Response of grasshoppers to the agricultural mosaics of the Cape Floristic Region biodiversity hotspot in South Africa

by

Samuel Adu-Acheampong

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Advisors: Prof. Michael J. Samways and Dr Corinna S. Bazelet

Department of Conservation Ecology and Entomology
Faculty of AgriSciences

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Disclaimer:

Kindly note that Chapters 2-5 of this thesis were written as stand-alone scientific publications, and therefore there is a possibility of detecting similarities in the methods and results.

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General abstract

Agricultural production is one of the main drivers of the on-going biodiversity crisis. This has resulted in research on the impact of agriculture on biodiversity being at an all-time high. This is critical given that the world must produce food for the ever-growing human population. This growing demand for food often demands increasing production areas at the expense of protected ones. Such trade-offs can potentially lead to dire consequences on biodiversity and its associated ecosystem function. In an attempt to minimise this potential negative impact, and also to conserve biodiversity and its associated ecosystem function, scientists and producers have developed a system that integrates natural with production patches as part of making agriculture more sustainable. In most instances, decisions on agro-natural schemes for sustainable food production are based on research conducted on larger animals at the expense of smaller ones, especially arthropods, even though they constitute the largest group of animals.

If humans are to achieve the aim of producing food to meet the growing demand at minimum cost to the environment and biodiversity, studies on smaller animals such as insects, which constitute more than 75% of all animals, and are also major contributors of terrestrial ecosystem function in the terrestrial world, must be considered a high priority. An insect group that has much value for the purpose of designing agro-natural schemes is grasshoppers (Orthoptera, Acridoidea). This is because they show high sensitivity to changes in vegetation type and structure, and have high potential for expressing changes in environmental conditions and vegetation. This is even more important in a biodiversity hotspot which is also known for intensive agricultural production, such as the Cape Floristic Region (CFR). In view of that, I embarked on a study to document the footprint of agricultural production types on biodiversity using grasshoppers as keystone species in four studies making up my four core chapters.

Firstly, I compared species richness, abundance, composition, diversity and evenness of grasshoppers among 46 sites in four geographical areas in the CFR. Here, I investigated three land-use types: fynbos, vineyards and deciduous fruit orchards, the main production types in the region. Results showed that grasshopper abundance were significantly higher in vineyards than in fynbos or orchards. Species richness, diversity, and evenness were highest in fynbos followed by vineyards and then orchards. There was overall high species similarity among all three land-use types, with high species assemblage similarities between vineyards and orchards. Species that preferred fynbos were mostly flightless and endemic to the CFR.

In the second chapter, grasshopper abundance was studied under agricultural land-use (vineyards) and in natural vegetation (fynbos) across two peak seasons (spring vs. summer). This study aimed at quantifying the level at which different grasshopper species utilise the different aspects of the landscape and how this range of utilisation among species relates to certain species' traits. My results showed that species traits play a major role in grasshoppers' ability to move between patches, and which also affects how they utilize various different patches on the landscape. Highly mobile, generalist species are able to utilise more aspects of the landscape. And depending on seasonality, these species will inhabit either vineyards or fynbos aided by their high ability to move between patches. On the other hand, low mobility, specialists lack the ability to move readily between patches, and as a result, they are confined to one or a few patches across the seasons.

In the third chapter, I developed species distribution models for four localized, CFR endemic flightless grasshopper species, *Euloryma larsenorum* and *E. lapollai*, *E. umoja* and *E. ottei*. The first two are associated with fynbos only, while *E. umoja* and *E. ottei*, the second two, are both associated with both fynbos and vineyards. I used the Maximum Entropy algorithm, which showed that vegetation type and soil characteristics were the most important environmental factors affecting local distribution of *Euloryma* species in the CFR. My models also showed that *Euloryma* species have very narrow, predicted, suitable habitats in the CFR. I also showed that there are no significant differences in the distribution of species associated with fynbos only as well as those associated with both fynbos and vineyards.

Lastly, in the fourth chapter, I investigated grasshopper species assemblage composition on three land-uses across the agro-natural mosaic landscape of CFR. This study documented species' level of occupancy and abundances in relation to their life history traits in order to assess the amount of change occurring on the landscape in the CFR. My results show that very few species, and mostly from Acrididae, dominated the landscape. It also shows that the species that dominated the transformed landscape were generalists. There was also a high correlation between generalists, high to medium mobility and widespread species on one hand, and specialists, low in mobility, and localised species on the other.

Conclusions

My study shows that protected areas still remain vital for maintaining the full complement of CFR grasshopper species, especially flightless endemics. I also show that highly mobile, generalist species are better adapted to heterogeneous and novel landscapes compared to low

mobility specialists. Surprisingly, agricultural production supports a wide variety of species, and hence contributes positively towards grasshopper conservation in the CFR. This study further shows that it is the poorly-mobile, specialist species that are particularly vulnerable to ongoing landscape change as they can only benefit from remnant patches of natural vegetation, unlike the highly mobile generalists which can move around the landscape and benefit both from anthropogenic patches and natural ones. To reduce future biotic erosion and homogenisation, there should be concerted efforts to protect grasshopper groups which occur in low abundance in this biodiversity hotspot.

Algemene opsomming

Landbouproduksie is een van die dryfvere agter die huidige biodiversiteitskrisis. Navorsing oor die impak van landbou op biodiversiteit is belangrik aangesien die wêreld moet aanhou om kos te produseer wat daartoe lei dat produksie areas dikwels groei ten koste van bewaarareas. Dit kan potensieel tot verdere verliese in biodiversiteit en ekosisteem funksie lei. In ‘n poging om die potensiele negatiewe impak van landbou te minimeer, het wetenskaplikes en produsente ‘n stelsel ontwikkel wat natuurbewaring en landbouproduksie integreer om landskappe meer volhoubaar te maak.

In die meeste gevalle word besluite oor sulke agri-natuurskemas vir volhoubare voedselproduksie geneem op grond van groter diere eerder as kleineres, soos geleedpotiges, selfs al vorm laasgenoemde meer as 75% van alle diere op aarde, en speel hulle ‘n belangrike rol in die funksionering van terrestriële ekosisteme. As mense graag die doel wil bereik om die groeiende vraag na kos te beantwoord sonder om die omgewing beduidend te benadeel, moet studies oor kleiner diere soos insekte ‘n hoër prioriteit word. ‘n Groep insekte wat groot waarde het vir die ontwerp van agri-natuurstelsels is springkane (Orthoptera, Acridoidea). Hulle is sensitief vir veranderinge in plantegroeitipe en –struktuur, en weerspieël ook veranderinge in omgewingstoestande. In ‘n biodiversiteitshittekol wat bekend is vir sy intensiewe landbouproduksie, soos in die Kaapse Floristiese Streek (KFS), is dit selfs nog belangriker om hierdie klein diertjies in ag te neem wanneer ‘n mens na die integrasie van natuurbewaring en landbouproduksie kyk. In die lig hiervan, kyk hierdie studie na die effek van verskillende landproduksietipes op biodiversiteit deur te fokus op springkane as ‘n sleutel takson.

In die eerste hoofstuk het ek spesiesrykheid, talrykheid, spesiesamestelling, diversiteit en getalgelykheid van springkane tussen 46 areas in vier geografiese areas in die Kaapse Floristiese Streek (KFS) vergelyk. Ek het na drie landsgebruiktipes gekyk: fynbos, wingerde, en vrugteboorde. Laasgenoemde twee landsgebruiktipes is ook die hoof produksietipes in die streek. Resultate dui aan dat springkane se talrykheid beduidend hoër is in wingerde as in fynbos of in vrugteboorde. Spesiesrykheid, diversiteit en getalgelykheid was egter die hoogste in fynbos, gevolg deur wingerde en dan vrugteboorde. Vrugteboorde het geen unieke spesies gehad nie, maar wingerde het twee, en fynbos het 14 unieke spesies gehad. Nogtans was daar ‘n hoë soortgelykheid in spesiessamestelling tussen die drie landsgebruiktipes, veral tussen wingerde en vrugteboorde. Spesies wat fynbos verkies het was meestal vlugloos en endemies tot die KFS.

Ek wys uit hoe landboustreke nie die volle komplement van spesies in natuurlike fynbos ondersteun nie, maar dat wingerde wel meer divers as vrugteboorde is. Ek wys ook hoe wingerde ‘n goeie geleentheid bied vir harmonie tussen landbouproduksie en natuurbewaring deur verbetering in grondbedekking en ander landboupraktyke. Minder geleenthede bestaan in vrugteboorde aangesien hulle ‘n digte blaredak het, en nie gekenmerk word deur ‘n gras grondbedekking of fynbosplante nie. In die tweede hoofstuk het ons gekyk hoe springkane se talrykheid van wingerde en natuurlike plantegroei (fynbos) varieer oor twee piek seisoene (lente vs. somer) in die Kaapse Floristiese Streek (KFS). Die doel van die studie was om te bepaal watter springkaanspesies watter dele van die landskap gebruik, en hoe dit verband hou met spesiespesifieke kenmerke in die KFS. My resultate toon dat spesiespesifieke kenmerke ‘n groot rol speel in springkane se vermoë om te beweeg en verskillende kolle natuurlike plantegroei in die landskap te gebruik. Hoogs beweeglike, algemene voeder springkaanspesies kan meer dele

van die landskap gebruik. Hulle kan tussen wingerde of fynbos beweeg, afhangende van die seisoensveranderinge. Aan die ander kant kan minder beweeglike spesialis springkaanspesies nie maklik tussen verskillende kolle nauurlike plantegroei beweeg nie. Hulle word grotendeels tot een of ‘n paar kolle beperk oor verskeie seisoene.

In die derde hoofstuk, ontwikkel ek ‘n spesiesverspreidingsmodel vir vier gelokaliseerde, vluglose springkaanspesies (*Euloryma larsenorum* and *E. lapollai*, *E. umoja* and *E. ottei*) wat endemies is tot die Kaapse Floristiese Streek (KFS). Die eerste twee assosieer slegs met fynbos, maar die ander twee (*E. umoja* and *E. ottei*) bewoon fynbos sowel as wingerde. Ek het die Maksimum Entropie algoritme gebruik wat getoon het dat plantegroeitipe en grondkenmerke die belangrikste omgewingsfaktore was wat verspreiding van hierdie vier spesies beinvloed het. My modelle het voorspel dat hulle ‘n baie nou geskikte habitat in die KFS het. Daar was geen beduidende verskil in die verspreiding van spesies wat met slegs fynbos, of met fynbos en wingerde geassosieer is nie. Beduidende pogings tot die bewaring van *Euloryma* spesies is nodig in die KFS, veral aangesien hulle geskikte habitat mag krimp in die geval van globale veranderinge. Omdat *E. larsenorum* en *E. lapollai* baie sensitief is vir veranderinge in die landskap vanaf fynbos na landbou, behoort hulle bewaring geprioritiseer word. Dit is onwaarskynlik dat die ander twee spesies (*E. umoja* en *E. ottei*) tot dieselfde mate beïnvloed sal word aangesien hulle kan oorleef in die huidige landbou omgewing.

Laastens, in die vierde hoostuk, oorweeg ek springkane se spesiesamestelling in drie landsgebruikstipes binne die agri-natuur mosaieklandskappe van die Kaapse Floristiese Streek (KFS). Ek het na spesies se vlak van okkupasie en talrykheid gekyk binne die konteks van spesiespesifieke kenmerke sodat ‘n mens ‘n beter idee kan kry van verandering wat binne die landskap gebeur. My resultate toon dat slegs ‘n klein hoeveelheid spesies (meestal Acrididae) die landskap domineer. Dit het ook getoon dat dominante spesies algemene voeders was. Daar was ‘n hoë korrelasie tussen algemene voeders, matige tot hoogs mobiele, en wydverspreide spesies aan die een kant, en spesialisvoeders wat minder beweeglik en gelokaliseerd is aan die ander kant.

Gevolgtrekkings

My studie het getoon dat bewaarareas belangrik bly om die volle komplement van springkane in die Kaapse Floristiese Streek (KFS) te bewaar. Dit is veral so vir vluglose endemiese spesies, want hulle het die nouste verspreidings en is baie sensitief vir antropologiese veranderinge. Ek het ook gewys dat hoogs beweeglike, algemene voeders beter aangepas is vir heterogene en nuwe landskappe as spesialisvoeders wat minder beweeglik is. Landbouproduksie areas ondersteun ‘n wye verskeidenheid spesies, en dra dus positief by tot die bewaring van springkane in die KFS. Hoogs beweeglike algemene voeders kan oor die hele landskap beweeg en baatvind by landbouproduksie en natuurlike kolle plantegroei, terwyl hulle optimeer vir seisoensveranderinge. Dit is meestal die minder beweeglike spesialisvoeders wat kwesbaar is vir veranderinge in die landskap, want hulle kan slegs oorblywende kolle natuurlike plantegroei bewoon. Die *Euloryuma* genus kan moontlik gebruik word as bio-indikatore vir grondstudies in die KFS. Om verdere vereenvoudiging van insekgroepe te verhoed moet daar gepoog word om springkaangroepe wat natuurlik teen lae getalle voorkom, te bewaar.

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CHAPTER 1: Introduction

1.1 Landscape context and biota

Agricultural production and urbanisation are the two main causes of fragmentation and reductions in quality of native habitats occupied by many species (Opdam *et al*. 2003; Opdam & Wascher 2004; Foley *et al*. 2005; Lindenmayer *et al.* 2013). As a result of fragmentation, different components of ecological landscapes outside of native habitat patches are no longer regarded uniform and natural (Ricketts 2001; Hilty *et al*. 2012). In spite of that the dispersal and persistence of spatially distributed meta-populations are mostly controlled by such components. For instance, aspects such as ecological networks and corridors have become vital for linking different populations (Hilty *et al*. 2012). In view of this, the landscape as a whole can be considered as a utilitarian device for species and at the same time be used to assess where human land-use effects dominate and cause changes (Opdam *et al*. 2003).

In addition to anthropogenic land-use (mostly agriculture and urbanisation), there is also the threat of global change (e.g. climate change, alien invasive species) on species persistence on the landscape (Masters & Norgrove 2010; Mainka & Howard 2010). Many studies on species' ability to respond to changes in their habitat and to shift accordingly via landscape connectivity to avoid the effect of fragmentation have been conducted (Bradshaw & Holzapfel 2006; Kettunen *et al*. 2007; Pascual-Hortal & Saura 2007). Despite these important studies, a key area that requires more attention in most ecological studies, especially species distributions models, is heterogeneity of the landscape (Opdam & Wascher 2004). Furthermore, most studies lack information on species' inherited traits that dictate their responses to habitat changes. In spite of this, there have been some studies that have focused on species responses to landscape change based on their inherited traits. For instance, in the case of widespread generalist vs localised specialist species (Brouat *et al*. 2004; Colles *et al*. 2009; Clavel *et al*. 2011).

This thesis aims to document the response of biodiversity, specifically grasshoppers, in a biodiversity hotspot (the Cape Floristic Region (CFR)) which also has intensive agriculture. It combines species responses with fragmentation and transformation of habitats, and predicts and measures grasshopper utilisation of different patches through their inherited traits and behavioural characteristics in an agro-natural mosaic. It also models their distributions taking into consideration features of the landscape and habitats which are fragmented by agriculture and urbanisation. Finally, it focuses on verifying that widespread, generalist grasshopper species occupy more patches in the landscape than do specialist species. My thesis also focuses on agriculture as one of the main causes of fragmentation in the CFR, a biodiversity hotspot of conservation priority in South Africa.

1.2 Biodiversity hotspots in South Africa

There are three major biodiversity hotspots of high conservation priority in South Africa. These hotspots largely follow round the rim of the country. Located on the east coast is the Maputaland-Pondoland-Albany (MPA) and two other hotspots are located in the south: the CFR and the Succulent Karoo hotspots (Mittermeier *et al.* 2004; Rutherford *et al*. 2014; Mittermeier *et al*. 2011; Esler *et al*. 2014). These biodiversity hotspots are based on the number of endemic plants, and on high species diversity that is mostly under threat in these hotspots (Myers *et al*. 2000). The CFR is home to a very high number of endemic plants, with an estimated 6210 species, followed by Succulent Karoo with 2439 species and 1900 for Maputaland-Pondoland-Albany (Mittermeier *et al.* 2004; Fonseca 2009).

Threats of land transformation and global change are major drivers causing habitat and biodiversity losses in these areas, and hence there is an urgent need for increased conservation efforts in these hotspots. For instance, it is estimated that 80%, 76% and 71% of habitats in CFR, MPA and Succulent Karoo, respectively, have been 'lost' through land transformation and global change (Mittermeier *et al.* 2004; Fonseca 2009). One of the most important types of land transformation and land-uses in these hotspots is agricultural production which is a means of livelihood and source of food production in South Africa (Myers *et al*. 2000; Esler *et al*. 2014). According to Greef & Kotze (2007), Cowling *et al*. (2003), Rouget *et al*. (2003) and Esler *et al*. (2014), agriculture has been a major driving force in the loss of an estimated 83% of the original extent of the dominant natural vegetation (fynbos) in the CFR.

1.3 Agriculture and biodiversity

A large proportion of terrestrial environment is covered by agricultural production which is also home to thousands of species worldwide (Vitousek *et al.* 1997; Foley *et al*. 2005). Although agriculture is vital for producing food to meet the demands of increasing human population (Godfray *et al*. 2010; Chaplin-Kramer *et al.* 2015; Wezel *et al*. 2016), the process is also a major cause of biodiversity loss. In order to meet this growing demand for food, more natural/protected lands are often converted to production lands, giving rise to conflicts between agriculture and biodiversity conservation (Zorrilla-Miras *et al.* 2014).

Transforming natural lands to agricultural production areas greatly alters ecosystems and species habitats (Foley *et al*. 2005; Forman 1995). In spite of this transformation, certain species have adjusted to agricultural ecosystems for survival, especially when there is low intensity and traditional production practice (Sutherland 2004). Under intensive agricultural production more plant species that occur naturally are replaced by often few and introduced ones. This situation alters the arrangement of wildlife of both flora and fauna and can even force some species into local extinction (Sax & Gaines 2008; Brook *et al*. 2008). More importantly, agriculture creates situations where geographically widespread and common species are dominant on production lands compared to the former natural areas that were dominated by more indigenous and endemic species. Furthermore, common and opportunistic species tend to inhabit ecotones between natural and agricultural areas which hitherto were not in existence in the former continuous natural vegetation (Vitousek *et al*. 1996; Vitousek *et al*. 1997; Panel 2011).

1.3.1 Effects of agriculture on biodiversity

The sudden change in land-use from intricate natural systems to often streamlined ecosystems that are managed intensively often affects both flora and fauna (Mayfield & Daily 2005; Zhang *et al*. 2007; Panel 2011). In agricultural systems, high emphasis is placed on resource use for the purpose of creating good conditions for few plant and animal species to thrive in order to maximise production (Swift *et al*. 2004). For instance, the use of agrochemicals and fertilisers are meant to create environmental conditions that will increase the competitive ability of the species of interest. On the other hand, these inputs are also meant to reduce the competitive ability (if not destroy) of other organisms that may be in conflict with the wellbeing of the species in question, and thereby affect selection pressure (McEwen & Stephenson 1979; Murphy & Lemerle 2006). Although these input activities might seem straight forward, the long term effect is often devastating due to the negative impact they have on the ecosystem. Agricultural production practices often lead to the destruction of non-target or beneficial organisms (Johnsen *et al.* 2001), leave chemical residues in soils, water bodies and plants (WHO 1990; Mullin *et al*. 2010) and cause a general decline in farmland biodiversity, especially of habitat specialists (Robinson & Sutherland 2002; Benton *et al.* 2003). Other agricultural production practices, such as genetic modification of crops, are further simplifying the ecosystem at the gene level (Uzogara 2000; Vanloqueren & Baret 2009).

At the landscape scale, agricultural production practices create homogeneous environments that are aimed at enhancing the efficiency of production. This leaves little natural vegetation for associations between organisms and hence depletion of ecosystem services (Foley *et al*. 2005; Tscharntke *et al*. 2005; Holzschuh *et al*. 2007). Agriculture also causes fragmentation of the otherwise continuous natural habitats, creating isolated and often small populations, and which eventually leads to a reduction in species (Verboom *et al*. 1991; Tscharntke *et al.* 2005). For instance, there has been widespread reporting of population declines of bees (an important ecosystem provider) due to adverse agricultural practices (Goulson *et al*. 2008; Rundlöf *et al*. 2008; Gallai *et al.* 2009; Kremen *et al*. 2002; Potts *et al*. 2010). In another study, in Scotland, reductions in farmland birds corresponded with a decline in invertebrate diversity because of increase in agricultural activities (Benton *et al*. 2002). Other ecosystem dis-services that emanate from agricultural production are an increase in production costs from control of ‘undesired’ species which compete with crops for nutrients, water etc. (Mayfield & Daily 2005; Mayfield *et al.* 2005; Zhang *et al*. 2007).

1.3.2 Importance of agriculture to biodiversity

Agriculture is not always detrimental. There is evidence of improvement in ecosystem functions and biodiversity in general as a result of certain, specific production activities (Tscharntke *et al*. 2005; Fahrig *et al*. 2011). It is also important to note that agro-ecosystems hold the major part of biodiversity in the world (Pimentel *et al*. 1992). Most importantly, it is widely known that traditional and low intensity agricultural production practices tend to improve biodiversity on farmlands. This is because such production practices give rise to a heterogeneous environment that creates many suitable habitats for a variety of organisms (Bignal & McCracken 1996; Mander *et al*. 1999). For instance, it has been reported that there are as many floral resources available in agricultural systems for pollinators as in the wild. Agroecological practices may also be characterised by plentiful supply of plant biomass such as palatable leaves and fruits for birds, mammals and insects (Kevan & Viana 2003; Tscharntke *et al*. 2005; Wratten *et al*. 2012). Low intensity agriculture also increases the competitive ability of less dominant species and reduces that of dominant species thereby increasing the number of organisms that can co-exist under such conditions (Hyvönen & Salonen 2002; Oehl *et al*. 2003). This means that agricultural production does not always increase the probability of species extinction but can provide important resources for increased diversity and co-existence. A few opportunistic species even prefer highly intensive agricultural production areas to thrive (Huston & Huston 1994).

1.3.3 Agricultural production and endemic species

Endemic and indigenous species respond to habitat transformation, especially agricultural production, in different ways. Some adapt to the newly created habitats and continue to persist in them (Corlett 1992; Midgley *et al*. 2003). Other species move away from the transformed environment (that is now considered hostile) to a friendlier environment and thus shift their range of occupancy (Corlett 1992; Midgley *et al*. 2003). Failure to either adapt to this newly transformed habitat or shift range can only mean a species will die out and possibly go extinct (Corlett 1992; Midgley *et al*. 2003; Samways 2007).

1.3.4 Agriculture production and insect conservation

There are many supporting ecosystem services that are provided by insects (Samways 2007; Zhang *et al*. 2007). For instance, bees, butterflies and beetles are among the most prominent pollinators of crops in agricultural ecosystems (Proctor *et al*. 1996; Zhang *et al*. 2007; Buchmann & Nabhan 2012). Other ecosystem services such as pest control and dung burial are prominent among certain beetles (Zhang *et al*. 2007; Sepp 2012). Dung burying beetles accelerate the decomposition of animal waste and act as a driver of nutrient recycling (Losey & Vaughan 2006; Zhang *et al*. 2007). Parasitoids, predators, entomopathogenic fungi and nematodes provide important ecosystem services in the natural suppression of pests in agricultural ecosystems (Gaugler *et al*. 1997; Cardinale *et al*. 2003; Malan & Moore 2016; Odendaal *et al*. 2016; Stokwe & Malan 2016). Intensive agricultural production practices such as insecticide application often have unintended negative consequences on biodiversity of these important ecosystem service providers. There is therefore an urgent need for a systematic approach towards the conservation of such ecosystem providers to avoid future collapse of agriculture production which humans are entirely dependent on for survival (Samways 2007).

