resilience across multiple scales.

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Table 4.1: Arthropod diversity of arboreal and nocturnal arthropods across agricultural landscapes.

Arthropod Order	Total Abundance	Arboreal Dwelling arthropods	Nocturnal Flying Insects	Feeding Traits[1]	Riparian - dominated *n* = 11	Woodland - dominated *n* = 8	Cropland Edge *n* = 17	Cropland Interior *n* = 14
Hemiptera	17086	10561	6525	H, Pr,	5004	4530	6492	5096
Hymenoptera	12295	8701	3594	Pr, Pa, Pol	4622	3852	6002	2926
Coleoptera	32852	5958	26894	H-, Pr	4618	3512	2246	1540
Diptera	6089	3839	2250	H, Pa, Po	502	738	2764	3674
Araneae	3416	3406	10	Pr	744	1088	2794	2186
Orthoptera	1560	1476	84	S	692	600	958	702
Acari	386	386	0	H, Pr	604	124	40	4
Blattodea	404	337	67	S	498	88	56	32
Mantodea	113	80	33	Pr	36	50	38	36
Neuroptera	154	66	88	Pr	12	4	68	48
Odonata	44	44	0	S	0	0	70	14
Phasmatodea	31	30	1	S	26	8	18	8
Solifugae	24	24	0	Pr	22	16	12	0
Pseudoscorpion	20	20	0	Pr	20	18	0	2
Dermaptera	193	17	176	Pr	0	16	2	16
Isopoda	17	17	0	S	22	10	2	0
Lepidoptera	6684	15	6669	H	0	0	0	30
Thysanoptera	6	6	0	H	12	0	0	0
Scorpiones	4	4	0	Pr	6	0	2	0
Isoptera	828	3	825	S	0	0	2	4
Chilopoda	1	1	0	S	0	0	0	2
Σ =	82207	34991	47216		17440	14654	21566	16320

[1] H = Herbivore (Leaf, stem, bark, Fruit, minor pest, major pest). Pr = Predator, Pa = Parasitoids, Po = Pollinator, S = Secondary group (decomposer, anthophilous, and uncommon).

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Throughout this thesis, the emphasis lies on the importance of landscape-scale factors in balancing agricultural productivity with environmental stewardship. This thesis firmly establishes the critical role of landscape structure in shaping arthropod diversity and influencing IPM strategies in citrus agroecosystems, particularly within subtropical developing regions. By demonstrating how natural and semi-natural habitats, such as riparian zones and woodlands, support beneficial arthropods and reduce pest pressures, the findings underscore the ecological and agricultural importance of maintaining habitat heterogeneity (Tscharntke et al., 2005; Jeanneret et al., 2021). The study highlights the complementary roles of arboreal-dwelling arthropods and nocturnal flying insects in ecosystem functioning, with both communities contributing to pest control, pollination, and nutrient cycling (Benton et al., 2003; Bianchi et al., 2006).

The evidence emphasises that landscape heterogeneity enhances biodiversity and supports functionally diverse arthropod communities that underpin sustainable agriculture (Tscharntke et al., 2007; Fahrig et al., 2015). Furthermore, including insectivorous vertebrates, such as bats and birds, as biocontrol agents highlights their importance in reducing reliance on chemical pesticides and promoting ecological stability (Taylor et al., 2017; Weier et al., 2018). The study reinforces the need for landscape management strategies that balance agricultural intensification with biodiversity conservation, such as preserving at least 20% of non-crop habitats and enhancing habitat connectivity (Chaplin-Kramer et al., 2011; Bommarco et al., 2013; Garibaldi et al., 2020).

Ultimately, this research advances our understanding of the interconnectedness between landscape features, biodiversity, and ecosystem services, providing actionable insights for IPM and sustainable farming. By prioritising biodiversity-friendly practices, farmers and policymakers can create resilient agricultural systems that maintain productivity while safeguarding the ecological integrity of agroecosystems. These findings are a foundation for future studies and policies to integrate biodiversity conservation into agricultural landscapes worldwide.

4.2. Study limitations and recommendations

Our study highlights several limitations that provide valuable direction for future research. We excluded ground- and ground cover-dwelling species inhabiting grasslands and lower vegetation strata, focusing instead on tree-dwelling arthropods. This limitation likely led to

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underrepresenting the full arthropod diversity in citrus agroecosystems. Ground-dwelling arthropods play critical roles in ecosystem processes, such as biological control, and their absence limits our findings. We confined the spatial scope to orchard perimeters, which did not account for the movement of arthropods between orchards and adjacent natural habitats, interactions that likely influence diversity patterns. Additionally, we restricted the temporal scope to a single growing season, which prevented us from capturing seasonal and interannual dynamics essential for understanding biodiversity trends and their effects on crop production.

We classified arthropods at broad taxonomic levels, which limited our ability to analyse their specific functional roles in the ecosystem. It was also a restriction in properly analysing species richness and assemblage compositional differences. Furthermore, we should have included the interactions between insectivorous birds, bats, and arthropods, which were likely overlooked, as important dynamics influencing pest populations and crop yields. These limitations underscore the need for a more holistic and integrated approach to studying ecological interactions within agroecosystems.

Future research should incorporate ground- and ground cover-dwelling arthropods to provide a more comprehensive understanding of the arthropod community and its role in ecosystem functioning. Expanding spatial sampling to include landscapes with varying degrees of heterogeneity and extending the temporal scope across multiple growing seasons would allow for a more robust analysis of biodiversity patterns and prioritising transect study design to capture arthropod movements. Researchers should also classify arthropods into functional guilds to better understand their ecological roles and the influence of landscape features on these functions. Employing species distribution or environmental niche modelling for pests such as FCM can enhance predictions of pest behaviour under varying climatic and landscape conditions, informing adaptive pest management strategies.

Exploring the effects of landscape management practices, such as maintaining plant diversity and conserving at least 20% of non-crop habitat (Garibaldi et al., 2020), will further elucidate the role of natural habitats in biodiversity conservation and pest control. The continuation of exclusion experiments can quantify the role of insectivorous birds and bats in pest regulation by measuring their impact on pest populations, crop damage, and yields. Investigating interactions between vertebrate predators and pest species under varying climatic scenarios and

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spatial scales will provide critical insights for refining IPM strategies tailored to specific ecological contexts, as their effects might vary regionally based on climate and prey availability. Given that predation by bats and birds tends to be higher near habitat edges while pest densities increase toward orchard interiors, we recommend designing smaller orchards (e.g., 1–4 ha) surrounded by 10–20 m wide margins planted with indigenous vegetation. These field margins could act as source habitats for natural enemies, facilitating rapid recolonisation and enhancing pest regulation. Indigenous tree species should be assessed for their capacity to support beneficial arthropods, with priority given to those sustaining high numbers of predators or parasitoids for future orchard planning. Additionally, installing bat boxes along orchard margins can provide roosting sites, encouraging bat residency and enhancing their contribution to biological control.

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4.3. References

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