Some of the useful strategies for insect conservation in agricultural systems are land sparing, use of cover crops, land sharing and the provision of natural corridors (Samways 2007; Phalan *et al*. 2011). These strategies are aimed at providing refuges and good habitats, to maintain soil conditions (especially moisture), provide alternative sources of food, link agricultural production sites and natural areas etc. Linking agricultural production to natural areas through corridors and also sparing adjacent lands for conservation purposes have been reported to affect pollination positively and hence increase yields (Klein *et al*. 2003).

1.3.5 Agricultural production and grasshopper conservation

As key insect herbivores, grasshopper species have mixed responses to land transformation, e.g. agricultural production (Torrusio *et al*. 2002; Kuppler *et al*. 2015; Adu-Acheampong *et al*. 2016), invasive alien plants (Yoshioka *et al*. 2010), grazing and fire (Gebeyehu & Samways 2003; Joubert *et al*. 2016) and land management and design (Gebeyehu & Samways 2002; Bazelet & Samways 2011b) etc. Like other terrestrial insects some generalist species, mostly flighted, widespread species (e.g. *Aiolopus thalassinus*), benefit, while specialist, and often native or endemic, flightless species (e.g. *Eremidium maius* and *Euloryma* sp. both endemic to South Africa) are impacted negatively (Rainio *et al*. 2003; Yoshioka *et al*. 2010; Adu-Acheampong *et al*. 2016; Joubert *et al*. 2016). According to Steck *et al*. (2007), grasshopper sensitivity and their subsequent change in diversity differs based on changing land-use and environmental scenarios.

In Tanzania, grasshoppers responded positively to vegetation with close to 100% increment in diversity and abundance as a result of increases in density of grass cover (Kuppler *et al*. 2015). The study also reports that a heterogeneous landscape such as a low intensive agro-natural mosaic has the potential of maintaining higher grasshopper diversity compared to a highly intensive and conventional agriculture land-use (Kuppler *et al*. 2015). These findings agree with the findings of Griebeler & Gottschalk (2000) on German bush crickets (Tettigoniidae), where species had very high persistent rates under heterogeneous habitats compared to homogeneous ones. These studies overall show that certain grasshoppers thrive better under well-managed agro-natural schemes compared to either pristine natural environment or a highly intensive agricultural production system alone. The most successful of these species in agro-natural landscapes are flighted species with high dispersal ability.

Grasshoppers were chosen for this study because they readily respond to changes in land-use and hence have previously been employed as indicators of environmental changes. Some of these important uses are within afro-montane grasslands (Crous *et al*. 2013), agricultural production fields (Kuppler *et al* 2015, Adu-Acheampong *et al*. 2016), grassland remnants within a timber plantation matrix (Bazelet & Samways 2011a), fire and grazing management (Gebeyehu & Samways 2003; Joubert *et al*. 2016), monitoring invasive alien plants (Yoshioka *et al*. 2010) and community succession within alluvial pine plantation (Fartmann *et al*. 2012; Helbing *et al*. 2014), succession and grass encroachment (Schirmel *et al*. 2011), restoration management (Gebeyehu & Samways 2002; Borchard *et al*. 2013), conservation (Gebeyehu & Samways 2006a and b) and developing tools to identify natural vegetation with high conservation priorities (Matenaar *et al*. 2015). Information on grasshoppers are also readily available and together with their relatively well understood biology, the group becomes one of the best candidates for a study in a biodiversity hotspot which doubles as an agricultural production area like the CFR.

1.3.6 Insect utilisation of different patches in agro-natural landscapes

Pressure from anthropogenic activities result in unexpected changes in resource allocation to various elements of a landscape. In this situation organisms are forced to change habitats in a bid to survive these impacted landscapes (Masters & Norgrove 2010; Mainka, & Howard 2010; Todgham & Stillman 2013). In such landscapes, animals move between habitats for the purpose of locating any available resources as the season changes. This is one mechanism that enhances the survival of species under such changing landscapes. This movement between seasons can be described as dispersal which is defined in animals as either a passive or active effort to shift from a resting or breeding site to another site (Clobert *et al*. 2009). A vivid example is the movement of natural enemies of pests between non-cropped and cropped areas based on need and seasonal allocation of resources (Duelli *et al*. 1990; Wissinger 1997, Tscharntke *et al*. 2007; Todgham & Stillman 2013).

More often, agricultural mosaics consist of semi-natural and cultivated patches (Westphal *et al*. 2003). This environment houses plants with different phenologies and life history traits that cause significant differences and seasonal shifts in available resources (Tscharntke *et al*. 2005). The production of crops creates sudden large availability of dry matter during a short period followed by a lean one. On the other hand, natural and semi-natural habitats exhibit moderate phenological changes in seasons. The combination of the different habitat patches arising from a combination of both agriculture and natural vegetation, as opposed to just one of these land-types, supplies most of the needed resources for species' persistence. Free moving organisms may access resources based on their availability in different patches in different seasons, unlike less mobile species. Under such conditions, these different patches produce resources that are complementary to each other in terms of supporting local diversity of insects (Pilliod *et al*. 2002; Mayfield & Daily 2005; Lonsdorf *et al*. 2009). One example of complementary use of resources from different patches in an agro-natural landscape was demonstrated in a study conducted in USA where there was strong movement responses of bees to temporal availability of floral resources (Mandelik *et al*. 2012). In this study, most of the wild bees foraged within fallow areas in early season, switched to crop production patches in the middle of the season, and later shifted towards old fields as the season drew to an end, with natural habitats not playing any significant role in this complementary support of bees (Mandelik *et al*. 2012).

1.3.7 Dispersal of grasshoppers in agro-natural landscapes

Dispersal plays a major role for grasshoppers in fragmented landscapes. This is mainly for the purpose of maintaining functional connectivity through genetic transfer between populations (Hanski & Gaggiotti 2004; Ortego *et al*. 2015). It also makes it possible for migration into new and suitable habitats and hence increases species persistence across a landscape (Ronce 2007; Ortego *et al*. 2015). This dispersal ability is more pronounced in highly mobile grasshoppers i.e. well-flighted species. The high correlation between dispersal ability and mobility in flighted species can be related to their wing morphology (Sekar 2012) which is also affected by habitat quality (Bazelet & Samways 2014) and hence can be inferred that the quality of habitat will have an indirect influence on dispersal ability of flighted grasshoppers. This explains partly the reason why wingless and less mobile grasshoppers have lower dispersal ability leading to less genetic transfer between isolated populations of such species (Ronce 2007; Sekar 2012; Hanski & Gaggiotti 2004; Ortego *et al*. 2015).

In view of this situation, we can deduce that less mobile grasshopper species are likely to be more affected by fragmentation than highly mobile species, through lack of gene transfer and ability to shift range, and hence are more likely to be less persistent in agricultural landscapes. The opposite is arguably more likely to be the case for highly mobile and flighted species. Such movement under agro-natural landscapes has the potential to be used to influence conservation actions (Ronce 2007; Ortego *et al*. 2015). Ecological niche modelling has the potential of helping understand the best habitat conditions (Pearson 2010) that can influence such grasshopper movements for effective prediction of potential destinations in agro-natural landscapes with changing seasons.

1.4 Species distribution modelling and biodiversity conservation

A very useful application tool for conservation purposes is developing a model that can be used to forecast or predict species distribution (Elith *et al*. 2006; Pearson 2010). This important model is constructed by combining environmental variables that affect the species in question and its occurrence records usually in modelling software (Franklin 2010; Pearson 2010). Some of the most important conservation decisions that can be taken based on species distribution modelling are forecasting the potential or current distribution of species on a landscape (Franklin 2010; Ferraz *et al*. 2012), estimating the suitability of environmental conditions where species can be maintained and finding the range of distribution (Anderson & Martínez-Meyer 2004; Chefaoui *et al*. 2005), identifying areas of conservation importance, (Thorn *et al*. 2009; Ferraz *et al*. 2012; Guisan *et al*. 2013), and predicting places of future invasion and forecasting climate change impacts (Peterson & Vieglais 2001; Guisan *et al.* 2013; Elith & Leathwick 2009; Elith *et al*. 2006; Hulme 2016) on species.

Characterising the most suitable environmental conditions has been the common approach for evaluating the potential or actual geographic range of a species (Pearson 2010). This characterisation can either be done using a mechanistic or correlative approach. Under a mechanistic approach, the modeller uses the species' tolerance level to certain physiological limitation under certain conditions, usually environmental, to predict its potential or actual distribution (Pearson & Dawson 2003; Kearney & Porter 2009; Pearson 2010; Rebaudo *et al*.

2016); for instance, reproductive success under certain conditions such as heat, cold and or moisture stress. With such an approach, the modeller is obliged to have a thorough knowledge on the organism's physiological reactions to various environmental factors (Pearson 2010). Correlative approaches on the other hand seek to match occurrence records with important environmental variables that are known to physiologically affect the species and its persistence under such locations (Ferraz *et al*. 2012; Hulme 2016; Jung *et al.* 2016).

Here I use the correlative approach for modelling the local distribution of grasshoppers where occurrence is matched with environmental variables such as rainfall, temperature, vegetation and altitude to predict the most suitable environmental niche and conditions for the persistence of grasshoppers in a heterogeneous agro-natural landscape. Using this approach, information of the most useful environmental conditions for occurrence of a species is derived from its observed distribution (Pearson 2010).

1.4.1 Species distribution modelling and conservation of insects

For successful modelling of species distribution, a key factor to consider is spatial scale. Spatial extent or geographic range is a necessary factor to consider in an attempt to account for all habitats that are required for life history traits of the species in question. Another important factor to consider is also key environmental variables suitable for the persistence of the species in question (Lin *et al*. 2016; Silva *et al*. 2016). Insects, especially terrestrial species like beetles, butterflies, bees and grasshoppers are mainly found in association with their food resources, and hence vegetation cover and/or amount of floral resources available in an environment which may be key for their distribution (Jung *et al.* 2016).

Other important factors such as temperature, rainfall, elevation, level of biological activities (e.g. predation, competition etc.) may be important for the distribution of insect species and hence these factors need to be considered when designing ecological niche models (Schemske *et al*. 2009; Kearney & Porter 2009; Franklin 2010). Usually, the population of insects occupying a unit area of land is higher than that occupied by other terrestrial animals like birds and mammals for a similar unit of land. Because of that, the exact spatial scale to consider for capturing the distribution of insects is often relatively small. According to Peters & Wassenberg (1983), relatively small animals often record higher population densities per unit area of land compared to larger ones. Inferring from this relationship, it can be extrapolated that the extent of an area to consider in order to cover the geographic ranges of insects will be relatively smaller compared to larger animals.

1.4.2 Species distribution modelling and grasshopper conservation

Although grasshoppers are mainly regarded as habitat specialists they are not necessarily limited by food sources because their feeding habits range from being omnivorous to polyphagous (Dadd 1963; Detzel 1998). The most likely determinant factors for their distribution in a habitat will be the capacity to provide necessary conditions for vital life history traits such a good soil conditions, ambient temperature and oviposition sites. Under a Mediterranean-type climate, as in the CFR, grasshoppers are usually seen in warmer places at the lowest part of mountains, and in dry and open habitats (Detzel 1998). For instance, the fynbos biome, a shrubland that occurs on both lowland and highland places in the CFR (Mittermeier *et al*. 2004; Myers *et al*. 2000; Esler *et al*. 2014) is this type of system.

Most grasshopper species tap resources from different vegetation types and structures throughout their life history, especially in open vegetation (Kemp *et al*. 1990), such as fynbos and grasslands. For example, they may use places with high temperature for hatching of eggs and others with long forbs and grasses for food and shelter (Detzel 1998; Hein *et al*. 2007). Therefore a measure of heterogeneity in the vegetation can approximate the number of grasshopper species present.

To be able to successfully model the distribution of grasshoppers, vegetation structure and type, temperature and soil conditions must play a vital role. This is even more important if conservation actions are to be based on distribution models. For instance, a study conducted in Germany reported that habitat type e.g. grassland and marshy areas were the most important factors that determined the occurrences of grasshopper species (Hein *et al*. 2007).

1.5 The main goals of this thesis

My thesis aims at gaining insights into conservation of insects (specifically grasshoppers) in a biodiversity hotspot (the CFR) which is also known for high agricultural production. I focus here on grasshopper diversity in different land-uses, mainly agriculture (vineyards and orchards), with protected areas as reference. Firstly, I determine the land-use type that is grasshopper friendly and which offers most opportunities for grasshopper diversity conservation in the CFR. Then I assess the dispersal ability of the various focal species and relate this to the life history traits of the various grasshoppers to ascertain the actual dispersal mode of each grasshopper major group for conservation planning purposes in the CFR. Finally, I identify the more important of two known environmental conditions (topography and vegetation) necessary for the distribution of an endemic grasshopper through species distribution modelling in agro-natural landscapes in the CFR for the purposes of designing proper conservation schemes.

1.6 Chapter outlines

***Chapter* 1** consists of the general introduction of the thesis. It touches on the study background, goals and specific questions asked and the outline of the thesis.

In ***chapter* 2** I analyse the extent to which an agricultural mosaic supports grasshopper species in an agro-natural landscape to ascertain the level at which biodiversity is impacted by land-use activities in the CFR. This study also determines the best agricultural environment and practices for conservation, and recommends practices to improve biodiversity in agro-natural landscapes in the CFR. This chapter is already published as a paper in the journal *Agriculture Ecosystems and Environment*.

In ***chapter* 3** I relate species life history traits of grasshoppers to their ability to utilise different patches in an agro-natural landscape of the CFR. Specifically, I link grasshopper species inherited traits with their ability to utilise agriculture and or natural patches through changing seasons.

In ***chapter* 4** I develop species distribution models for the grasshopper genus *Euloryma* and focus on four species, *E. umoja*, *E. ottei E. lapollai* and *E. larsenorum.* I aim to identify the most important environmental variables that determine the distribution of these flightless, endemic species which have small geographical ranges in the CFR, and as such, are highly vulnerable to habitat transformation. This study also determines the extent of vulnerability of four species groups to extinction (i.e. species associated with agriculture only vs. species associated with agriculture and natural areas). I also make recommendations on the appropriate conservation practices to be used.

In ***chapter* 5** I investigate the relationship between grasshoppers' type of distribution and level of site occupancy and link these to mobility. I aim to prove an anecdotal observation that highly mobile, widespread species occupy more habitats compared to low mobility and localised species. I will then use this relationship as a baseline indicator for accessing landscape change in the CFR. I make recommendations towards developing a biotic index based on species mobility and type of distribution in the CFR.

In ***chapter* 6** I develop a synthesis and draw general conclusions for the thesis. I connect the various chapter findings to arrive at the general conclusion for the thesis.

1.7 The main research hypothesis

I first test the hypothesis that agricultural production has no impact on biodiversity of insects (using grasshoppers as a test case) and follow with a second hypothesis that irrespective of the agriculture production type (either vineyards or orchards), the impact on grasshopper diversity is similar. This hypothesis is also used for chapter 2.

My hypothesis for chapter 3 is that, mobile, generalist species will migrate in between agricultural and natural patches in response to changes in habitat conditions aided by their life history traits of high mobility and seasonal change in vegetation structure. On the other hand, narrow-range endemic species will not be able to move through different habitat patches due to their less mobile ability and hence will be confined to a small area throughout changing seasons.

In chapter 4 I hypothesise that both topography and type of vegetation (both widely known environmental factors affecting grasshopper distribution) affect the distribution of *Euloryma* species equally. I also predict that the more sensitive a species is to likely climatic change, the lower the chances of it occurring in a transformed habitat (e.g. vineyards) other than fynbos, with the reverse being the case for less sensitive species. I also hypothesise that species that occur only in fynbos (and not in agricultural fields) are more sensitive to future land-use and climate change than species which commonly occur in both fynbos and agricultural fields.

In Chapter 5 I hypothesise that widespread and generalist grasshopper species are abundant and occupy more sampling sites and land uses compared to localised and specialist ones. Here I assume that the high abundance and or occupancy of generalist and widespread species, is as a result of occupying more diverse habitats and sites over the course of evolutionary time.

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CHAPTER 2: Extent to which an agricultural mosaic supports endemic species-rich grasshopper assemblages in the Cape Floristic Region biodiversity hotspot

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Abstract

The impact of expansion and intensification of agriculture on biodiversity requires quantification, especially in areas of exceptionally high biodiversity like the Cape Floristic Region (CFR). In the CFR, landscape mosaics consist of agriculture alongside Mediterranean-type fynbos scrubland natural vegetation rich in endemic insect species. However, little is known about how ground-dwelling insect herbivores utilize the various elements of the mosaic. I compared species richness, abundance, species composition, diversity and evenness of grasshoppers among 46 sites in four geographical areas in the CFR. I investigated three land-use types: fynbos (the historic condition as reference), vineyards and deciduous fruit orchards, the main production types in the region. Grasshopper abundance was significantly higher in vineyards than in fynbos or orchards. Species richness, diversity, and evenness were highest in fynbos followed by vineyards and then orchards. Orchards had no unique species, vineyards two, and fynbos 14 unique species. Nevertheless, there was overall high species similarity among all three land-use types, with high species assemblage similarities between vineyards and orchards. Species that preferred fynbos were mostly flightless and endemic to the CFR. I show that agricultural areas do not support the entire species assemblage of natural vegetation, although

vineyards are more diverse than orchards, probably because of the presence of often grassy ground cover and an open canopy. Vineyards provide the greatest opportunity for improved harmony between production and biodiversity conservation through continuing to improve the ground cover quality and other farming practices. Fewer opportunities are provided by orchards in view of their closed canopy and absence of grassy ground cover (for generalist species) and fynbos plants (for endemic species). However, protected areas still remain vital for maintaining the full complement of species, especially flightless endemics.

2.1 Introduction

Biodiversity is threatened by increasing human stressors (Crains & Lackey 1992; Corker 2011; de Baan *et al*. 2013). The threats come from increasing demands for food, fibre and fuel, necessitating the expansion of agricultural lands at the expense of natural vegetation (Norris 2008; Pagiola *et al*. 1998). Agricultural production is considered to be one of the strongest drivers of this biodiversity loss (Lindenmayer *et al*. 2013).

The Cape Floristic Region (CFR) is a world biodiversity hotspot, with high diversity of endemic plants and other organisms which face high levels of threat (Mittermeier *et al*. 2004; Myers *et al*. 2000). The CFR is also known for intensive agricultural production (Esler *et al*. 2014). Over 30% of the land mass of the CFR has been transformed by agriculture, urbanisation and alien invasive plants, with only 17% of the original extent of the primary natural vegetation (fynbos) still remaining (Cowling *et al*. 2003; Rouget *et al*. 2003). Furthermore, 47.7% and 78.6% of South Africa’s vineyards and apple orchards, respectively, are located in the CFR (Greef & Kotze 2007). These production types, together with potato and melon production, are responsible for the loss of the majority of the original extent of fynbos vegetation, mostly lowland fynbos (Esler *et al*. 2014) and there is still potential for expansion of agricultural holdings and further pressure on biodiversity within the CFR (Rouget *et al*. 2003).

While agriculture is known to adversely affect biodiversity, if good management practices are observed, they may be able to benefit biodiversity through mitigating the effects of transformation. This can be done by land sparing, such as conserving remnant patches (as has been done in the CFR; Gaigher *et al*. 2015) or provision of large scale ecological networks

(Pryke & Samways 2012; Samways *et al*. 2010), or it can be done by land sharing such as the instigation of biodiversity-friendly farming methods such as organic farming (e.g. in the CFR; Gaigher & Samways 2010; Kehinde & Samways 2014), or a combination of both land sparing and land sharing into an agro-ecological matrix. Interestingly, it is estimated that half of all species in Europe are dependent on agricultural habitats (Kristensen 2003).

Previous research conducted in vineyards in the CFR recorded high arthropod diversities with minimal declines in relation to neighbouring natural vegetation (Gaigher & Samways 2010; Kehinde & Samways 2012; Magoba & Samways 2011; Vrdoljak & Samways 2014). Other studies conducted by Bailey *et al*. (2010) in Switzerland, Brown (2012) in the U.S.A. and Horak *et al*. (2013) in the Czech Republic, on the impact of deciduous orchard production on biodiversity produced mixed results. These mixed results support the notion that the impact of agriculture on biodiversity depends mostly on the type of agricultural production, production practices, surrounding landscape features and in particular the taxon under consideration (Badenhausser & Cordeau, 2012; Bailey *et al*. 2010; Bruggisser *et al*. 2010; Horak *et al*. 2013; Liu *et al*. 2015; Norris 2008). Some taxa (e.g. snails and lichen) prefer a cold, wet and closed canopy with tall trees and dense vegetation (e.g. forests) (Bailey *et al*. 2010; Horak *et al*. 2013), while others (e.g. grasshoppers) prefer open, dry and warm relatively short vegetation (e.g. grasslands) (Uvarov 1966).

Grasshoppers are good indicators of changes in environmental quality. For instance, grasshopper species assemblages showed strong responses to changes in semi-natural grasslands within the exotic timber plantation matrix in South Africa (Bazelet & Samways 2011b, 2011c) and community succession in steppe grasslands and alluvial pine woodland in Germany (Fartmann *et al*. 2012; Helbing *et al*. 2014). Grasshopper diversity in grasslands of South Africa (Gebeyehu & Samways 2002), grassland remnants within a timber plantation matrix (Bazelet & Samways 2011a, 2011b, 2011c) and rocky afromontane grasslands (Crous *et al*. 2013) have been shown to be high. However, grasshopper ecology or diversity has been little studied in fynbos or agricultural areas of the CFR biodiversity hotspot (but see Matenaar *et al*. 2014). In neighbouring xeric succulent thicket (Fabricius *et al*. 2003) and sugarcane plantations (Bam *et al*. 2013) in South Africa, natural and cultivated lands in Eurasia (Sergeev1998), small scale farms adjacent to savannah vegetation in Tanzania (Kuppler *et al*. 2015) and lac plantations in China (Chen *et al*. 2011), high grasshopper diversities were reported, especially on agricultural lands but without focus on narrow-range endemics such as those which occur in the CFR.

Here, I aim to assess the extent to which the main agricultural land-use types in the CFR (grape vineyards and fruit orchards) are able to support indigenous grasshopper assemblages, including the CFR's characteristic high levels of endemic species, relative to historic fynbos in protected areas. I tested two hypotheses: (1) that agricultural production in the CFR has no impact on grasshopper diversity; and (2) that different agricultural production types (vineyards vs. orchards) have similar impacts on grasshopper diversity. I compare grasshopper species richness, composition, diversity and evenness among the three land-use types in four geographical areas in the CFR.

2.2 Methods

2.2.1 Geographical areas and sites

Forty-six sites were selected belonging to three land-use types: historic Fynbos (F) in formally protected areas, Vineyards (V) and Orchards (O). The elevation of sites ranged from 90 m to 592 m asl. All sites were located in one of four geographical areas within the CFR: Grabouw, Somerset West, Stellenbosch and Paardeberg (Fig. **2.1**). The four areas constituted four independent landscape mosaics because they were either distant from each other (the farthest inter-site distance within an area was 23km, while the closest inter-site distance between areas was 35km), or separated by mountain ranges which probably acted as movement barriers to grasshoppers. Such distances, while seemingly short for northern-hemisphere temperate regions, are biogeographically highly significant for the CFR (Vrdoljak & Samways 2014). The area has many folded mountains with valleys and rivers. It has cold, wet winters and warm, dry summers. Forty-six sampling sites were selected. The selected areas were Stellenbosch (33° 55' 56" S, 18° 51' 37" E), Somerset West (34° 04' 33" S, 18° 50' 36" E), Paardeberg (34° 27' 00" S, 19° 36' 00" E) and Grabouw (34° 09' 08" S, 19° 00' 13" E) (14-16 sites each) (Fig. **2.1**). The selected farms were Vergelegen at Somerset West, Paul Cluver at Grabouw, Delvera, Delheim and Timbalea at Stellenbosch and Slent and Vondeling at Paardebeg. All fynbos sites were located in protected areas (PAs): Hottentots Holland at Grabouw, Jonkershoek at Stellenbosch, Helderberg at Somerset West and Limietberg provincial nature reserves at Paardebeg.

All selected vineyards were conventional wine grape vineyards (*Vitis vinifera*) that followed pesticide and irrigation management regimes based on IPW guidelines (Tromp 2006). All vineyard sites were interspersed with one or more cover crops, mostly legumes (*Vicia* spp.) that are annual, *Raphanus raphanistrum* annual or biennial and also grows in the wild, rye grasses (*Lolium* spp.) with both wild and cultivated species, oats (*Avena fatula*) which is considered an agricultural weed worldwide, *Hypochoeris radicata* which is a perennial cover crop, *Bidens pilosa* cultivated and also grows in the wild and is also known to be a weed on agricultural fields and *Erodium moschatum* which is also a weed which occurs both in natural environment and cultivated lands. Deciduous fruit orchards were mostly closed canopy apple trees. All selected apple orchard sites practiced conventional production that involved mostly the use of broad spectrum pesticides, although they were based on market standards and requirements (see Hortgro 2015).

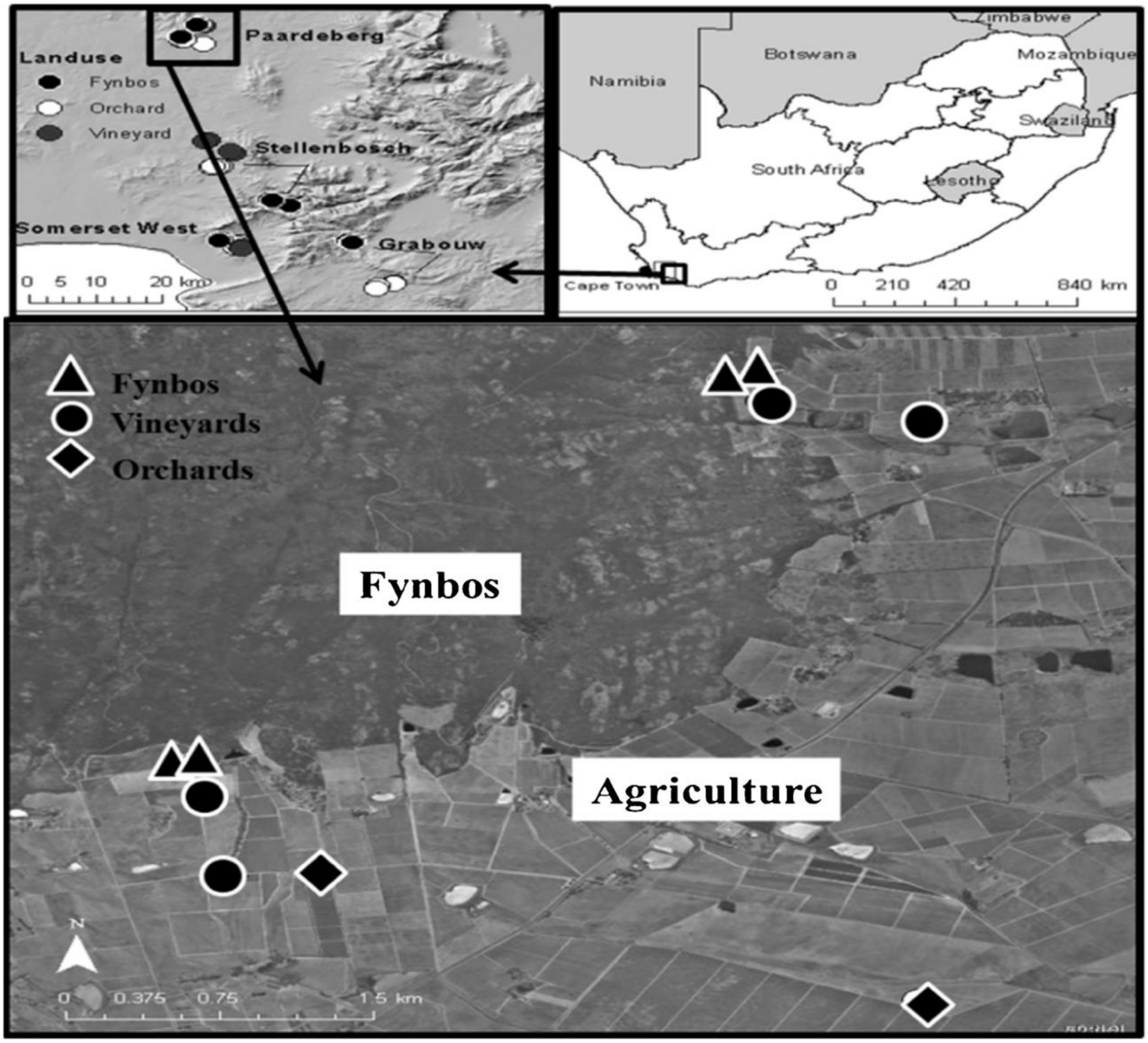

Fig.2.1. Map of the study area in the Cape Floristic Region, South Africa. Forty-six sites were sampled in four geographic regions and of three land use types. The map shows how the forty-six sites are distributed across the four study areas. It also shows the proximity of fynbos, vineyards and orchards within a geographic area (e.g. Paardeberg).

Most of the selected orchards had little to no cover crops. The few interspersed cover crops in orchards were mostly rye grasses, alfafa (*Medicago sativa*) a perennial cover crop and legumes. Irrigation application for my selected apple orchard sites were mostly based on soil moisture and plant requirements, with irrigation being much more frequently used in orchards than in vineyards. My sampled farms either used drop, microjet irrigation or both in all orchard sites. Fynbos sites were all located in protected areas (PAs): Hottentots Holland, Jonkershoek, Helderberg and Limietberg provincial nature reserves and were adjacent to vineyards and orchards (Fig. **2.1**). Fynbos is a scrubland, high in endemic plant species and dominated by Proteaceae, Restionaceae, and Ericaceae (Esler *et al*. 2014; Mittermeier *et al*. 2004).

2.2.2. Grasshopper sampling

Grasshoppers were sampled on four different occasions between November 2013 to April 2014 between 09:00 and 17:00 on sunny days with low wind speed and cloud cover. A 50x50 m quadrat was delineated in the centre of each site >30 m from the edges, to avoid edge effects (Bieringer *et al*. 2013; Pryke & Samways 2011). The choice of quadrat size was based on successful use elsewhere in South Africa (Bazelet & Samways 2011a, 2011b). Each site was sampled for 30 min on four occasions by two collectors (i.e. four person hours per site). Sites were sampled repeatedly at different times of day and across seasons in order to eliminate bias and ensure that samples collected were an adequate representation of total grasshopper diversity at a site. All four samples were pooled per site. Grasshoppers were initially flushed out of their swards and individuals seen hopping, walking or flying were caught with an insect net (Bazelet & Samways 2011a, 2011b; Larson *et al*. 1999). The timed quadrat count method was appropriate for scrubland vegetation (fynbos), vineyards and orchards (see Bazelet & Samways 2011a, 2011b; Gardiner *et al*. 2005). Captured grasshoppers were killed and identified in the laboratory using keys of Dirsh (1965), Eades *et al*. (2015), Jago (1994), Johnsen (1984), Johnsen (1991) and Spearman (2013).

2.2.3 Statistical analyses

Sample-based and individual based rarefaction curves were plotted for each land-use type separately and for all sites together to verify the completeness of sampling using EstimateS (Colwell 2005; Gotelli & Colwell 2011; Moreno & Halffter 2000). Rarefaction curves showed that sampling was sufficient within each land-use type and for all land-use types combined. Sample-based and individual-based curves reached near asymptotes in all cases (Fig. **2.2**).

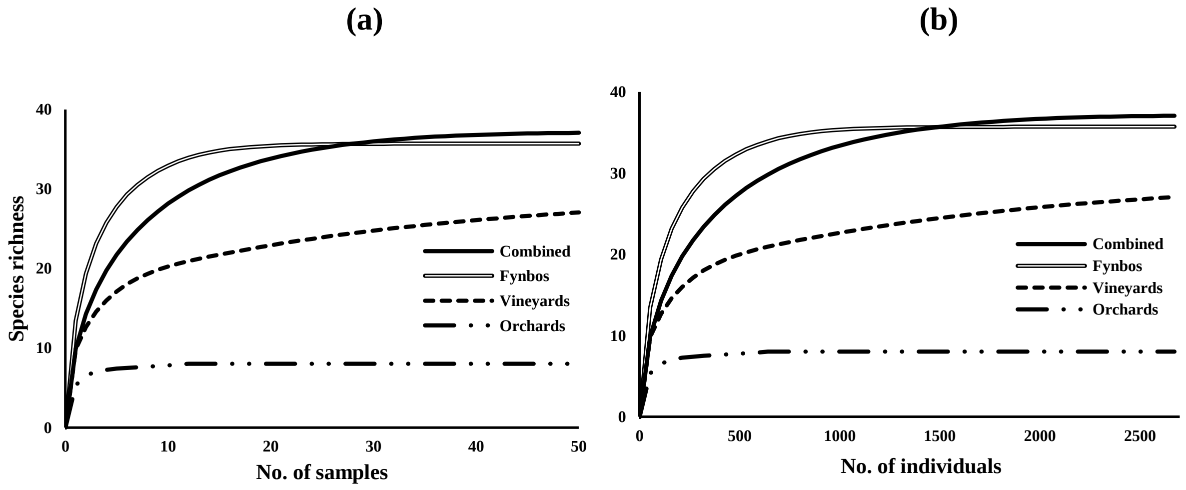

Fig. 2.2 Sample (a) and individual (b) based rarefaction curves for all (combined) vegetation types, fynbos sites, vineyard sites, and orchard sites.

To characterise community differences among the various land-use types and areas of study, we calculated species richness, abundance, density of grasshoppers in 2500 m^2, Shannon-Wiener Diversity index (H'), and Pielou’s evenness (J) (dependent variables) by hand in Excel (Fishel 2014) and EstimateS. Two-way ANOVA was performed in Statistica 12.6 (Hill & Lewicki 2007; StatSoft 2013) to compare diversity indices of grasshoppers among geographical areas and land-use types and their interaction term (independent variables). This was after a Shapiro-Wilk’s test of normality showed that the data were normally distributed (Shapiro-Wilk’s W = 0.94, p = 0.13). When the interaction term was significant, one-way ANOVA was performed to compare land-use types within each area. I chose to analyze my data using two-way ANOVA as this method is intuitive and easy to interpret, I had a simple two-way factorial design, and my data fit the assumptions of ANOVA.

To illustrate the similarity of grasshopper assemblages among the three land-use types, a Venn diagram showing the percentage and the number of shared and unique species per land-use was constructed. The Bray-Curtis similarity index (Kindt & Coe 2005; Magurran 2013) was calculated in EstimateS to assess species assemblage similarity among each pair of land-uses based on study areas. Bray-Curtis was used because it is influenced by the most abundant species and it is assumed that the most abundant species in ecological studies are well sampled, and thus express differences among sampling sites and land-uses better than less abundant ones (Kindt & Coe 2005). The values of the Bray-Curtis similarity index range from 0 to 1 with 1 indicating sites have the same species composition and 0 indicating that sites have no common species. I compared differences in Bray-Curtis similarity indices (dependent variables) for each pair of sites classified by whether they were in the same or different geographic area and land-use type (independent variable with four levels: same area-same type, same area-different type, different area-same type, different area-different type) using one-way ANOVA and Tukey's multiple comparison test in Statistica 12.6.

These results were corroborated using a Mantel's test performed in Pattern Analysis, Spatial Statistics and Geographic Exegesis (PASSaGE; Rosenberg & Anderson 2011). Three matrices were constructed: one with pairwise Bray-Curtis dissimilarity of species assemblage composition for each pair of sites (for Mantel's tests, we required a distance matrix to compare with geographic distance, and therefore used Bray-Curtis dissimilarity rather than similarity for this set of analyses only). Two binary dissimilarity matrices were constructed to indicate differences among sites. In the first, a score of 0 was given to a pair of sites in the same land-use and a score of 1 to each pair of sites of different land-uses; in the second binary matrix, a score of 0 was given to each pair of sites within the same geographic area and 1 to each pair of sites in different geographic areas.

Mantel's test in PASSaGE was also performed to test for the effect of geographical proximity (spatial autocorrelation) on species assemblage composition of the 46 sites (Legendre & Fortin, 1989). The species composition matrix using Bray-Curtis dissimilarity was compared with a matrix with pairwise geographical distance in kilometers between each pair of sites. All Mantel's tests were run using 1000 permutations. A two dimensional Multidimensional Scaling ordination (MDS) was constructed to show the relatedness of grasshopper assemblages per land-use using Bray-Curtis similarity index in Statistica 12.6 (StatSoft 2013). All species for which fewer than four individuals were collected were eliminated from the MDS due to lack of confidence in these results. These species were not removed from diversity analyses because the rare species are an important component to consider for species richness, diversity and evenness yet have a negligible effect on abundance and density.

2.3 Results

A total of 2453 grasshopper individuals belonging to 37 species, 25 genera, and 3 families, were collected (Table **2.1**). The most speciose sampled family was the Acrididae and the most speciose genus was *Euloryma*.

2.3.1 Effect of geographical areas and land-use types

There was a significant interaction between geographical area and land-use type for grasshopper abundance (two-way ANOVA F = 14.94, P < 0.001). Grasshoppers were significantly more abundant in vineyards than in orchards and fynbos (which did not significantly differ) at Stellenbosch (one-way ANOVA F = 16.98, P < 0.001) and Paardeberg (one-way ANOVA F = 45.15, P < 0.001) but significantly less abundant in orchards than in fynbos and vineyards (which did not significantly differ) at Somerset West (one-way ANOVA F = 13.98, P = 0.002) and Grabouw (one-way ANOVA F = 12.75, P = 0.002; Fig. **2.3a**).

The interaction between geographical area and land-use type on species richness was also significant (two-way ANOVA F = 11.45, P < 0.001). Mean species richness was highest in fynbos followed by vineyards and then orchards (one-way ANOVA F = 41.55, P < 0.001). This was true for all geographic areas except for Paardeberg, which had significantly higher species richness in vineyards followed by fynbos and then orchards (one-way ANOVA F = 31.88, P < 0.001; Fig. **2.3b**). There was a significant interaction between geographic area and land-use type for Shannon-Wiener diversity (two-way ANOVA F = 4.21, P = 0.003). Fynbos had significantly higher Shannon-Wiener diversity than vineyards which in turn had significantly higher Shannon-Wiener diversity than orchards overall (one-way ANOVA F = 53.86, P < 0.001). This pattern was consistent in all four geographic areas. The four geographic areas did not differ significantly in terms of their Shannon-Wiener diversity (one-way ANOVA F = 0.32, P > 0.05; Fig. **2.3c**).

There was a significant interaction between land-use and geographic area for Pielou’s evenness (two-way ANOVA F = 2.65, P = 0.03). Pielou’s evenness was significantly higher in fynbos than in vineyards, with orchards not differing significantly from either of the other land-use types (one-way ANOVA F = 3.92, P = 0.03). Grabouw sites had significantly higher Pielou’s evenness than the three other geographic areas (one-way ANOVA F = 5.59, P = 0.003; Fig. **2.3d**).

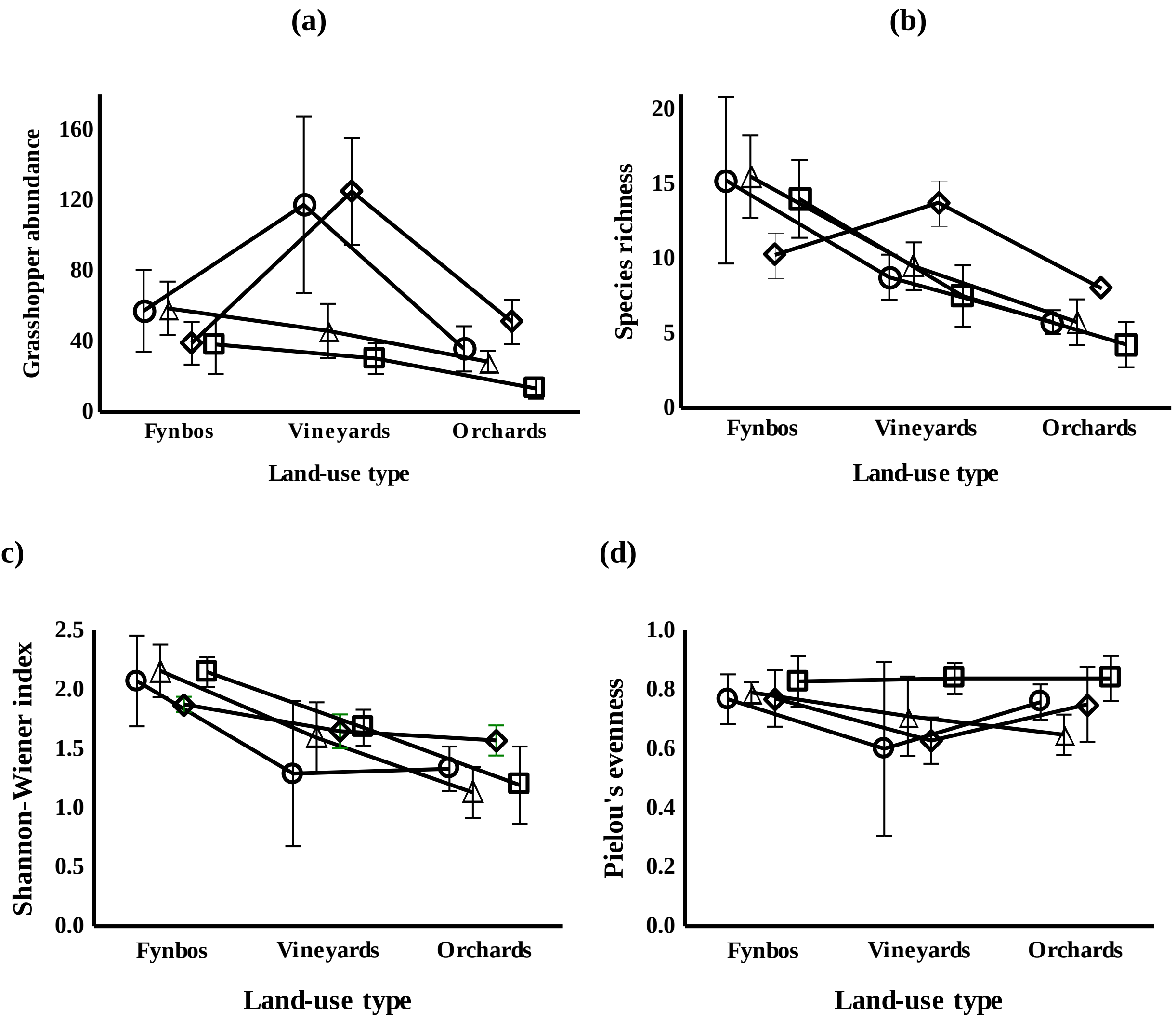

Fig. 2.3. Mean abundance (a), species richness (b), Shannon-Wiener diversity (c) and Pielou’s evenness (d) of geographical area by land-use interaction. △ = Somerset West, ○ = Stellenbosch, ◇ = Paardeberg and □ = Grabouw.

There was no significant interaction among land-use type and geographic area in mean grasshopper density in 2500 m^2 (two-way ANOVA F = 1.87, P > 0.05). Likewise, there was no significant difference in grasshopper density among the geographic areas (two-way ANOVA main effects F = 0.45, P > 0.05). However, orchards had significantly lower grasshopper density than fynbos and vineyards which did not differ from each other (two-way ANOVA main effects F = 24.81, P < 0.001).

2.3.2. Grasshopper similarity among land-use types

In total, 35 species belonging to all recorded families and subfamilies were observed in fynbos, 23 species were observed in vineyards, while nine species were sampled in orchards. Fourteen species belonging to three families and six subfamilies were observed in fynbos only, while only two species of Acrididae were sampled in vineyards only (Fig**. 2.4**). There were no species confined only to orchards. The average Bray-Curtis similarity index between fynbos vs. vineyards was 39%, fynbos vs. orchard was 38% and vineyard vs. orchard was 47%.

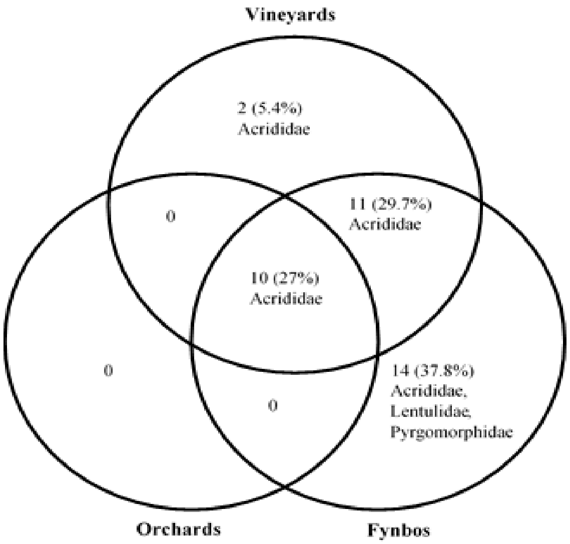

Fig. 2.4. Venn diagram showing percentages and numbers of unique and shared grasshopper species between fynbos, vineyard and orchard sites. Grasshopper families found in each land-use type are also denoted.

Sites within the same land-use types located in the same geographical area shared mean Bray-Curtis similarities of grasshopper assemblage composition of 70%, while sites within the same land-use types located at different areas shared mean Bray-Curtis similarity of only 50%. Sites in different land-uses located either in the same or different geographic areas shared 40% Bray-Curtis similarities. Bray-Curtis similarity values for each pair of sites were significantly higher when the two sites were in the same land-use and same geographical area than for sites within the same land-use type but different geographical areas (Tukey's F = 0.000, P < 0.05). Bray-Curtis similarity was consistently low and did not differ significantly for any pair of sites from different land-use types regardless of whether the sites were in the same or different geographical area (Tukey's F = 0.90, P < 0.05; Fig. **2.5**).

A Mantel's two-tailed test produced similar results, with a distance matrix of species assemblage composition (Bray-Curtis dissimilarity) being significantly correlated with a binary matrix for sites of same vs. different land-use types (Mantel's test t = 3.89, P < 0.01) and same vs. different geographic areas (Mantel's test t = 15.92, P < 0.01). There was no significant spatial autocorrelation in the grasshopper assemblage, with no evidence that geographically closer sites had more similar species compositions than geographically distant sites (Mantel's test t = 1.64, P = 0.10).

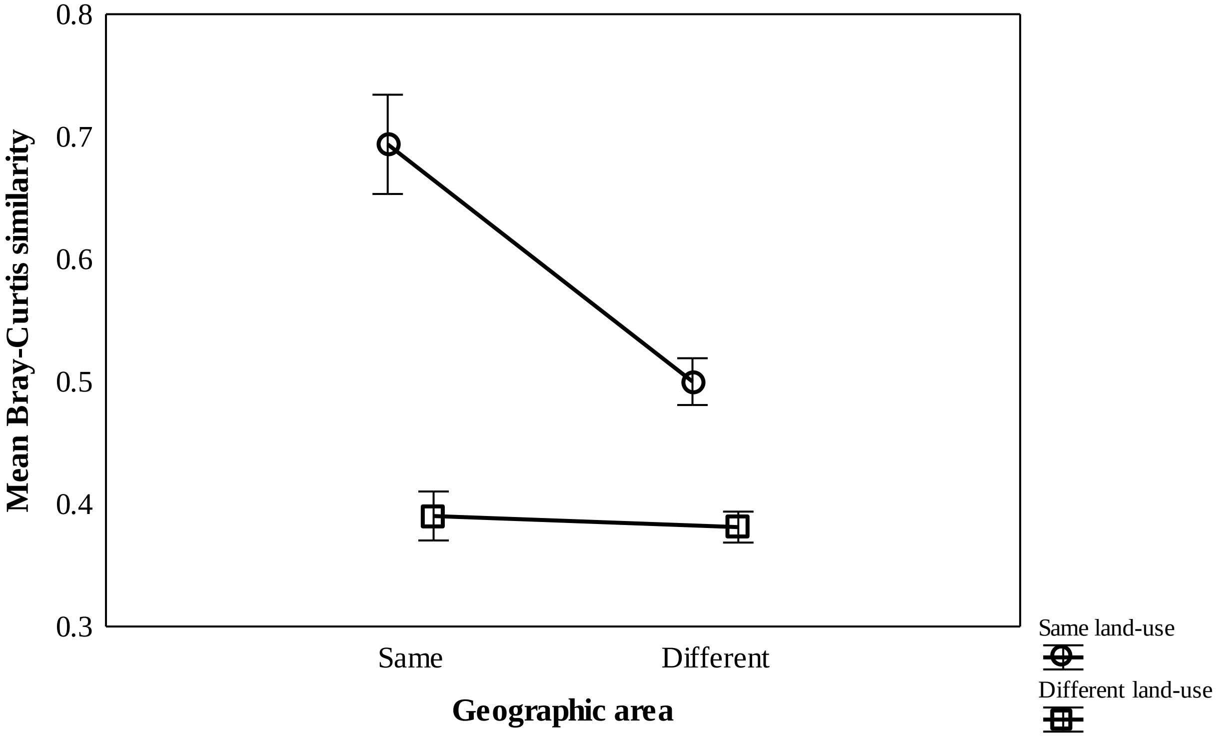

Fig. 2.5. Mean Bray-Curtis similarities of grasshopper species composition comparing sampling sites from different vs. same land-use types and geographic areas.

A Multidimensional Scaling (MDS) analysis of the three land-uses showed that each land-use type had similar species composition to each other, which was different from other land-use types. Vineyards had intermediate species assemblages between orchards and fynbos sites (Fig. **2.6**).

2.4 Discussion

More than half of the grasshopper species were associated with more than one land-use type and one quarter was associated with all three land-use types. These are similar results to those from Switzerland, where species overlap between agriculture and various degrees of natural and semi natural land-uses was high for wild bees, true bugs and ground beetles (Diekötter & Crist 2013).

Heterogeneity in habitats is vital for grasshopper life history requirements, such as mating in one microhabitat and grazing in another (Sergeev 1998; Gebeyehu & Samways 2003). This heterogeneity coupled with some species only being present in a combination of more than one plant cover type could be responsible for the high species similarities across the three land-use types (Fahrig *et al*. 2011; Tews *et al*. 2004).

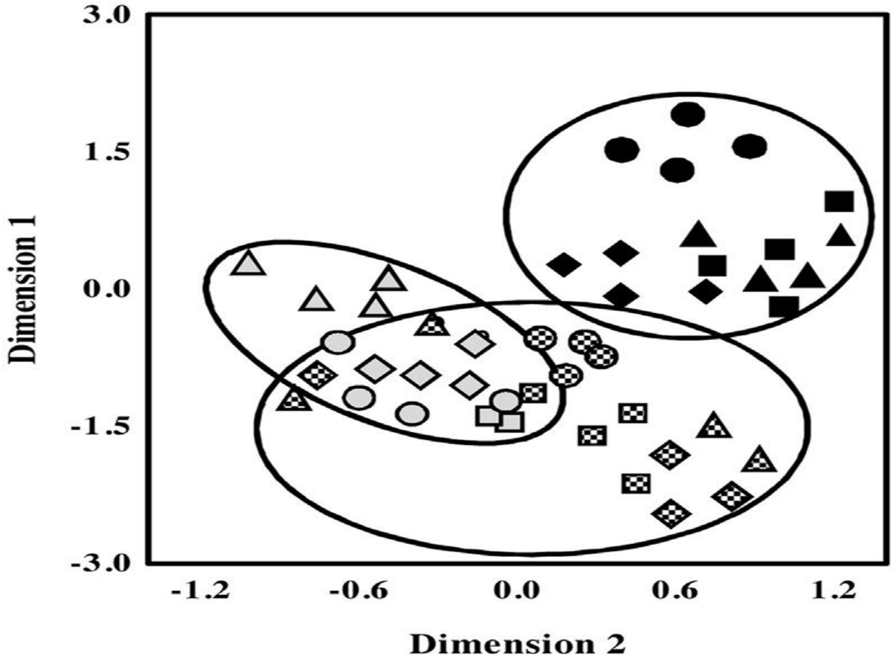

Fig. 2.6. MDS ordination plot showing assemblage similarities among geographic areas and land-use types. Gray fill = orchards, Black fill = fynbos, spotted pattern fill = vineyard sites. Somerset West, = ○ Stellenbosch, = △ Paardeberg and = ◇ Grabouw= □.

Although there was high species overlap among the three land-use types, species assemblages were distinct for each land-use. This was depicted by three distinct clusters in our MDS plots (see Fig. **2.6**). Furthermore, close to 43% of all grasshopper species collected for this study were distinctly associated with either the agricultural sites or fynbos. Of the 14 species which were specific to fynbos, seven are flightless endemics to the CFR (*Eulorymа* sp.1, *E. lapollai*, *E. larsenorum*, *D. bothai*, *D. coryphistoides*, *Gymnidium* sp.1, *G. cuneatum*) and two are flighted and probably endemic to the CFR (*K. capicola* and *P. rufipes*). The remaining five species are widespread, strong flyers (*C. aeruginosa*, *G. linea-alba*, *G. determi-natus vitripennis*, *G. crassicollis*, and *P. tricolor tricolor*). This high number of unique species underscores the value of protected areas and perhaps even historic remnants (Gaigher *et al*. 2015) for conservation of the endemic grasshopper fauna. At the other end of the spectrum was one species confined to vineyards despite being widely distributed throughout southern Africa and flighted (*T. nasuta*), illustrating that vineyards can increase the area of occupancy albeit for an already widespread species. Even though there was high overlap in grasshopper assemblages between the various land-use types, there were differences in diversity (species richness and Shannon-Wiener diversity) of indigenous assemblages among the land-use types, with type of agricultural activity emerging as an important driver of compositional biodiversity. This shows the importance of type of land-use on grasshopper assemblages (Hahn & Orrock 2015; Koch *et al*. 2015; Kuppler *et al*. 2015). Here the fynbos was the most species diverse, followed by vineyards and orchards. Fynbos also had higher evenness compared to vineyards, a manifestation of vineyards being dominated by many individuals of a few species in contrast to fynbos. Therefore, my results support others on arthropod diversity in the region, where spiders, ants, beetles, bees, bugs, butterflies and other terrestrial arthropods all had moderate richness in vineyards compared to fynbos (Gaigher & Samways 2010; Kehinde & Samways 2012; Magoba & Samways 2011; Vrdoljak & Samways 2014). The low diversity in orchards might be due to the closed canopy of most sampled orchards, creating less favourable conditions for undercover grass and herb growth from lower solar penetration. This is due to the reported reduction in the ambient local climatic conditions of plants with closed canopies (Smith & Capinera 2005) and expecially apple orchards that are reported to be 2 degrees less compared to nearby sourrounding air temperature

(Tanny *et al*. 2008). It also results in a relatively cool microclimate compared to vineyards. A grasshopper's growth and life activities are directly proportional to temperature, with cool conditions being less favourable for development (Uvarov 1966; Chapman & Joern 1990). Reduced undercover grass and herb growth, as was the case here in orchards, is also deleterious to some specialist feeders and less mobile species (e.g. wingless groups) (Davis *et al*. 1995). Although diversity of grasshoppers was relatively low in vineyards in comparison with fynbos, grasshopper abundance and density were highest in vineyards followed by fynbos and then orchards. Most of the high abundance and low evenness of grasshoppers in vineyards could be attributed to the species *A. dorsalis*, a strong flying oedipodine known for its association with bare ground for ovipositing and basking (see Bazelet & Samways, 2011a for species traits of close relative, *Aiolopus meruensis*), which was far more abundant in vineyards than in orchards. Its abundance in the vineyards can be explained by the open and bare ground within rows of vineyards which permit high sunlight penetration necessary for basking. Paardeberg had highest species richness and abundance in vineyards, a departure from the general patterns elsewhere in the CFR. Based on our MDS, where vineyards clustered somewhat with orchards, we conclude that this departure from the other geographical areas may be an indication of fynbos vegetation losing its naturalness in this area.

2.4.1 Conclusions and conservation recommendations

Although I found that agriculture has a negative impact on grasshopper diversity, there was high overlap of species between agricultural production areas and historic fynbos. Half of the species found only in fynbos were flightless CFR endemics, while those dominating the agricultural patches were winged, strong flyers and mostly more widespread species. These dissimilarities in grasshopper assemblages also varied according to crop type and production practices, with the greater the divergence of the crop from the natural fynbos (the harder the filter) the lower the species richness of grasshoppers in that crop. This distinctive species composition associated with the various land-uses substantiates that grasshoppers can potentially be used for monitoring changes in availability of production patches in the CFR towards or away from the historic fynbos condition. Our evidence suggests that vineyards provide an opportunity for improving the land sharing approach for grasshopper conservation in the CFR. This is mainly because the vineyard floor has high insolation, as with fynbos. Furthermore, vineyard management practices usually involve the planting of cover crops, mostly legumes, rye grasses and oats, to preserve soil structure and conserve water. This favours grasshoppers, especially the widespread, flighted ones, at the expense of flightless, narrow range endemics. It will also favour the endemic species if alien cover crops were replaced by fynbos vegetation. Deciduous fruit orchards provide less opportunity than vineyards for land sharing, mostly because of the dense canopy shading the ground and making it unfavourable for grasshopper-friendly vegetation and for grasshoppers themselves. Management practices in orchards, especially high levels of irrigation and continuous application of pesticides, may have compounded the situation. In the case of both vineyards and orchards, land sparing will be an important management intervention to conserve endemic species in particular. Although rehabilitation and expansion of this historic land and its inclusion into the protected areas network would better conserve the endemic fauna, this seems unlikely given current human requirements for production landscapes. However, some degree of land sparing on farms in the form of remnant patches is possible, and likely to be positive for grasshoppers as it is for parasitoids (Gaigher *et al*. 2015) and monkey beetles (Donaldson *et al*. 2002).

Table 2.1 Abundance and relative abundances of grasshopper species across sites among fynbos, vineyards and orchards in the Cape Floristic Region, South Africa.

Family/sub-family /species	**Abundance Fynbos**	**Abundance Vineyards**	**Abundance Orchards**	**Rel. abd. Fynbos (%)**	**Rel. abd. Vineyards (%)**	**Rel. abd. Orchards (%)**
ACRIDIDAE						
Acridinae						
Acrida sp.1	32	16	8	1.30	0.65	0.33
Anaeolopus dorsalis	60	573	177	2.45	23.36	7.22
Gymnobothrus carinatus	21	4	1	0.86	0.16	0.04
Gymnobothrus linea-alba	8	0	0	0.33	0	0
Keya capicola	8	0	0	0.33	0	0
Gomphocerinae						
Paragymnobothrus rufipes	14	0	0	0.57	0	0
Thyridota nasuta	0	4	0	0	0.16	0
Oedipodinae						
Acrotylus apricarius	4	2	0	0.16	0.08	0
Acrotylus bilobatus	3	31	0	0.12	1.26	0
Acrotylus deustus	4	1	0	0.16	0.04	0
Aiolopus thalassinus	13	78	31	0.53	3.18	1.26
Gastrimargus crasicollis	5	0	0	0.20	0	0
Gastrimargus determinatus vitripennis	5	0	0	0.20	0	0
Heteropternis couloniana	88	35	7	3.59	1.43	0.29
Heteropternis pudica	20	3	10	0.82	0.12	0.41
Morphacris fasciata	8	1	0	0.33	0.04	0
Oedaleus nigrofasciatus	21	32	0	0.86	1.30	0
Paracinema tricolor	3	0	0	0.12	0	0
Sphingonotus nigripennis	3	16	0	0.12	0.65	0
Cyrtacanthacridinae						
Acanthacris ruficornis	3	32	9	0.12	1.30	0.37
Cyrtacanthacris aeruginosa	2	0	0	0.08	0	0

…cont’

Cyrtacanthacris tatarica	2	3	0	0.08	0.12	0
Catantopinae						
Vitticatantops humeralis	18	74	31	0.73	3.02	1.26
Eyprepocnemidinae						
Eyprepocnemis calceata	226	256	138	9.21	10.44	5.63
Euryphyminae						
Calliptamicus semiroseus	104	54	0	4.24	2.20	0
Plegmapterus sinuosus	1	0	0	0.04	0	0
Hemiacridina						
Euloryma sp.1	2	0	0	0.08	0	0
Euloryma cederbergensis	0	2	0	0	0.08	0
Euloryma lapollai	12	0	0	0.49	0	0
Euloryma ottei	25	48	0	1.02	1.96	0
Euloryma umoja	16	8	0	0.65	0.33	0
Euloryma larsenorum	16	0	0	0.65	0	0
LENTULIDAE						
Lentulinae						
Devylderia bothai	7	0	0	0.29	0	0
Devylderia coryphistoides	2	0	0	0.08	0	0
Gymnidium sp.1	1	0	0	0.04	0	0
Gymnidium cuneatum	6	1	0	0.24	0.04	0
PYRGOMORPHIDAE						
Pyrgomorphinae						
Dictyophorus spumans	3	1	0	0.12	0.04	0

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CHAPTER 3: Seasonality and life history traits affect grasshopper utilisation of different patches in an agro-natural mosaic of the Cape Floristic Region, South Africa

Abstract

Understanding the link between species inherited traits and the utilisation of different elements in a heterogeneous landscape such as an agro-natural mosaic has value for conservation planning. Key among traits is species' mobility which determine species' ability to navigate in between different patches in a heterogeneous landscape. Furthermore, change in seasonality also affects the dynamics of resource allocation for herbivorous insects such as grasshoppers. Such traits are likely to be highly selected over long periods of time in biodiversity hotspots, and may not be adaptive in the face of landscape change. Studying grasshopper species traits, seasonality and how these factors affect their utilisation of the various aspects of the landscape will further increase our understanding of biodiversity conservation, especially in biodiversity hotspots. Grasshopper abundance was studied here under agricultural land-use (vineyards) and in natural vegetation (fynbos) across two peak seasons (spring vs. summer) in the Cape Floristic Region (CFR) biodiversity hotspot. My aim was to quantify the level at which different grasshopper species utilise the different aspects of the landscape and how this range of utilisation among species relates to certain species' traits in the CFR. My results showed that species traits play a major role in their ability to move in between patches which also affects how they utilize various different patches on the landscape. Highly mobile, generalist species are able to utilise more aspects of the landscape. And depending on seasonality, these species will inhabit either vineyards or fynbos aided by their high ability to move between patches. On the other hand, low

mobility, specialists lack the ability to move readily between patches, and as a result, they are confined to one or few patches across the seasons. Highly mobile, generalist species are better adapted to heterogeneous and novel landscapes compared to low mobile specialists. I also show that agricultural production supports a surprisingly wide variety of species. It is the poorly-mobile, specialist species that are particularly vulnerable to ongoing landscape change as they can only benefit from remnant patches of natural vegetation, unlike the highly mobile generalists which can move around the landscape and benefit both from anthropogenic patches and natural ones while optimising on season for doing this.

3.1 Introduction

Linking landscape patterns and species traits to ecological processes is important in landscape ecology (Chen *et al*. 2008; Smith *et al*. 2015). For instance, animal dispersal which is often dictated by inherited traits is vital for understanding how organisms effectively utilize different resources and features located in different habitats in an agro-natural landscape (Ewers & Didham 2006; Griebeler & Gottschalk 2000). This is especially important for species that require heterogeneous habitats on a landscape for sustaining their future (Taylor 1993; Brooker *et al*. 1999; Schirmel *et al*. 2010.; Mandelik *et al*. 2012).

Landscapes are made up of all natural elements that differentiate one part of the earth's surface from another. Examples of such elements are forest patches, hills and water bodies, with matrices, corridors, and patches (Sayer *et al*. 2013). By extension, an agro-natural landscape consists of agricultural production patches alongside natural patches and other natural features.

In the Cape Floristic Region (CFR) the natural areas are composed of a sclerophyllous vegetation known as fynbos, with agricultural areas of mostly grapevines and deciduous fruit orchards (Wesgro 2015). In these agro-natural landscapes, there are often competing interests: economic, environmental and biodiversity conservation. This means that management factors become necessary to maintain population levels of highly impacted animals (Sayer *et al*. 2013). These competing priorities of land-uses, coupled with different responses of the various host biota to seasonal changes in an agro-natural landscape, has the potential of creating different patches with different survival probabilities for different species that inhabit them. Studies of agro-natural landscapes, especially those inhabited by different species, are important because of the need to improve production without expanding agriculture into protected areas (Hutton 2010).

A study conducted in the USA showed that wild bees utilised both agriculture and old fallow fields in different seasons although they visited natural fields less often (Mandelik *et al*. 2012). Similarly, a study in Sweden suggested that semi natural pastures acted as population sources for the dispersal of butterflies to agricultural fields (Öckinger & Smith 2007). Furthermore, another study conducted in Germany on grasshoppers reports that Ensifera (Orthoptera: Acridiodea) require a mixture of dwarf shrubs and sand dunes for their persistence on the landscape (Schirmel *et al*. 2010). Findings from these studies reiterates the importance of heterogeneous landscapes for the life history traits of terrestrial insects. In addition to the importance of heterogeneous landscapes for these species, such studies also increase our understanding of how to improve conservation of animals, especially threatened ones, and to be able to protect ecosystem processes e.g. pollination, pest and vector control, and to monitor their biodynamics for bio-indication (Hansen 2011).

The CFR is a biodiversity hotspot with an exceptional number of endemic species experiencing great threats (Myers *et al*. 2000). This situation increases conservation concerns considering that the area is also used for intensive agricultural production (Rutherford *et al*. 2014; Mittermeier *et al*. 2004). In such a landscape, the identification of the relative importance of the various aspects of the landscape in terms of habitat selection and patch utilisation has the long term effect of helping in planning for conservation purposes (Morris *et al*. 1992). This is even more important for planning community interactions of species e.g. biological control and food web dynamics. In the CFR, close to 19% of the total land cover has been transformed for agriculture production (Maree & Govender 2013). Among the agricultural land-uses, several regions are dominated by vineyards which constitute approximately 17% of total agriculture by area (Wesgro 2015). Nevertheless, 78% of the total land mass is still covered by natural vegetation (Maree & Govender 2013). These differences in vegetation type and land-use directly and indirectly affect grasshopper population dynamics in the CFR (Adu-Acheampong *et al*. 2016).

In addition to differences in vegetation type and land-uses, seasonal variations of temperature and other abiotic factors also influence grasshopper population dynamics directly (Uvarov 1966) while resource availability can affect them indirectly (Smith & Capinera 2005). For instance, sprouting of leaves in vineyards is ephemeral due to its deciduous nature. This situation causes defaunated habitats over certain seasons (Mullins *et al*. 1992) thereby affecting grasshopper diversity indirectly through lack of food and microhabitats for their life history traits, although there may still be inter-cropping with either alien or exotic vegetation. Most fynbos vegetation on the other hand is evergreen, although recurring fire regimes can temporarily reduce leaf cover (Allsopp 2014; Rutherford *et al*. 2014), and possibly also create defaunated islands which reduce grasshopper population. Grasshoppers are supplied with high quality resources necessary for development during good conditions in a favourable habitat. They respond to these good conditions with an increase in population normally higher than the population in adjacent and relatively poor habitats (Adu-Acheampong *et al*. 2016). This behaviour is sometimes regulated by their mobility, food preferences and distribution.

Interestingly, mobility and food preferences also affect the distribution of grasshoppers and how they utilise the various aspects of agro-natural landscapes. Species with high mobility have a higher ability to migrate in between different patches on a landscape, and as such, are able to utilise different habitats (Hansson *et al*. 2014), especially winged and well-flighted species. Wingless species on the other hand, are mostly limited in movement and are confined to specific habitats on the landscape. Due to these physical limitations they are not able to utilise different patches or at best just a few. Food requirements also become a limitation for monophagous and often sedentary specialist insect species because they are often confined to their food sources or host plants. This is because they only feed on a single species or a single family of plants which are often located in few places (Wahlberg *et al*. 2002). Hence they are only able to utilise few habitats on the landscape. In contrast, polyphagous and often mobile generalist insect species are able to utilize more than one family of plant species for their life history requirements and hence are able to move in between different habitats more freely (Wahlberg *et al*. 2002). This feeding behaviour increases their ability to utilise different aspects of the landscape and to reside in more patches.

Here I investigate grasshopper utilization of vineyards and natural fynbos in an agro-natural landscape mosaic of the CFR across two seasons of grasshopper abundance, spring/early vs. summer/late season, and related this utilization to functional traits of species. Specifically, I investigate how different habitat patches are utilised by various grasshopper species in different seasons under agro-natural landscapes. I also test whether species inherited traits are related to grasshoppers ability to inhabit and utilise different vegetation patches in agricultural landscapes.

I hypothesize that often mobile generalist species will have elevated abundances in vineyards compared to fynbos. This is because vineyards are mostly interspersed with more attractive cover crops especially during good conditions. Assuming this is true, I expect higher abundances of mobile, generalist grasshoppers in vineyards only, during the late/summer season, when conditions are optimal in the vineyards because conditions do not change much in the fynbos. I also hypothesize that there will not be any significant change in grasshopper abundance across seasons in the fynbos because a high proportion of fynbos plants are sclerophyllous and evergreen, as opposed to the deciduous vineyards and their cover crops. I expect decreased numbers of grasshoppers in vineyards during harsher times (early summer). I also hypothesize that low mobile specialist, narrow-range endemic species adapted to CFR conditions will have approximately similar abundances within fynbos across seasons. Similarly, I also hypothesise that generalist, broad-range, widespread and highly mobile species will have elevated abundances in different patches (vineyards vs. fynbos) depending on seasons (early vs. late). Based on the results of the study I make recommendations regarding grasshopper conservation in this CFR agro-natural landscape.

3.2 Methods

3.2.1 Geographical areas and sampling seasons

Two land-use types, natural fynbos vegetation and vineyards, were sampled at 32 sites within four geographic areas in two sampling seasons. The elevation of sampling sites ranged from 90 m to 592 m asl. The selected geographical areas within the CFR were Grabouw, Somerset West, Stellenbosch and Paardeberg. The four areas constituted four independent landscape mosaics because they were either distant from each other (the farthest inter-site distance within an area was 23km, while the closest inter-site distance between areas was 35km), or separated by mountain ranges which probably acted as movement barriers to grasshoppers. Such distances, while seemingly short for northern-hemisphere temperate regions, are biogeographically highly significant for the CFR (Vrdoljak & Samways 2014). The two sampling seasons consisted of an early one, (late spring to late summer, called “spring” throughout) starting from November to February and a late one, (late summer to early autumn, called “summer” throughout) starting from February to April.

3.2.2 Sampling of grasshoppers

Sampling was conducted on clear sunny days with low wind speed by two collectors on four occasions (two per each season) between 09:00 and 17:00. A 50x50 m quadrat was delineated at the centre of each site >30 m from the edges, to avoid edge effects (Bieringer *et al*. 2013). The choice of quadrat size was based on successful use elsewhere in South Africa (Bazelet & Samways 2011a, 2011b).

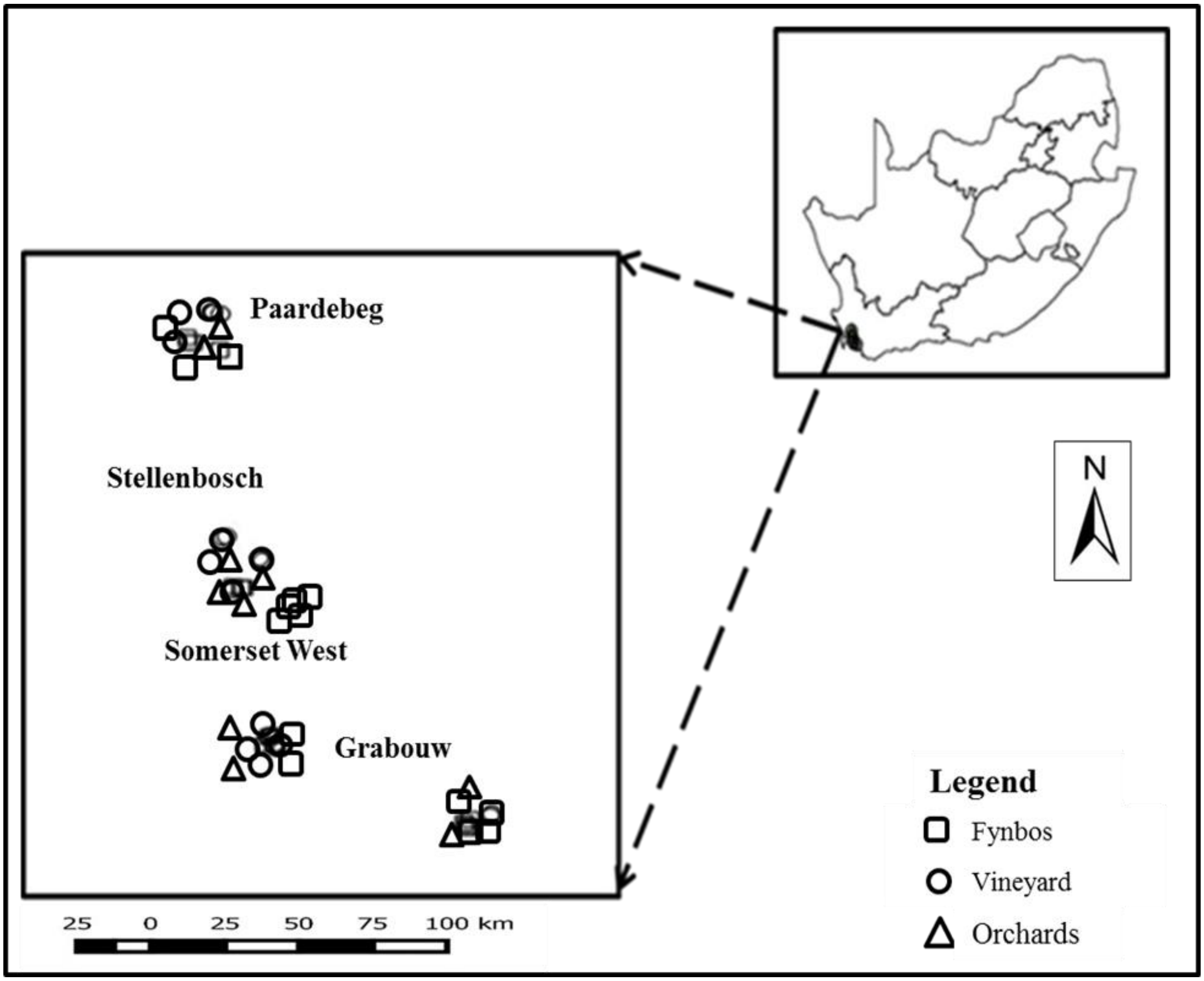


Figure 3.1 The study area in the Cape Floristic Region, South Africa. Thirty-two sites were sampled at four locations and in two land-use types. The map shows how the thirty-two sites are distributed across the four study areas.

Grasshoppers were initially flushed out of their swards with individuals seen hopping, walking or flying caught with an insect net (Bazelet & Samways 2011a, 2011b; Larson *et al*. 1999). The timed quadrat count method was appropriate for scrubland vegetation (fynbos) and vineyards (Bazelet & Samways 2011a, 2011b; Gardiner *et al*. 2005). Captured grasshoppers were frozen and later identified in the laboratory using keys of Dirsh (1965), Eades *et al*. (2015), Jago (1994), Johnsen (1984), Johnsen (1991) and Spearman (2013) among others. The six most abundant species in my samples were selected for further analysis: *Anaeolopus dorsalis*, *Heteropternis couloniana*, *Eyprepocnemis calceata*, *Calliptamicus semiroseus*, *Euloryma ottei* and *Aiolopus thalassinus* (Table **3.1**). These species were chosen for analysis because they were sampled in both fynbos and vineyards throughout the two seasons. Further consideration for the selection of these species was based on representation of the major groups of grasshopper species in the CFR (i.e. distribution, trophic level, mobility). Also these species were the most abundantly sampled groups. Commonly sampled species are expected to express differences among sampling sites, geographic areas and land-uses better than less abundant ones (Kindt & Coe 2005; Maurer & McGiII 2011).

Three life-history traits: geographic distribution, trophic level, and degree of mobility were chosen to characterize species (Bazelet & Samways 2011a; Iverson *et al*. 2011; Henle *et al*. 2004). These life history traits were taken from all available articles, and books on life history traits of grasshoppers (Grunshaw 1986; Bazelet & Samways 2011a; Dirsh 1965; Johnsen 1984, 1991, Matenaar *et al*. 2016). Extrapolations based on closest relatives were the only possible means for evaluating traits of species that did not have enough information from available materials. Categorisation of grasshopper distributions into widespread, regionalised or localized was based on the extent of occurrence in South Africa. Species that are known to occur worldwide are categorised as widespread, those known to occur only in the southern African region are termed regionalised and those known to occur only in South Africa are termed localised. For trophic levels, grasshoppers were placed into either one of three groups: mixed-feeder, graminivorous, or forb-feeder (Bazelet & Samways 2011a). Grasshoppers belonging to subfamilies, Acridinae, and Oedipodinae are strong fliers and hence arbitrarily considered high in mobility and those belonging to Eyprepocnemidinae consists of medium fliers and hence are arbitrarily considered to be medium in mobility (Ritchie 1981). On the other hand, apterous to brachypterous sedentary grasshopper species such as lentulids and hemiacridines were categorised as the low mobility group.

All vineyard sites selected for this study observed conventional production approach and application of pesticide and irrigation management regimes based on IPW guidelines (Tromp 2006). These vineyards were also interspersed with several green leafy cover crops during the late season (Fig. **3.2a**) but devoid of any or at best have few dry cover crops in the early season (Fig. **3.2b**). Notably amongst these cover crops were *Raphanus raphanistrum* (wild radish), *Lolium* spp. rye grasses, *Vicia* spp., *Hypochoeris radicata*, *Bidens pilosa*, *Erodium moschatum*, and *Avena fatula* (oats). Fynbos, defined as a scrubland that is dominated by Restionaceae, Ericaceae and Proteaceae, and high in endemic plant species (Rutherford *et al*. 2014; Mittermeier *et al*. 2004), was the natural mosaic used for this study.

Figure 3.2. Interspersed dry leafy (a) and green leafy (b) cover crops in between rows of vines in early (spring) and late (summer) seasons respectively, as well as fynbos vegetation in early (c) and late (d) seasons.

Sites selected within the fynbos were located in Helderberg, Jonkershoek, Cederberg and Hottentots Hollands nature reserves. The fynbos phenologies did not differ significantly between the two seasons (Fig. **3.2c** and **d**).

All selected vineyards were managed under the Integrated production of wine program in South Africa (IPW). The IPW management practice mainly includes the use of selected pesticides for the control of key pests such as weevils and fruit flies. Other precautionary spray programmes are also conducted to control fungal diseases such as powdery mildew under this scheme mainly at the latter season. Pesticides application is entirely dependent on levels of pest attacks on the grapes under IPW scheme. With increasing stirngent export requirements for export integrated pest management schemes, farmers are advised to apply pesticides with caution under this scheme (Tromp 2006) . Some of the important pesticides Chloropyrifos for the control of ants at 400ml/vol endoslfan for the control of mites at 125ml/vol and Mancozeb for the control of *Plasmopara viticola* at 200g/100L on the field.

3.2.3 Statistical analyses

Generalized linear mixed model (GLMM) fit by maximum likelihood (Laplace Approximation) were constructed in RStudio version 3.2.5 to compare total grasshopper abundance (dependent variable) among seasons and land-use types. Poisson distribution was used because my response variable is discrete count data and GLMM was used to account for the underlying spatial structure in the experimental design (RStudio 2015). Here, abundance was my dependent variable, while season and land-use type were my independent variables. I also constructed Wilcoxon matched paired test in Statistica 13.0 (Hill & Lewicki 2007; StatSoft 2013) to assess whether there were significant differences in species abundance between early vs. late season for each land-use separately.

3.3 Results

There was a significant difference in total abundance of all species between seasons at all study sites ($Z=6.60$, $p<0.01$). Also total abundance between land-uses at all study sites was significantly different ($Z=8.29$, $p< 0.01$). However, there were no significant difference in seasonal abundance in fynbos for all selected species, although there was a significant difference in vineyards in the majority of the selected species. Abundance was significantly higher in late season compared to early season for *H. couloniana*, *A. dorsalis*, *C. semiroseus* and *E. calceata* (Fig. **3.4**).

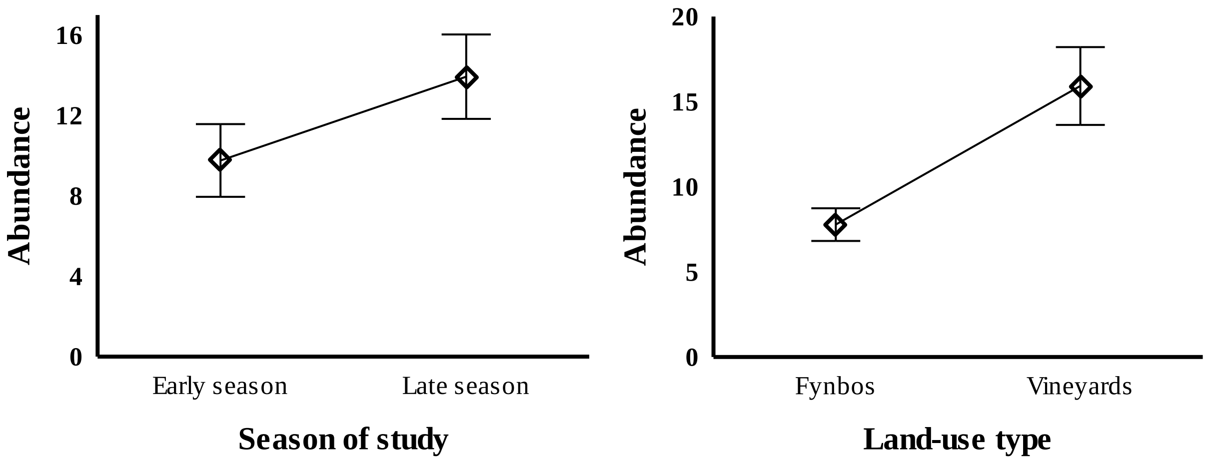
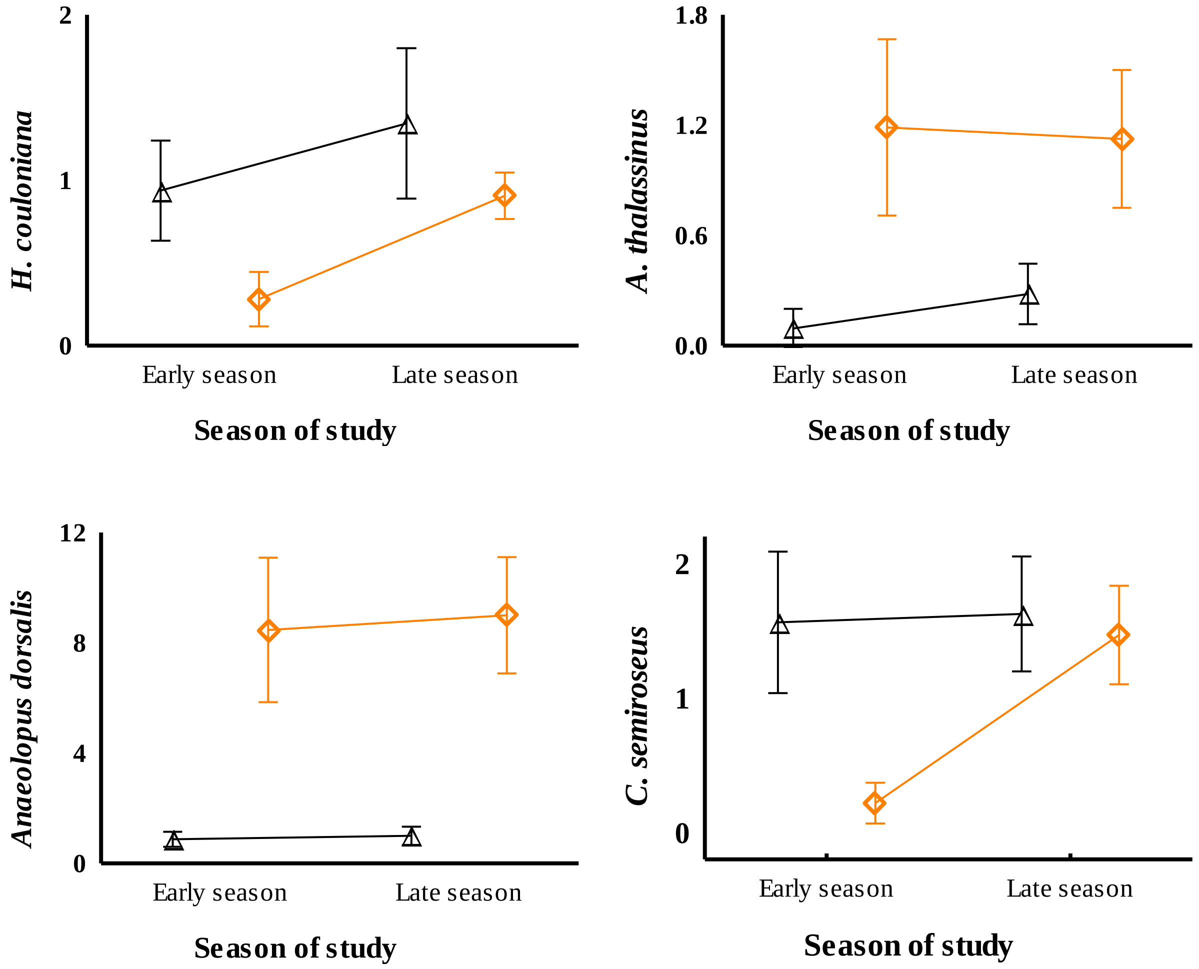


Figure 3.3 Mean (±SE) of abundance of grasshoppers per study season and land-use type in the Cape Floristic Region.



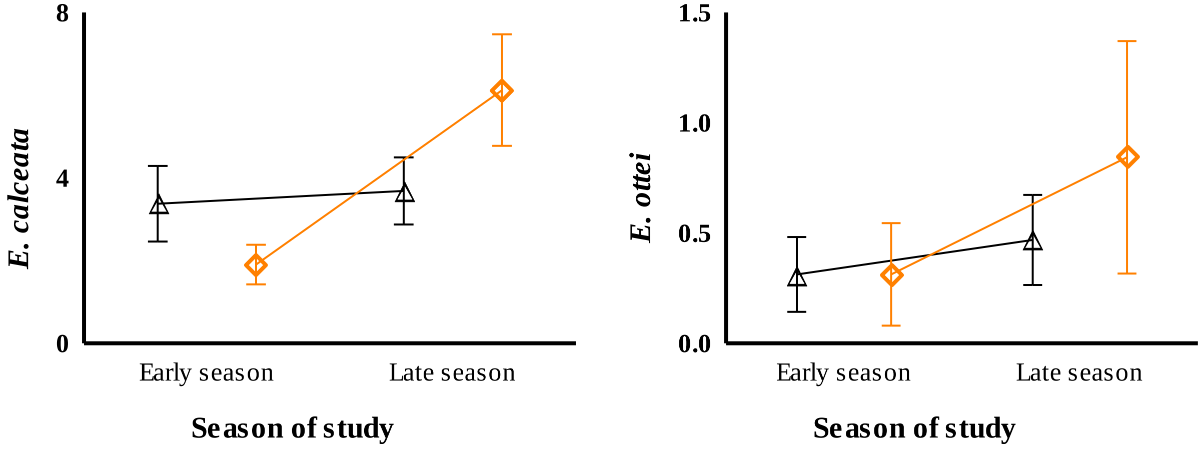


Figure 3.4 Mean (±SE) of abundance of six grasshopper species in early and late seasons in the Cape Floristic Region. Fynbos= △ vineyard= ◇

Table 3.1: Results of Wilcoxon's matched-pairs test of abundance for the two seasons in vineyards and fynbos.

Grasshopper species	**Wilcoxon matched paired test (Vineyards only)**		**GLMM by maximum likelihood (Land-use*Season interaction)**
Heteropternis couloniana	$Z_v=3.65$ $p<0.01$ **	$Z_F=1.77$ $p=0.08$	$Z=5.456$ $p<0.01$ **
Anaeolopus dorsalis	$Z_v=4.94$ $p<0.01$ **	$Z_F=0.59$ $p=0.55$	$Z=4.80$ $p<0.01$**
Calliptamicus semiroseus	$Z_v=4.13$ $p<0.01$ **	$Z_F=0.23$ $p=0.82$	$Z=4.156$ $p<0.01$**
Eyprepocnemis calceata	$Z_v=4.50$ $p<0.01$ **	$Z_F=0.73$ $p=0.46$	$Z=5.456$ $p<0.01$**
Euloryma ottei	$Z_v=1.45$ $p=0.15$	$Z_F=1.27$ $p=0.20$	$Z=1.078$ $p=0.28$
Aiolopus thalassinus	$Z_v=0.07$ $p=0.94$	$Z_F=1.53$ $p=0.13$	$Z=-1.646$ $p=0.10$

Abbreviations: Z_V=Z value in vineyard, Z_F=Z value in fynbos, **=significantly different

Wilcoxon matched paired test as well as the generalised linear mixed model results are summarised above in (Table **3.1**). Significant Z value for both sets of tests means significant differences in abundance between seasons on the same land-use type by the species involved. Here, the abundances of *H. couloniana, A. dorsalis, C. semiroseus* and *E. calceata* were all significantly different between the two seasons in vineyards but not fynbos. This can be interpreted as them occupying different patches on the landscape in different seasons. Because a shift in abundance from late to early in vineyards clearly is an indication of movement in and out. Therefore, a shift in abundance in vineyards was the most important determinant of movement in between patches because abundances in fynbos did not differ significantly between seasons.

Table 3.2. Three life history traits and predicted dispersal mode of six grasshopper species in the Cape Floristic Region.

Grasshopper species	**Distribution**[a]	**Trophic**[b]	**Mobility**[c]
Heteropternis couloniana	W	M	H
Anaeolopus dorsalis	R	G	H
Calliptamicus semiroseus	W	M	M
Eyprepocnemis calceata	W	M	M
Euloryma ottei	L	F	L
Aiolopus thalassinus	W	G	H

Abbreviations (Distribution): L, localized; R, regional; W, widespread

Abbreviations (Trophic type): G, graminivorous; M, mixed-feeder; F, forb-feeder

Abbreviations (Mobility): L, low; M, medium; H, high

Of the six species, three, *H. couloniana*, *C. semiroseus*, and *E. calceata*, were widely distributed, with good mobility and also mixed feeders. They were also found to be most abundant in the late season in vineyards when there was little or no pesticide application. Two additional species, *A. thalassinus* and *A. dorsalis*, were relatively widely distributed, graminivorous, highly mobile and most abundant in vineyards in the late season. Only one species among the selected group, *E. ottei*, was an endemic, flightless, forb-feeder which was most abundant in fynbos, regardless of the season (Table **3.2**).

3.4 Discussion

Highest grasshopper species richness and abundance was recorded in late season in vineyards in all geographic areas. This contrasts with the early season results which show lower abundance in vineyards in comparison with the late season's abundance. This underscores that there is distinct grasshopper diversity and abundance in each season, although the seasonal variation was far less in fynbos than in the vineyards. The late season also coincided with the peak plant production, with grasshopper richness and abundance of *A. dorsalis, H. couloniana, E. calceata* and *C. semiroseus* being influenced by the increase in edible cover crops as reported elsewhere (Kruess & Tscharntke 2002; Joern 2005) and little or no pesticides application. Early season conditions in the vineyards (e.g dried leaves, high pesticide application) could be less suitable because of little edible cover crop and high pesticides application within. At this time, there are few or no individuals of these species in vineyards but they are present in fynbos which offers alternative life supporting conditions. In spite of this alternative habitat occupancy, there is little change in population levels of these species in fynbos compared to when conditions are good in vineyards. Favourable (e.g. less pesticides pressure and high temepreture) conditions in vineyards return late season, leading to a population increase in vineyards. At this time, populations are low in fynbos.

The characteristic dispersion patterns, coupled with medium to high mobility traits, suggest migration in between patches based on suitability because they have the ability to move across the landscape. Also, being graminivourous or mixed feeders, means that *A. dorsalis, H. couloniana*, *E. calceata* and *C. semiroseus* can survive in both fynbos and in vineyards when palatable grasses are present in both patches (Table **3.2**). Although mobility by adults and even nymphs is possible, the overall differences in abundance between the two seasons could have been influenced by the natural seasonal dynamics of grasshoppers in this type of climate, where egg diapause during winter and adults emerge to complete their life cycle during spring-summer-autumn seasonal cycles (Uvarov 1966). Also, it is not clear at this stage if these species are utilising either one or both vineyards and fynbos for breeding and the other strictly for browsing or foraging. Nevertheless, it is certain that both vineyards and fynbos patches are utilised in different seasons.

In contrast to the above four species, *E. ottei* and *A. thalassinus* showed no significant differences in abundance between the two seasons. Relating the species traits and seasonal abundance across the two seasons in both fynbos and vineyards suggest these species are not utilising vineyards to any extent. This could be the result of their high sensitivity towards land transformation and agricultural production. Their characteristic traits of low to medium mobility could also play a role in their inability to migrate among patches. The high fragmentation of the agricultural environment might have also created barriers to movement for these relatively less mobile species. Another possible reason why these species are not able to utilise vineyards might be due to the absence of their preferred host plants. Furthermore, other biotic interactions such as predation and competition from other species might have played a role in these species which seemingly do not move between patches and do not take advantage of the different patches on the landscape. With these characteristic traits, the two species maximise their search for good life conditions by occupying the best habitat or patch type where foraging efficiency will be higher (especially in the fynbos for *E. ottei*) (Pyke *et al*. 1977), especially during harsh conditions because of their limited mobility.

The fynbos leafy vegetation changes little in phenology during the different seasons (although the flowers change greatly). This could mean that the fynbos biome is the best and surest patch to find food if these species are to expend less energy in the searching process, even if they can still utilise vineyards. Under such circumstances the species will only occupy the best possible habitats in both early and late seasons to further reduce the energy expended on searching for food. These findings also suggest that heterogeneous landscapes e.g. agro-natural mosaics are vital for the persistence of grasshoppers. This means such landscapes can potentially serve to complement each other in the provision of resources and vital habitats at different stages of grasshoppers' life cycle and in different seasons. For instance, the most suitable soil conditions that determine breeding sites may not necessarily be the preferred soils for the host plants. Also different life stages of grasshoppers may require different resources for development e.g. early instar nymphs may prefer a different type and structure of food compared to later ones and so on (Uvarov 1966: Gardner *et al*. 1995; Jeanneret *et al*. 2003). A study conducted on German bush crickets (Orthoptera: Tettigoniidae) reported that they have higher rate of persistence under optimal habitats surrounded by sub-optimal habitats than optimal habitats only (Griebeler & Gottschalk 2000). Similarly, it seems heterogeneous habitats are vital for the development and life history traits for some orthopteran species. Indeed, vineyards and fynbos appear to provide just such a heterogeneous environment for these life history traits, with seasonality of the CFR also being important.

Species in the Lentulidae, Hemiacridinae, Eyprepocnemidinae and Pyrgomorphidae (i.e. wingless, localised/endemic, forb feeders to mixed feeders with limited to medium mobility) would be expected to utilise only one or few habitat patches in heterogeneous landscapes. This is because most species that belong to these groups, especially Hemiacrididae species (Spearman 2013) and Lentulidae species (Matenaar *et al*. 2015, 2016) are only associated with fynbos with slight changes in densities throughout seasons. A few Hemiacridinae species are also associated with vineyards. Even so, their abundance does not vary significantly between seasons in both fynbos and vineyards. Under optimum environmental conditions these species will locate the best possible habitats in the fynbos or any other patch on the landscape at a particular time of the year for best living conditions. However, the quality of habitats varies with time of year and it is necessary to move to find optimal conditions at any time (Loreau *et al*. 2013). Here, densities of *E. ottei,* and *A. thalassinus* did not differ much between seasons.

3.4.1 Conclusions and conservation recommendations

Grasshopper species that are highly mobile, widely distributed and mostly grass to mixed feeders utilise a greater variety of patches on the landscape. They characteristically establish in good quality habitat (vineyard) for a short time during favourable conditions but decrease there greatly during unfavourable conditions. Nevertheless, the life history traits of overwintering as eggs, hatching as nymphs during spring, and then reaching adulthood in a different habitat may also play a role in the seasonal dynamics of these species. Further studies are required to ascertain which species are abundant in vineyards due to the presence of good conditons in vineyards or as a result of life cycle traits. Other species, especially the wingless, localised endemics that display little to medium mobility, that eat mostly forbs or are mixed feeders, utilised relatively low variety of patches on the landscape. This is because they were either encountered on few occasions or not at all in vineyards across the changing seasons. These species can potentially be used as bio-indicators of high quality habitats, with vineyard seemingly a lower quality habitat for their persistence. The dynamics of hemiacridines for example, could be used for fynbos quality surveillance. Furthermore, a biodiversity conservationist could use the life history traits of a particular grasshopper species to help design conservation schemes in agro-natural landscapes. These species could be used to determine the quality and the quantity of fynbos/forb vegetation in and around vineyards to see whether these are sufficient to maintain population levels without any ecological relaxation. My study also shows that agricultural land is of high importance for the persistence of certain species, especially those that are generalist, widespread and mobile. Under large-scale expansion of agriculture into natural vegetation, low mobility habitat specialists will be at risk of extinction, because of their limited ability to move between optimal patches to escape harsh conditions.

3.5 References

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CHAPTER 4: Endemic grasshopper species distribution in an agro-natural landscape of the Cape Floristic Region, South Africa

Abstract

Conservation biologists and ecologists often make use of models to identify important biotic and abiotic factors that constrain species distributions for conservation decisions to be taken. In line with such practice, I developed species distribution models for four localized, Cape Floristic Region (CFR) endemic flightless grasshopper species. *Euloryma larsenorum* and *E. lapollai* are associated with fynbos only, while *E. umoja* and *E. ottei* both associated with fynbos and vineyards. I used Maximum Entropy algorithm, which showed that vegetation type and soil characteristics were the most important environmental factors affecting local distribution of *Euloryma* species in the CFR. Models also showed that *Euloryma* species have very narrow predicted suitable habitats in the CFR. I also show that there are no significant differences in the distribution of species associated with fynbos only as well as those associated with both fynbos and vineyards. This calls for concerted efforts for conservation of *Euloryma* species in the CFR. In spite of the fact that all modelled species may suffer range constriction in the event of a global change, *E. larsenorum* and *E. lapollai* may require higher conservation priorities since they are sensitive to land-use change. *E. larsenorum* and *E lapollai* are likely to be the most affected species in the event of further habitat transformation from fynbos to agricultural production. This is not likely to be the case for *E. umoja* and *E. ottei* which can tolerate agriculture environment, although they might survive both sets of environments according to their life history traits. The *Euloryma* species group can potentially be used as bioindicators for soil assessments in the CFR.

4.0 Introduction

Conservation biologists and ecologists are often faced with the difficult task of identifying important factors (biotic and abiotic) with high implications for species distributions under the current biodiversity crisis (Rangel & Loyola 2012; Lin *et al*. 2016). Such models are often referred to as species distribution, habitat suitability or ecological niche models (Dormann 2012; Porfirio *et al*. 2014). Species distribution models (SDMs) often link species' known occurrences with certain environmental conditions peculiar to sites where they were recorded to predict possible locations where populations could be maintained on the landscape (Pearson 2010; Peterson *et al*. 2011). This is in accordance with the ecological niche theory where species' tolerance to certain environmental factors limit their persistence on a landscape (Soberón 2007; Colwell & Rangel 2009). Most ecological correspondence analyses and species distribution models are aimed at describing mathematical or statistical patterns underlining species occurrences with fitted models (Franklin 2010; Peterson *et al*. 2011). In view of this, species distribution models can be described as the quest to simplify complex realities involving observed biological phenomena with a model. Consequently, species distribution models (SDMs) have become important instruments for generating simplified expected responses to potential future impacts of environmental change on biodiversity (Howard *et al*. 2014). This is particularly important in a biodiversity hotspot which is also heavily utilized for agricultural production, such as the Cape Floristic Region (CFR) with its high conservation priorities (Rutherford *et al*. 2014; Mittermeier *et al*. 2004; Esler *et al*. 2014). For instance, application of SDM's will help design ecological survey guides that have the potential to increase sampling precision through enhanced efficiency of data capture. Guided and precise data capture can have many applications in conservation biology especially for rare and threatened species (Elith &

Leathwick 2009; Pearson 2010; Simaika & Samways 2015; Silva *et al*. 2016). It can also be used to identify important ecological factors that affect species persistence on a landscape (Lin *et al*. 2016) and predict the geographic range expansion of species, especially invasive ones (Calatayud *et al*. 2016; Kanturski *et al*. 2016). This is even more important for under-studied groups such as insects (Ballesteros-Mejia *et al*. 2016) many of which are highly threatened on the landscape. Such threatened species can be used as surrogates for determining and/or designing conservation strategies for other such species that appear to occupy same geographic space. This is because such species often display similar physiological responses to environmental constraints similar to conditions which affect the focal surrogate species (Brooks *et al*. 2006; Mace *et al*. 2008). Surrogate species are usually referred to as indicator species (Caro 2010; Rodrigues & Brooks 2007) because they play a vital role in monitoring the organisational structures of ecological communities in locations of interest (Menon *et al*. 2012).

For such a study to be successful, especially in an agro-natural landscape (e.g. CFR), an ideal group of insects to focus on as surrogates for accessing land-use change or land transformation are grasshoppers (Orthoptera: Acridoidea). This is because of their reasonably well understood biology, high responsiveness to environmental changes (changes in vegetation and land-use) and readily available information on distribution and abundances worldwide. In spite of the available information, grasshopper studies are few in the CFR. However, there are some studies on grasshopper behaviour and ecology in this region (Matenaar *et al*. 2014), geographic distribution (Spearman 2013), conservation in natural systems (Gebeyehu & Samways 2002; Matenaar *et al*. 2015) and agro-natural mosaic (Kuppler *et al*. 2015; Adu-Acheampong *et al*. 2016), grazing and fire (Gebeyehu & Samways 2003; Joubert *et al*. 2016), land management and design (Gebeyehu

& Samways 2003; Bazelet & Samways 2011c) diversity (Gebeyehu & Samways 2002) and utilisation of different patches in agro-natural mosaics (Chapter 3). Notably absent from this list of studies is ecological niche or species distribution models e.g. models that can predict their potential distribution based on known environmental factors and predict suitable areas where they could occur.

One such important potential surrogate grasshopper species endemic to the CFR are the flightless, narrow range Hemiacridinae of the genus *Euloryma*. Their value lies in their high sensitivity to environmental changes and their tight coupling to the dominant natural fynbos vegetation in the CFR. Most importantly, their biodynamics on this landscape can be translated into changes in habitat or land-uses. The majority of these flightless endemic *Euloryma* species are associated with only the dominant native vegetation (fynbos) in the CFR (Spearman 2013). Nevertheless, few species in this group are also associated with agriculture production e.g. vineyards (Adu-Acheampong *et al*. 2016). Because they are particularly sensitive to changes in environmental conditions, it is important to develop a model that describes the set of environmental conditions that are necessary to support the persistence of a viable population for bioindication in the CFR.

In this study, I use SDM techniques to identify the most important variables that constrain the occurrence of *Euloryma* species in the CFR. Such studies focus on patterns of biodiversity and geographical distribution, and which have often been used to describe the relationships between biodiversity indices and a number of environmental variables. Studies involving modelling of an organism's responses to habitat constraints mostly highlight the contributions of abiotic components only and often neglect biotic interactions. However, in real life situations, species distribution focuses on the interaction between the two (Soberón & Peterson 2005; Soberón 2007). This has generated much debate over the appropriateness of projecting species range in space using SDM techniques only (Virkkala *et al*. 2013; Russo *et al*. 2014). Despite these practical difficulties, SDM's are still relevant in filling the knowledge gaps in species distribution, especially with regards to groups with limited information for conservation purposes (De Almeida *et al*. 2010; Bosso *et al*. 2013; Silva *et al*. 2014). This is even more important in an agro-natural landscape that is dominated by highly endemic vegetation, and subsequently classified as biodiversity hotspot with many undescribed insect groups (Rutherford *et al*. 2014; Mittermeier *et al*. 2004). According to Adu-Acheampong *et al*. (2016) there are species of *Euloryma* grasshoppers associated with only natural vegetation and others that are associated with both natural vegetation and with agriculture. If the *Euloryma* genus is to be protected, identifying the precise environmental conditions and areas with high probability of maintaining viable populations in the fynbos could assist conservation efforts in CFR. This is even more important to ensure their protection in the event of land transformation or climate change.

The main objective of this study was to determine the environmental variables that affect the distribution of *Euloryma* species (both associated with fynbos only and with both agriculture and fynbos) and to establish what the effects might be of agricultural expansion on these species. I first hypothesise that there are important environmental variables that influence the distribution of *Euloryma* in the CFR. I also hypothesise that the set of environmental variables that influence species associated with fynbos only are different for those species associated with both fynbos and agriculture. I further suggest that species that occur in fynbos only (and not in agricultural fields) are more sensitive to future land-use change than species which occur in both fynbos and agricultural fields. I go on to develop species distribution models for the flightless CFR endemic grasshopper species.

4.1 Methodology

4.1.1 Study area

The dominant natural vegetation in the CFR is a sclerophyllous shrubland referred to as fynbos (Esler *et al*. 2014; Mittermeier *et al*. 2004), with this biome also being classified as a global biodiversity hotspot (Cowling *et al*. 2003; Frazee *et al*. 2003). Although the CFR is known for its diverse and unique natural vegetation, it is also an area of intensive agricultural production (Rebelo *et al*. 2006; Rutherford *et al*. 2014). This agricultural production and other anthropogenic processes have led to the transformation of parts of the historic natural vegetation, especially in the case of lowland fynbos (Rutherford *et al*. 2014). There has been a reduction in biodiversity in agricultural production areas compared to natural areas in the CFR (Gaigher & Samways 2010; Kehinde & Samways 2012; Magoba & Samways 2011; Vrdoljak & Samways 2014, Adu-Acheampong *et al*. 2016).

The study area is located in the Western Cape in south-western part of South Africa. The area has many folded mountains with valleys, rivers and beaches. It has cold, wet winters and warm, dry summers. Thirty-two sampling sites were selected, comprising of 16 vineyards and 16 fynbos sites. The prioritised areas were Stellenbosch (33° 55' 56" S, 18° 51' 37" E), Somerset West (34° 04' 33" S, 18° 50' 36" E), Paardeberg (34° 27' 00" S, 19° 36' 00" E) and Grabouw (34° 09' 08" S, 19° 00' 13" E) (Figure **4.1**). This area was selected because a previous study on

Euloryma reported that they are endemic here and confined to certain specific geographic locations (Spearman 2013).

4.1.2 Description and sampling of *Euloryma* species

Euloryma is an endemic, flightless South African grasshopper genus (Acrididae, Hemiacridinae). The species are highly sensitive, narrow-range grasshoppers, small (12.62 mm, males) to medium in size (37.94 mm, females). There are two proposed species-groups of *Euloryma*. The Karoo group mostly found in the Succulent Karoo biome and the Fynbos group is often associated with fynbos biome. Currently, there are 11 known species inhabiting the Karoo and 10 known species in the Fynbos group (Spearman 2013). Only Fynbos-species group was used here as it was the only group present (Spearman 2013). Diet requirements of *Euloryma* genus can only be likened to that of their close relatives in Hemiacridinae subfamily (e.g. genus *Kassongia* that are specialist feeders) because of lack of information on *Euloryma* genus (Dirsh 1965; Grunshaw 1986).

Four species, *E. larsenorum*, *E. umoja*, *E. lapollai* and *E. ottei*, were selected, which fell into two sub-groups: 1) those associated with both agriculture and fynbos, and 2) those associated with fynbos only. In addition, the total number of occurrence of all species that were found associated with fynbos only and the total for those associated with both fynbos and vineyards were each modelled separately. Also the total number of all occurrence records of *Euloryma* genus was also modelled. Two of these species, *E. umoja* and *E. ottei*, were selected because of their association with both vineyards and fynbos, while *E. larsenorum* and *E. lapollai* were chosen to represent the group associated with fynbos only.

Although the geographic range of *Euloryma* is known (Spearman 2013), details of the ecological niches and environmental variables that affect the specific occurrences and persistence of each species on the landscape are still unknown. The relatively small geographic area of distribution, the low mobility, coupled with their probable high sensitivity to environmental change, increases the vulnerability of species of the genus. *E. lappolai* was first described at Klondyke, of Swaarmoedpas (near east of Warm Bokkeveldt north of Hexrivierberge) (S33°18.486', E19°35.375'), while *E. larsenorum* and *E. umoja* were first described from Somerset West and south Helderberg (S34°03.833, E018°52.453') and *E. ottei* is known from Tulbagh (west of Witsenberg) and Malmesbury (S33°19.800', E19°09.572).

Field sampling of grasshoppers was conducted on clear sunny days with no or low wind between 09:00 and 17:00. Within each sampling site, I laid out a 50 m x 50 m quadrat >30 m from the edges (Bieringer *et al*. 2013; Pryke & Samways 2012) to quantify grasshopper abundance and density (Bazelet & Samways 2011a, 2011b). Insect nets were used to trap and collect *Euloryma* species that were walking or hopping (Larson *et al*. 1999).

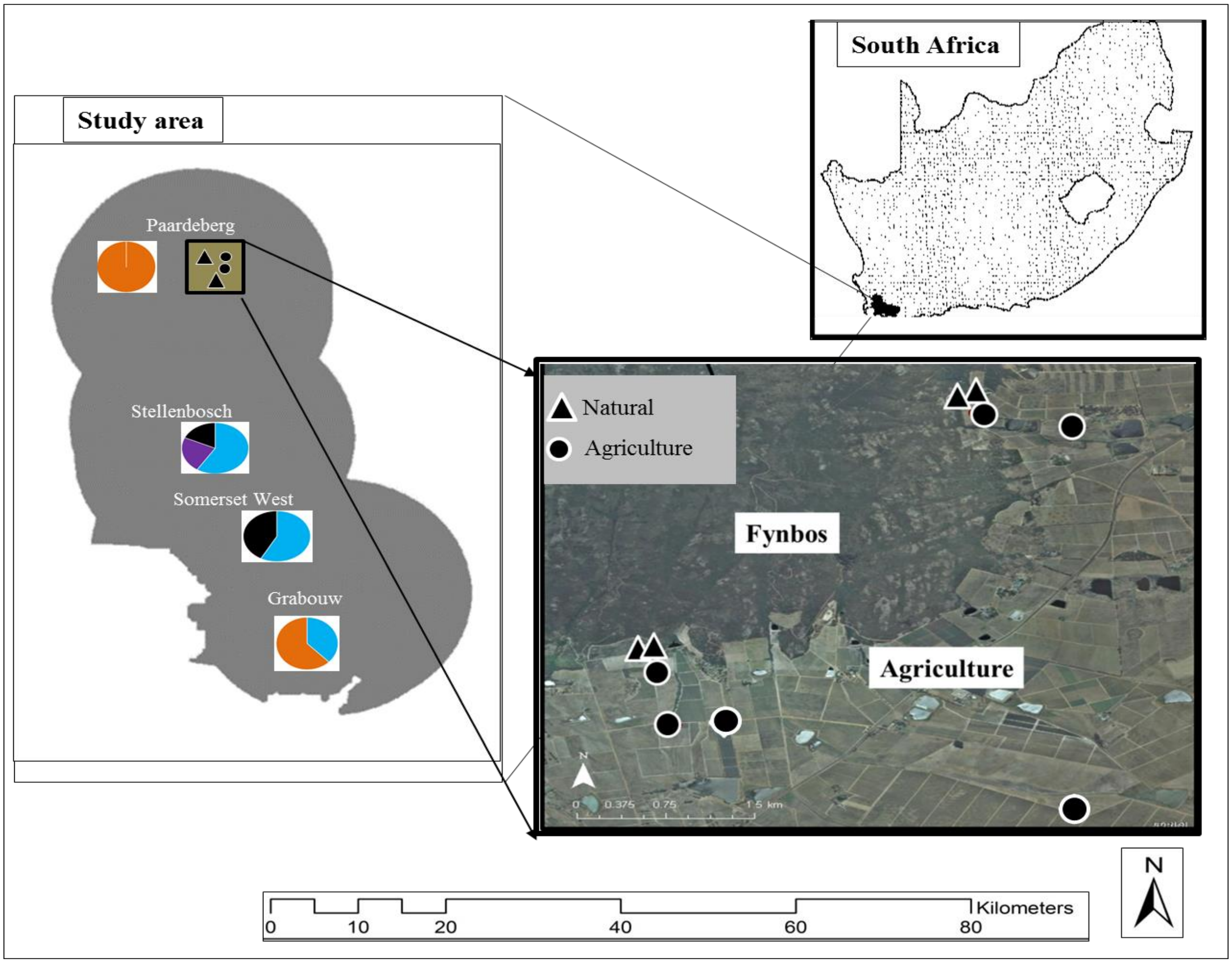

Figure 4.1 Study area for *Euloryma* species distribution showing the sampled fynbos and vineyard sites. It also shows which species were sampled at each location and their proportional occurrence in the samples in the Cape Floristic Region, South Africa. Colours of the pie charts represent *E. lapollai* (black), *E. umoja* (blue), *E larsenorum* (purple) and *E. ottei* (orange).

Each site was sampled for 30 min on four occasions by two collectors. The surveyed sites were chosen randomly within fynbos and vineyards based on geographic location (eight sites per geographic area). Collected specimens were stored in a -40 degree deep freezer, and later identified using Spearman (2013). During the sampling process, geographic position system (GPS) coordinates of these sampling sites were also recorded for the modelling process. These data were used for the ecological niche modelling of the four species, the two *Euloryma* groups (those associated with fynbos only and fynbos and vineyards), and the genus as a whole.

4.1.3 Selection of environmental variables

Sets of environmental raster layers at 90 m^2 grid resolution, and a shapefile constructed from 1 km^2 grid cell sizes for the Western Cape and South Africa, respectively, were acquired from Van Niekerk & Joubert (2011) and Development of a Soil and Terrain database for Southern Africa (SOTERSAF) website (http://www.isric.org/projects/soter-southern-africa-sotersaf). The 90 m^2 grid raster layers were: altitudes, mean annual minimum and maximum temperatures, mean annual rainfall, mean annual relative humidity, and vegetation cover. The 1 km^2 vector (shapefile) layer, acquired from SOTERSAF, was for soil types. The selection of these sets of layers was based on the physiological requirements and/or limitations of grasshoppers, and especially *Euloryma* spp., in the environment. The geographic points and extent of the study sites was clipped and cut out from all layers and converted into an appropriate file type for easy input into the model algorithm (Young *et al*. 2011). All selected variables were used for the initial training, and after the most important variables were selected and used for the actual modelling process.

4.1.4 Algorithm selection and habitat suitability modelling

The most desirable attribute for this study was precision, because according to Spearman (2013) *Euloryma* spp. occur in specific, limited places and in small numbers. Such a task required an algorithm that prioritizes on precision. To explain further, high precision algorithms are referred to as “vault” models by their lack of transparency in modelling and interpretability (Rangel & Loyola 2012). Alternative modelling algorithms, classified under “fish bowls” and “turbines” are known for their high to medium transparency, high to low generality and low to medium precision (Franklin 2010; Rangel & Loyola 2012). Maximum Entropy (MaxEnt, Phillips *et al*. 2006; Phillips & Dudík 2008) which falls under "vault models", and with particularly easy to fit settings, was selected for modelling the distribution of *Euloryma* because it has the potential of achieving high precision (Elith *et al*. 2006) which is the desired attributed being sought for the characteristic distribution of *Euloryma* spp. across the landscape. In short, by selecting MaxEnt, the easy interpretability and generalisation features were sacrificed for high precision (Jiménez-Valverde *et al*. 2008). Another reason for this choice comes from the few known occurrence records for *Euloryma* spp. in my study area. Under such low occurrence records, MaxEnt has a high probability of producing more reliable results (Hernandez *et al*. 2006; Phillips & Dudík 2008; Pearson *et al*. 2007). This is because Maximum Entropy employs generative means compared with other algorithms such as Generalised Linear Models that use more discriminative means, since it is already known that generative methods perform better under situations with small training data (Ng & Jordan 2001).

Maximum Entropy models were constructed in MaxEnt 3.3.3.k (Phillips *et al*. 2006; Phillips & Dudík 2008) under all default settings (Anderson & Gonzalez 2011; Merow *et al*. 2014). This allowed for the processing of both categorical and continuous variables in the sets of environmental layers used for the modelling (Phillips *et al*. 2006). There were background and pseudo-absence data generated throughout the study area. Before model development, Spearman's Rank-Order Correlation test was conducted in Statistica 13.0 (Hill & Lewicki 2007; StatSoft 2013) to check for multicollinearity of the selected environmental variables. Under such circumstances and also the fact that the selected environmental variables consisted of both categorical and continuous values, Spearman's Rank Order Correlation is deemed appropriate because it is a non-parametric test. This was necessary to check for overfitting of models as a result of environmental variables' association that can create uncertainty in the interpretation of the results (Phillips *et al*. 2006; de Oliveira *et al*. 2014; Merow *et al*. 2014; Varela *et al*. 2014). Values >0.7 for Spearman's Rank Order Correlation (r) between any two variables suggests collinearity and hence they may be excluded from the modelling process (Dormann *et al*. 2013). Nevertheless, the ecological relevance of variables to the organism or phenomenon under study is given prominence over collinearity and hence can still be included in modelling processes (Dormann *et al*. 2013). Jackknife tests were employed to pre-select the most significant variables for the actual modelling after the initial training of the data. Because of the few occurrences that characterise *Euloryma* species distribution, all records for all species were put together as a group (*Euloryma* genus), all those associated with fynbos only, and those that occurred in both fynbos and vineyards were also modelled separately. In previous studies elsewhere, occurrences and few additions for poorly sampled and rare species proved important for model performance (De Almeida *et al*. 2010; Silva *et al*. 2013). Because of the very few occurrences of *Euloryma* spp. in general, all species random records were used for training and also for validation of models in 100 replicated runs. Because of the very small geographic ranges of *Euloryma* spp. and also this study being the first for this group of grasshoppers, there was more emphasis on places where they actually or could potentially occur, with less concern over autocorrelation of sampling sites.

Area under the receiver operating characteristic curve (AUC) was used to validate as well as compare results between models. The AUC statistic evaluates the ability of models to differentiate between absences and presences with values >0.7 being good, <0.5 being poor and

0.5 showing random predictions (Pearce & Ferrier 2000; Elith *et al*. 2006; Newbold 2010). Furthermore, a comparison of occurrences and distribution of *Euloryma* spp. was made between this study and Spearman (2013).

4.2 Results

At the beginning of this study, the aim was to develop models for the four *Euloryma* spp. *E. umoja*, *E. ottei*, *E. lapollai* and *E. larsenorum* from data that was collected from field surveys. Before the actual modelling process, results from Spearman's Rank-Order Correlation test showed that minimum temperature, maximum temperature, relative humidity and mean annual rainfall variables were highly correlated with each other. However, these variables were still included in the initial modelling process due to their high physiological importance to the life history traits of grasshoppers. Table **4.1** is a summary of results of the Spearman’s-Order Correlations tests.

Table 4.1 Spearman’s Rank-Order Correlation test for environmental variables in the Cape Floristic Region, of South Africa (P<0.05)

	Alt.	Max. Temp	Min. Temp.	Vg. Cover	Ann. Rain	Rel. Humidity	Soil types
Alt.	1.00						
Max. Temp	-0.30	1.00					
Min. Temp	-0.66	0.74*	1.00				
Vg. Cover	-0.27	-0.43	-0.19	1.00			
Ann. Rain	0.31	-0.91*	-0.82*	0.41	1.00		
Rel. Humidity.	-0.38	0.88*	0.77*	-0.40	-0.80*	1.00	
Soil types	0.10	-0.72*	-0.37	0.46	0.55	-0.58	1.00

*=significant correlation

The initial search for environmental variables that limits the distribution of these species showed that, vegetation cover, soil type and altitude are the most important limiting factors for the distribution of *Euloryma*. This was similar for all selected species and groupings. The temperature variables, rainfall and relative humidity were rejected after the jack-knife tests because they contributed close to nothing to model development of each individual species, the various groupings based on land-use associations, as well as the *Euloryma* genus as a whole. Figure **4.2** shows the initial contributions (percent and permutation) of each of the variables to the model building process.

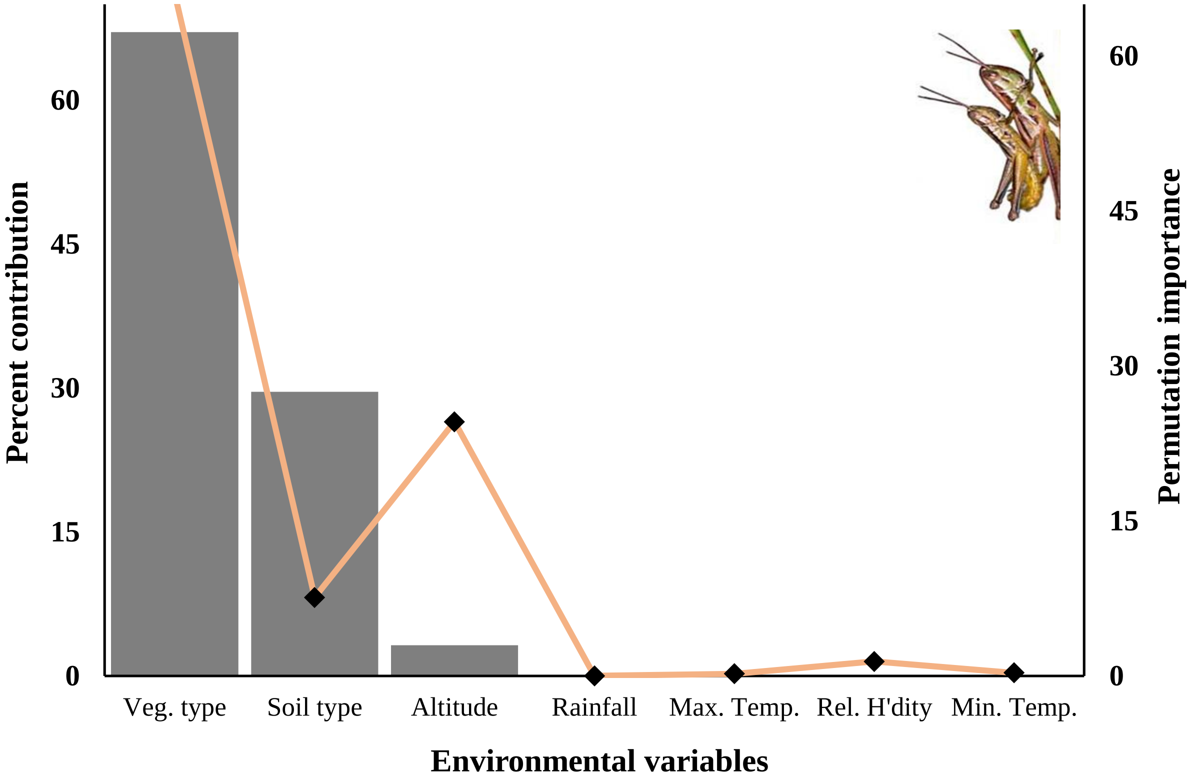

Figure 4.2 Initial percent (bar chart) and permutation contributions (line chart) of environmental variables of each individual as well as all species (same results for all groups) of *Euloryma* in the Cape Floristic Region, of South Africa.

A single model was developed for each of the selected species, the genus *Euloryma* in general, species associated with both vineyards and fynbos, and for species associated with fynbos only (Figures **4.3** and **4.4**). Vegetation type, altitude and soil types emerged as the most important variables contributing the most in explaining species distribution. This result was same for all individual species and groups. Temperature, rainfall and relative humidity were discarded because of their small contribution to the actual models for all species and groups. The environmental variables that influenced species that were associated with both agriculture and fynbos sites were not different from variables that influenced species that were associated with fynbos only, as well as the *Euloryma* genus as a whole.

Maps generated from the models show that all *Euloryma* spp. have very small geographic ranges Also, species that are associated with both agriculture and fynbos (*E. ottei*, *E. umoja* and a combination of these two) differed only little in distribution compared to those species that are associated with fynbos only (*E. larsenorum* and *E. lapollai* and their combination) The map also shows that there are areas outside the sampling sites with the probability of *Euloryma* occurrences in the CFR. Results of the Area under the receiver operating characteristic curve (AUC) values from MaxEnt models developed for this study was approximately 0.97 for all species indicating very good performances in terms of predicting the distribution of *Euloryma* spp. in the CFR.

4.3 Discussion

I show the relative importance of certain environmental parameters as key predictors of suitable habitats for the occurrence of an endemic grasshopper group in a biodiversity hotspot which is also an important agricultural production area in the CFR. I also show how a conceptualised idea can be used to evaluate a possible future event, using species distribution modelling techniques for ecology. The evaluation of the species distribution models here also enabled easy assessment of implications of a possible expansion of agriculture into fynbos on an endemic insect group in the CFR.

I found the most important environmental variables that determine the occurrence of *Euloryma* species groups to be vegetation types, soil characteristics and altitude. Grasshopper species are known to be strongly associated with type and structure of vegetation (Kruess & Tscharntke 2002; de Wysiecki *et al*. 2011). The majority prefer vegetation with open spaces, with grassy to shrub-like forms that allow enough sunlight penetration. Importantly, specialist species can be confined to a small geographic location because of their feeding behaviour which is strictly associated with their specific host plants (Clavel *et al*. 2011), which contributes to limiting *Euloryma* spp. to small areas of the CFR and Karoo, in case their host plants are also located in a small geographic location. *Euloryma* spp. are suspected to be specialist feeders (based on the feeding habits of close relatives e.g. genus *Kassongia*, Dirsh 1965; Grunshaw 1986) and also only weakly mobile. Due to the combination of these life history traits, they have become more vulnerable to increasing threats from habitat change, especially when it affects vegetation cover. The results of the MaxEnt models confirm a previous study in the CFR which reported that grasshoppers are affected by land-uses (Kemp *et al.* 2002; Torrusio *et al*. 2002; Adu-Acheampong *et al*. 2016) because, by extension, land-use can be a proxy measure of vegetation cover.

Soil properties can directly affect the persistence of grasshoppers on a landscape, with soil moisture, temperature, texture etc. affecting the choice of breeding sites (Uvarov 1966; Chapman & Joern 1990; Schell & Lockwood 1997). Indirectly, soil conditions can also limit a grasshopper's development and persistence on a landscape via their effect on the type of plants that can grow in a particular geographic location. This situation can be especially pronounced for specialist feeders where their host plants can only grow in particular type of soil which are confined to a specific geographic location. This finding agrees with a study conducted in Germany where sand dune type is reported to be a key determinant of habitats for grasshoppers (Schirmel *et al*. 2010). At this stage, it is not clear whether soil conditions in the Western Cape affect the distribution of *Euloryma* directly through breeding sites or indirectly via host plants, but likely to be both.

Because grasshoppers are ectothermic and mesophilic animals, their physiology is controlled directly by their surrounding temperature conditions (Hunter-Jones 1964; Uvarov 1966; Chapman & Joern 1990; Schell & Lockwood 1997), but temperature variables here did not contribute significantly to the models, owing to lack of variability among the small areas to which the grasshoppers were naturally confined. Relative humidity and rainfall variables also did not contribute to model development, for similar reasons as temperature (i.e. lack of variability in a small geographic location of occurrence). Altitude is also a known factor which affects grasshopper distribution and hence its significant contribution to the model building process. This is because the relatively low temperatures make habitats less conducive for grasshoppers at

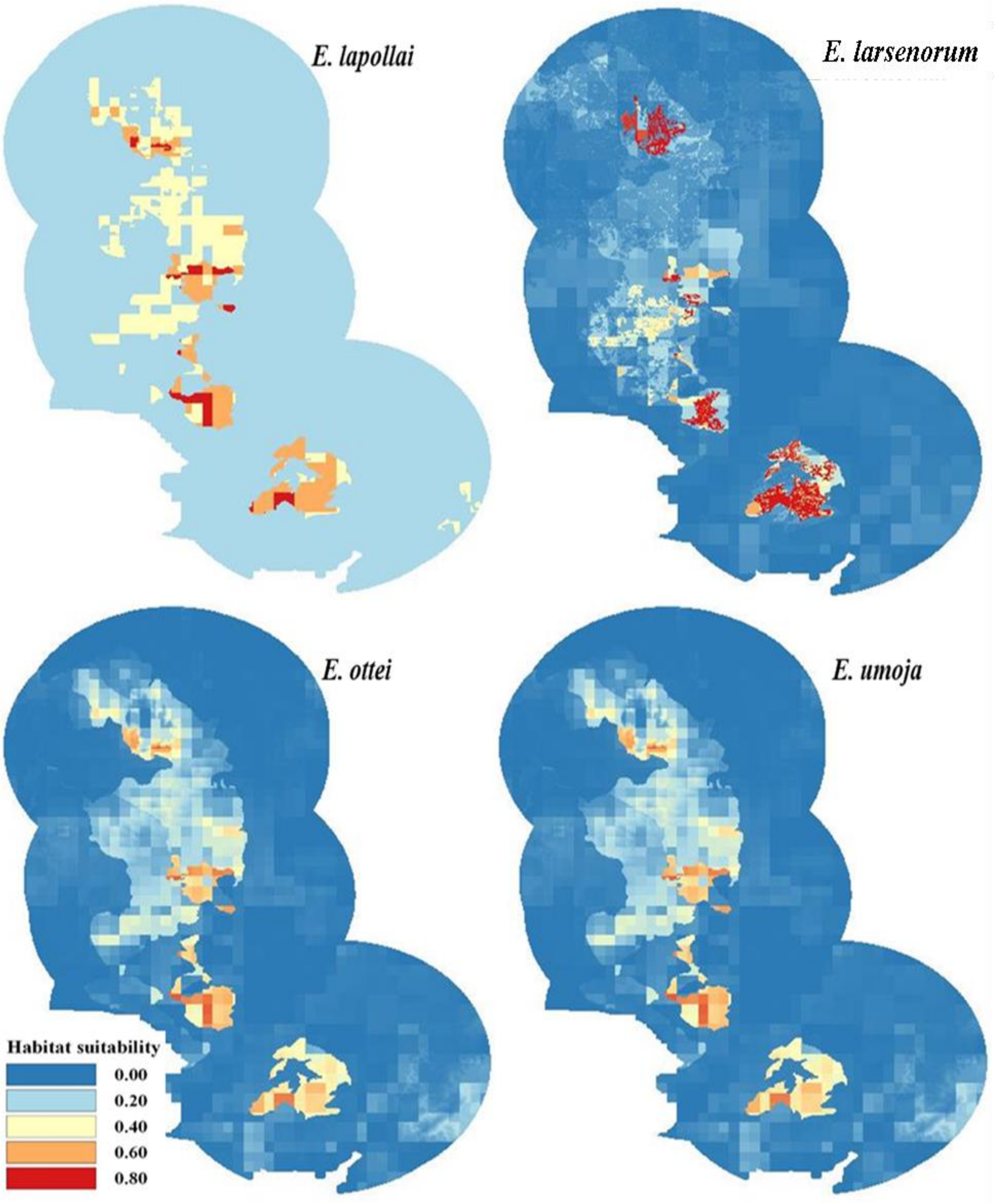

Figure 4.3 Distribution of *Euloryma* species, *E. umoja*, and *E. ottei* (both fynbos and vineyards) and *E. larsenorum* and *E. lapollai* (fynbos only) in the Cape Floristic Region of South Africa. Colour range shows less likelihood of occurrences (blue) to very high probability of occurrence (red).

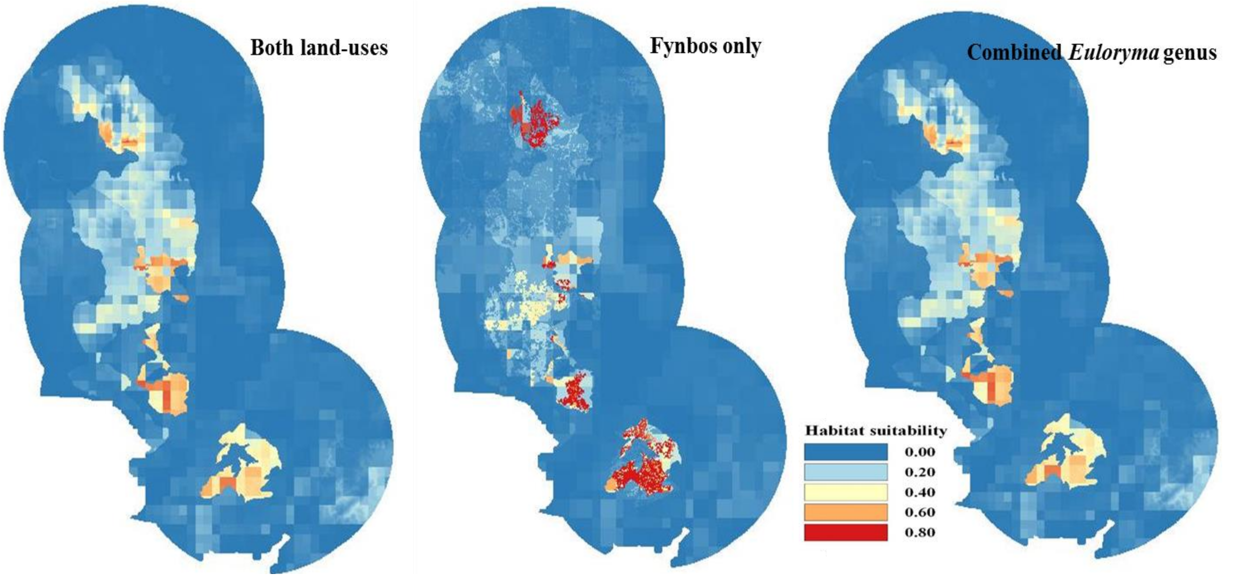

Figure 4.4 Maps of distribution of the general *Euloryma* genus, species associated with both fynbos and vineyards (both land-uses) and those associated with (fynbos only) in the Cape Floristic Region of South Africa. Colour range shows less likelihood of occurrences (blue) to very high probability of occurrence (red).

high altitudes and hence they are less likely to inhabit high altitudes (Wettstein & Schmid 1999; Gebeyehu & Samways 2006).

Maps generated from the study area show that for the categories all species *E. larsenorum*, *E. lapollai, E. umoja, E. ottei,* total occurrence in both fynbos and vineyards together, total sampled in fynbos only, and the *Euloryma* occurrence in general, all show that there is a very narrow geographic range in the CFR. Each individual species has a very small actual and predicted ecological niche that can enhance their persistence on the landscape (Figures **4.3** and **4.4**). These modelled occurrences agree with findings from previous work conducted on *Euloryma* genus, which reported that *E. larsenorum* and *E. umoja* occur in Somerset West (Spearman 2013). This further validates the accuracy or correctness of models produced from this study. In addition, models produced through occurrence records also show that these species (*E. larsenorum* and *E.*

umoja) are also present in Stellenbosch, with high probability of occurrence at Grabouw and Malmesbury but with moderate likelihood of occurrence at Paardeberg. The study also confirms the geographical location of *E. ottei* to be near Malmesbury (Paardebeg) but also have suitable habitats at both Somerset West, and Stellenbosch. Grabouw and Somerset West are predicted to have highly suitable habitats for each individual species and for all groups of species. Although the previous study mapped the distribution of *Euloryma* and in particular their associations based on certain geographic locations, it did not give reasons why they are specifically assigned to those locations.

Further interpretation of maps generated from all of the species show that the fundamental niche for each *Euloryma* species and groups exceeds their realised niches. This could be as a result of geographic restriction imposed on their movement and dispersal through barriers e.g. mountains historically, and roads today etc., and their low dispersal capabilities. Biotic interactions among organisms e.g. competition for resources, predation and even human transformation of the landscape likely play a role in them occupying small habitats in their fundamental niche (Phillips *et al*. 2006; Pearson 2010). Interestingly, the distribution of *E. lapollai* shows that all of the modelled geographic space is at least 20% suitable for their persistence on the landscape. This shows that although *E. lapollai* is only associated with fynbos and hence highly vulnerable to land transformation, it also has a higher rate of expansion and subsequent establishment in new suitable areas under possible future planned introduction programs.

From the relative contributions of each variable to the model development, it can be argued that expanding agriculture into fynbos is likely to have a negative impact on sensitive species that are associated with fynbos only (*E. lapollai* and *E. larsenorum*). This is because agricultural expansion into fynbos will cause changes in the vegetation cover and possibly destroy their habitats and host plants. *Euloryma* spp., being suspected to be specialists, means a possible reduction of food sources and area of occupancy. A change in vegetation which has been reported to also affect grasshopper persistence on the landscape (Kuppler *et al*. 2015, Adu-Acheampong *et al*. 2016) will likely accelerate their decline, especially in view of their relative immobility. This contrasts with highly mobile species that can change their area of occupancy or shift range easily, and often diet (Hansson *et al*. 2014).

E. umoja and *E. ottei* occur in both fynbos and vineyards, their occurrences of which can be translated into higher tolerance of land transformation and specifically from relatively benign local viticultural practices. They occupy larger geographic ranges and heterogeneous habitats compared to *E. larsenorum* and *E. lapollai* although the models predict similar ranges and hence are unlikely to have any changes in population dynamics as evidenced from their comparatively low sensitivity to land-use change. Expanding agriculture into fynbos might not affect the dynamics of *E. umoja* and *E. ottei* since they can equally dwell in both agriculture and Fynbos.

4.3.1 Conclusions and conservation implications

The most important environmental factors which accounted most for *Euloryma* species distribution patterns in the CFR were vegetation and soil characteristics, with altitude a secondary contributor. The distribution models showed that *Euloryma* species have very narrow ranges of predicted habitat suitability. My results suggest that *E. larsenorum* and *E. lapollai* should be a higher conservation priority than, say, *E. umoja* and *E. ottei*, because of their sensitivity to land-use change and hence are more vulnerable to habitat transformation.

Cultivating the host plant (requiring further study) of *E. larsenorum* and *E. lapollai* at the farm level as cover crops has the potential of attracting them into the farm environment to promote farm biodiversity and reduce the risk of their extinction. But at this stage there are no informations on the host plants of *Euloryma* genus and hence further studies e.g. feeding preferences are recommended to be able to find out their prefered host plants. These species can possibly also be used as surrogate species for designing conservation schemes for species with similar life history traits in the CFR. *Euloryma* species groups can also be used as bioindicators to measure type of soil and or most importantly its quality in the CFR. Further studies are required to ascertain if soil conditions affect *Euloryma* directly through breeding sites or indirectly through host plant regulation.

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CHAPTER 5: Grasshopper assemblage shifts relative to selected traits in the Cape Floristic Region biodiversity hotspot

Abstract

Landscape change is a phenomenon caused by both anthropogenic and natural factors and often results in change in the constituent biodiversity. One critical impact of landscape change is taxonomic and functional modification of biological communities, with specialist species usually being disfavoured and generalists less so, and in some cases even being given new opportunities. Proportions of specialist vs. generalist (feeding traits) species can reflect level of change in biotic communities. Another measure, proportions of widespread vs. localised (distributional traits) species, can also indicate impact of landscape change on biodiversity. Relating these two traits (as often anecdotally observed to be positively correlated) will help increase understanding on the impact of landscape change on structure of biological communities. I investigated grasshopper species assemblage composition on three land-uses across an agro-natural landscape of CFR. The study documentmented species' level of occupancy and abundances in relation to their life history traits in order to assess the amount of change occurring on the landscape in the CFR. My results show that very few species, mostly from Acrididae, dominated the landscape. They also show that the species that dominated the transformed landscape were generalist. There was also a high correlation between generalists, high to medium mobility and widespread species on one hand, and specialists, low in mobility and localised on the another hand. There is a need for concerted efforts to protect groups that occur in low abundance, especially the many endemic specialist species, to reduce possible future biotic erosion and homogenization in this hotspot.

5.1 Introduction

Landscape change is a phenomenon often associated with change in biodiversity, with altered biotic roles and forms of ecosystems that in turn affect human livelihood (Chapin *et al*. 2000; Fisher *et al*. 2009; Cardinale *et al*. 2012). Anthropogenic landscape change usually means urbanisation and agricultural production (Forman 1995; Pickett & Cadenasso 1995; Lambin *et al*. 2003), with climate change and invasive alien species also being drivers of landscape change (Vitousek *et al.* 1997; Anderson *et al*. 2004). Agriculture and urbanisation often lead to fragmentation of previously continuous landscapes, with negative consequences for resident biota (Foley *et al*. 2005; Ewers & Didham 2006; Lindenmayer & Fischer 2013). Infrastructural development, farming activities and other anthropogenic transformation of the landscape often deprives species of key life resources and habitats for their continuous persistence (Ricketts & Imhoff 2003; Kim *et al.* 2006; Lindenmayer & Fischer 2013). This either drives them towards extinction, forces them to shift geographic range, or to adapt to the new environment (Elmhagen *et al*. 2015). Climate change affects landscape and biota by altering environmental conditions that dictate the type of species that can inhabit and or persist in the area in question (Dale *et al*. 2001). In addition, invasive alien species alter the dynamics of resource availability by often outcompeting native ones (Levine *et al.* 2003; Gurnell *et al*. 2004). Furthermore, climate change affects the synchrony of biological features such as life cycles of invertebrates especially insects and appearance of leaves and inflorescences of their host plants (Dixon *et al*. 2009; Traill *et al*. 2010). Such structural changes on the landscape often affect species adversely, especially short distant migrants (Kullberg *et al*. 2015).

There is a direct correlation between landscape structures and or design and abundance of several taxa (McGarigal & McComb 1995; Van Buskirk 2005; Pardini 2005). Of key importance to these relationships are the different elements and the scale and geographic range under which they occur (Gaston & Lawton 1990; Kunin 1998; Schaffers *et al*. 2008). This is because there are many differences in species reactions to these different elements and the extent to which they occur in the surrounding landscape (Hunter 2002; Jeanneret *et al*. 2003). These reactions are often dictated by the functional traits and mobility characteristics of the species involved. In general, insects are among the most impacted animals with anthropogenic landscape change (Schaffers *et al*. 2008). Impacts such as habitat loss and degradation can cause reduction in local species richness, especially of specialists in comparison with generalists, with increased extinction risks for some of these specialists (Clavel *et al*. 2011).

According to evolutionary theory, diet specialisation develops over long periods of stable environmental conditions. However, generalist species traits develop as survival mechanisms against a more disturbed and or heterogeneous environment over a long period of time (Bernays & Graham 1988; Futuyma & Moreno 1988; Kassen 2002, Scheiner 2002; Julliard *et al*. 2006). Species often described as widespread, are those that are also mostly generalist. This is also because they are successful immigrants. Due to their generalist approach towards feeding, they have a relatively high establishment rate under a novel or introduced environment. Compared to generalists, specialist species are often geographically localised with a very low rate of establishment in novel environments. In the absence of their preferred host plants they will not survive due to their non-flexibility in choosing diets (Fisher & Owens 2004; Colles *et al*. 2009). Widespread generalists establishing in novel environments often have much genetic variability and high levels of adaptation, going hand in hand with high abundance and high survival rates, with the reverse being the case for specialist, localised species (Kattan 1992; Blackburn & Duncan 2001; Duncan *et al.* 2003; Zayed *et al*. 2005).

Effect of landscape change on insects and other terrestrial invertebrates is often pronounced compared to other taxa as they are the largest group of terrestrial animals and often have relatively high densities per unit area. A small change in habitat conditions often corresponds to high impact on their relative abundance (Hunter 2002; Tscharntke & Brandl 2004; Klein *et al*. 2007). Landscape change also creates isolated patches that restrict gene flow and reduce species persistence (van Strien *et al.* 2014), especially insects with low mobility (Kullberg *et al*. 2015). Pollution from agricultural production, urbanisation and other land transforming or landscape change drivers can further increase stress on insects, often affecting host plants, soil conditions, and water quality (Mohamed *et al*. 2009; Edokpayi *et al*. 2010; Conway & Pretty 2013). Under such altered conditions insects may be forced to shift their range, die out or adapt (Elmhagen *et al*. 2015). Species of dragonflies and worms, for example, require specific chemical composition of water and soil conditions for breeding and feeding, respectively (Watson *et al.* 1982; Lagadic & Caquet 1998; Lee Foote & Rice Hornung 2005). Another sensitive insect group that is gaining recognition in use for bioindication of landscape change are grasshoppers (Gebeyehu & Samways 2002, 2003, 2006a and b; Jonas & Joern 2007; Yoshioka *et al*. 2010; Bazelet & Samways 2011a, b and c, 2014; Branson 2010; Hill 2012; Borchard *et al*. 2013; Fartmann *et al*. 2012; Crous *et al*. 2013; Helbing *et al*. 2014; Kuppler *et al*. 2015; Hao *et al*. 2015; Adu-Acheampong *et al*. 2016; Joubert *et al*. 2016).

Grasshoppers are important insect herbivore assemblages on the landscape, especially grasslands (Gillon 1983; Cigliano *et al*. 2000; Batáry *et al*. 2007; Schaffers *et al*. 2008). Their feeding behaviour in combination with some other features (e.g. ease of sampling, and high sensitivity to environmental change), coupled with their often high abundance makes them good bioindicators of landscape change (Samways & Moore 1991; Samways & Kreuzinger 2001; Gebeyehu & Samways 2002; Joern 2005; Yoshioka *et al*. 2010; Fartmann *et al*. 2012; Helbing *et al*. 2014; Hao *et al*. 2015). Their abundance and distribution (which is often dictated by differences in vegetation patches) are used to measure landscape change (Hao *et al*. 2015), land use type and topography (Gebeyehu & Samways 2006a and b; Hill 2012; Crous *et al*. 2013; Kuppler *et al*. 2015; Adu-Acheampong *et al*. 2016), fire, and grazing management (Gebeyehu & Samways 2003; Jonas & Joern 2007; Branson 2011; Joubert *et al*. 2016), effect of invasive alien plants on native biota (Yoshioka *et al*. 2010); importance of restoration and design of land management for conservation purposes (Gebeyehu & Samways 2002, 2003; Bazelet & Samways 2011a and b), habitat quality assessment (Bazelet & Samways 2011c, 2012, 2014), and for prioritisation of conservation areas (Matenaar *et al*. 2015).

An important consideration when choosing grasshopper species for bioindication of landscape change is their life history traits. Grasshopper species life history traits that can be used for well-informed conservation decisions are mobility, geographical distribution, trophic level, and habitat preferences. A species' ability to move in between habitat patches greatly influences their response to changes in the landscape. Species with high mobility (e.g. winged and flighted) are able to move in between different patches easily in response to changes in their habitats compared to those of low mobility (e.g. wingless and flighless) (Ewers & Didham 2006; Fischer

& Lindenmayer 2007). Grasshoppers also respond differently according to whether they are specialist or generalist feeders. Specialist feeders and or habitat specialists are more vulnerable to landscape change compared to generalist feeders. Furthermore, habitat specialists risk local extinction when their host plants and/or habitats are modified or destroyed as they are not flexible to shift host plants or habitats. Generalists, in contrast, are more flexible in shifting host plants and habitats and hence are more tolerant of landscape change (Hunter 2002; Bolwig *et al*. 2006; Laaksonen *et al*. 2008; Hinsley *et al.* 2009).

In terms of species traits, grasshoppers can be categorised into two groups: widespread and localised species. Widespread species occur over large geographical areas and occur mostly in a variety of habitats because of their flexibility for adapting to many local environments. In contrast, localised species occur at specific locations and often in restricted or particular habitats along with low ability to survive different environments. However, there is little evidence that these relatinships hold for grasshoppers, especially in Africa (Bazelet & Samways 2012).

There are few studies of grasshoppers in the Cape Floristic Region (CFR), with those in natural habitats being investigated by Spearman (2013) and Maternaar *et al*. (2015), and relative to land use by Adu-Acheampong *et al*. (2016), and along riparian corridors by (Pronk *et al*. 2016). However, there is a need to improve our understanding of the relationship between grasshopper species geographical distribution, and type of mobility in relation to the number of habitats that species occupy, in order to be able to access the level of change in the landscape. In response, I investigate here the number of sites occupied by each individual species in both natural and cultivated lands (fynbos vs agriculture). I then relate grasshopper species' known distribution or type of mobility to their level of occurrence or occupancy on all of the study sites across a 90 km agro natural landscape in the CFR. Specifically, I aim to find out which grasshopper assemblages are most abundant at sampling sites under different land uses. I then relate the number and type of sites occupied by grasshoppers to their mobility type (high, low or medium) and their known distribution (widespread or localised). Finally, I draw conclusions in the grasshopper assemblage relative to degradation of the landscape. I hypothesise that widespread and generalist grasshopper species are abundant and/or occupy more sampling sites and land uses compared to localised and specialists ones. This high abundance and/or occupancy of generalist and widespread species, is assumed to be as a result of occupying diverse habitats and sites that include both natural and transformed sites.

5.2 Methods

5.2.1 Study areas and sampling sites

Data were collected from 46 sites from four areas: Somerset West, Grabouw, Stellenbosch and Paardeberg (14-16 sites each), and each comprised of three components: natural Fynbos vegetation, vineyards, and apple fruit orchards (Figure **5.1**). All sites were >23 km apart, which can be biogeographically significant in this area of rugged topography and narrow endemism (Vrdoljak & Samways 2014).

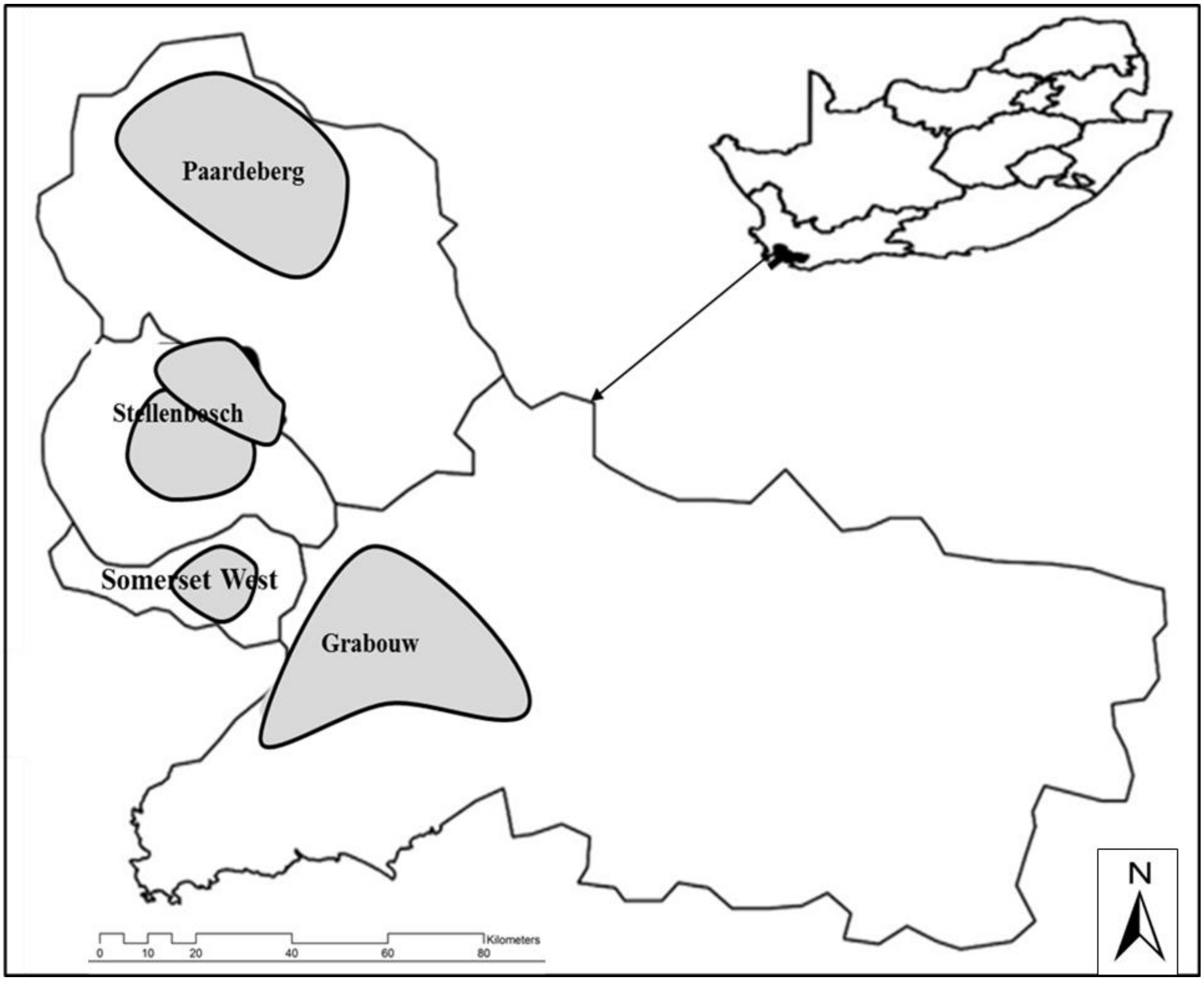

Figure 5.1 Study area in the Cape Floristic Region with the four sampling areas indicated in grey.

5.2.2 Grasshopper sampling

Grasshopper sampling was conducted between 09:00 and 17:00 on sunny days with no or little cloud cover and wind. I laid a 50x50 m sampling quadrat on each sampling plot at least 30 m from the edges (Bieringer *et al*. 2013). Two persons sampled each site for 30 min on four occasions (a total of four person hours per site). Insect nets were used to capture grasshoppers after initial flushing out of their swards (Bazelet & Samways 2011a and b; Larson *et al*. 1999). Specimens were then transferred into a zip lock bag and transported into a deep freezer for later identification using Dirsh (1965), Eades *et al*. (2015), Jago (1994), Johnsen (1984), Johnsen (1991) and Spearman (2013).

Geographic distribution and the degree of mobility traits of grasshoppers were selected from all available articles, and books on life history traits of grasshoppers (Dirsh 1965; Johnsen 1984, 1991, Henle *et al*. 2004; Bazelet & Samways 2011a; Iverson *et al*. 2011; Matenaar *et al*. 2016). Categorisation of grasshopper distributions into widespread or localised was based on the extent of occurrence worldwide and in South Africa. Species that are known to occur worldwide are categorised as widespread, those known to occur only in South Africa are termed localised. Grasshoppers belonging to subfamilies, Acridinae, and Oedipodinae are strong fliers and hence arbitrarily considered high in mobility and those belonging to Eyprepocnemidinae consists of medium fliers and hence are arbitrarily considered to be medium in mobility (Ritchie 1981). On the other hand, apterous to brachypterous sedentary grasshopper species such as lentulids and hemiacridines were categorised as the low mobility group.

5.2.3 Statistical analyses

Rank abundance curves were constructed in Statistica 13.0 (Hill & Lewicki 2007; StatSoft 2013) for the total grasshopper abundance as well as their abundances relative to the various land-uses. Four natural or biological cut offs of species abundances were identified: (1) species with >100 individuals (highly abundant species, Hh), (2) species with 50-90 individuals (medium abundance, Md), (3) species with 15-40 individuals (low in abundance, Lw), and (4) species with <15 (very low or rare (Vl/Rr).

A histogram of (log abundance + 1) was constructed in Excel (Fishel 2014) involving all species so as to minimise the visual effect of the large disparities in these biological classifications. To be able to relate species distribution type and mobility with the total number of sites that species occupied, a table was constructed followed by cluster analysis from Bray-Curtis dissimilarity distance in Statistica 13.0 (Hill & Lewicki 2007; StatSoft 2013). The Bray-Curtis dissimilarity cluster analysis was done from a combination of species abundance in fynbos, vineyard, orchard, their mobility and the number of sites that they occupied (Kindt &Coe 2005; Magurran 2013). Bray-Curtis cluster analysis was used in view of its sensitivity to differences in abundance and ability to distinguish between different species, study sites and land-uses from differences in occurrences (Kindt & Coe 2005). Species with similar abundances in all of the various land-uses, type of mobility and number of occurrences in all of the study sites have a very low dissimilarity index, often close to zero, and those with values closer to 1 are highly dissimilar. Generalized linear mixed model (GLMM) fit by maximum likelihood in R-studio version 3.2.5 was used to compare total number of occupied sites and abundance of grasshoppers (response variable) by widespread vs. localised species and high vs. medium or low, mobile species from all study sites. Poisson distribution was used because the response variable was discrete positive count data. Also, to account for the underlying spatial structure in the experimental design, GLMM was used. Spearman’s Rank-Order Correlation test was used to quantify the relations between grasshopper abundance and number of sites occupied by each species (RStudio 2015). Also to account for the underlying spatial structure in the experimental design, GLMM was used. Spearman’s Rank-Order Correlation tests were used to quantify the relations between grasshopper abundance and number of sites occupied by each species (RStudio 2015).

5.3 Results

The species rank abundance curve constructed for total individuals sampled showed that species richness was high (S=37) relative to total abundance (N= 2400) of the sample. Evenness was low, with only two species *A. dorsalis* and *E. calceata* making up 60% of the total sample. These same two species constituted 77% of total abundance in orchards, 67% in vineyards and 40% in fynbos. A histogram of (log+1) of species abundance showed that species of Acrididae dominated all samples, and classified as high to medium in abundance. All other species in other groups were classified as rare to medium in abundance. Of particular importance are the wingless species, with a majority falling into the very low or rare species group. Table **5.1** shows that only widespread species occupied >40% (19-46 sites) of all sites.

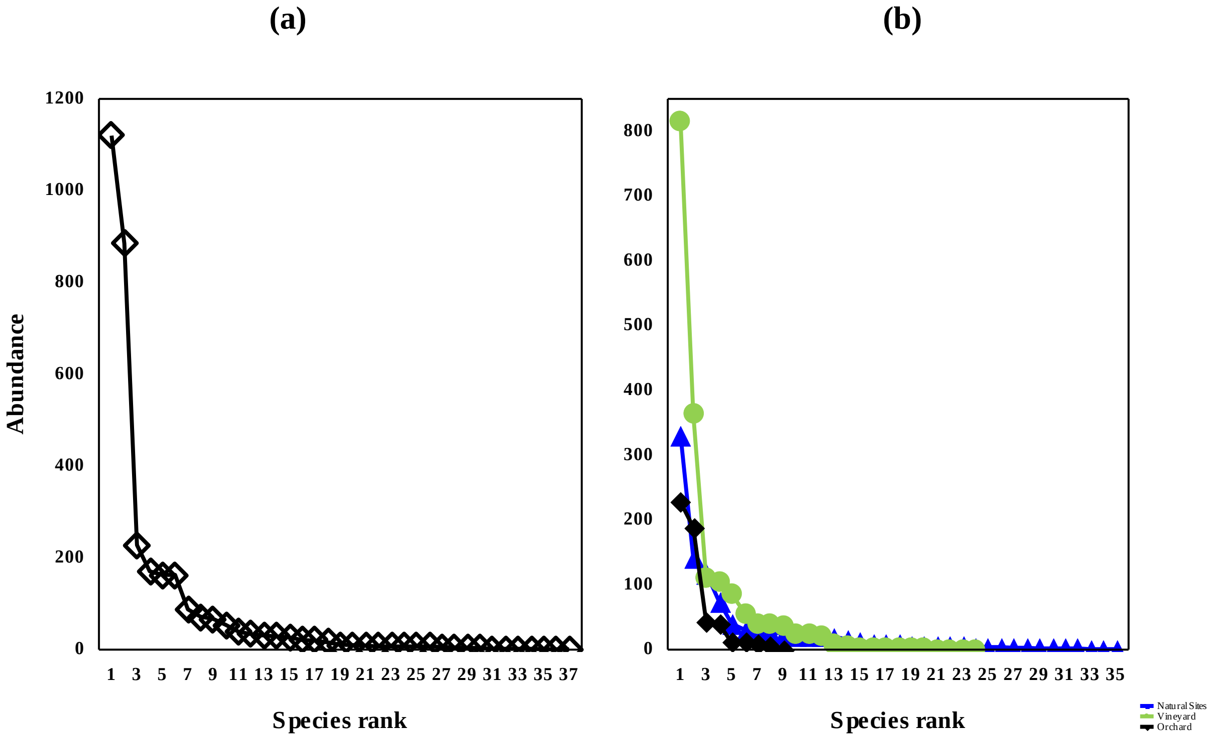

Figure 5.2 Species rank abundance curves for total grasshopper abundance (**a**), and for land-uses (vineyards, orchard and fynbos) **(b).**

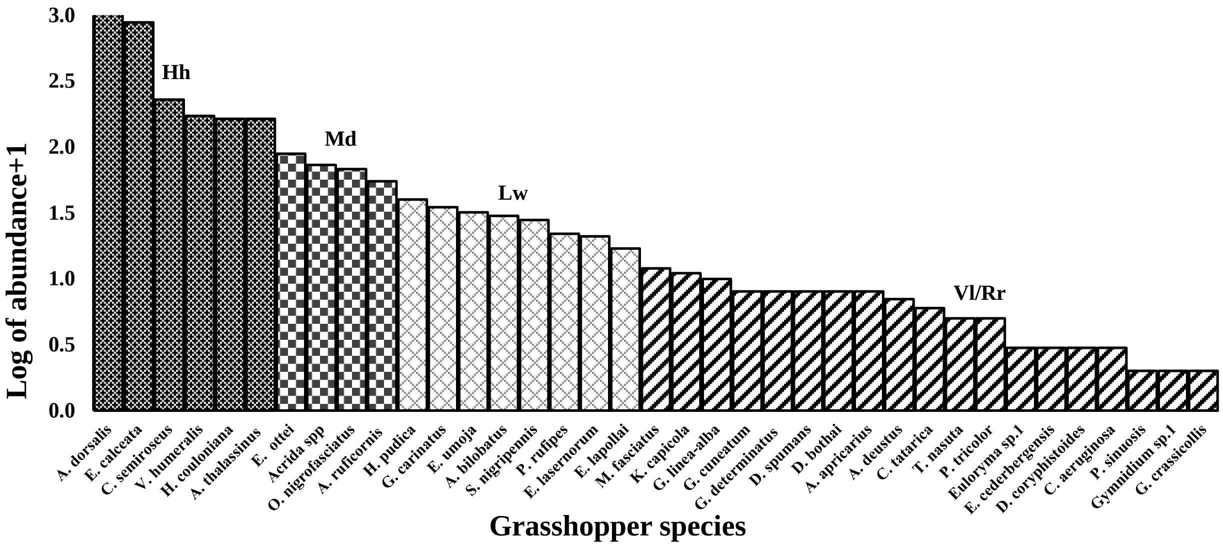

Figure 5.3 Log abundance + 1 of grasshopper species in the entire study. Hh=High; Md=medium; Lw=low; Vl/Rr=very low/rare.

The highest number of sites that a species classified as 'localised' occupied was 16 or 35% of all sampled sites (*E. ottei* in Table **5.1**). Although all species which occupied >40% of all sites were classified as widespread species, twice as many of this widespread group also occupied <30% of all sites. Most localised species occupied only 1-11 sites, out of 46. Furthermore, widespread species mostly fell into the high to medium mobility category, while all localised species were in the less mobile category (Table **5.1**). In general, species with lager abundances or high number of individuals also occupied the highest number of sites (Fig. **5.4a**). Also, widespread species occupied more sites compared to localised species (Fig. **5.4b**). Furthermore, widespread species in general were the most abundant of the two distribution groups (Fig. **5.4c**) while medium to highly mobile species occupied more sites compared with low mobility species (Fig. **5.4d**).

The GLMM results showed that for each site occupied by a localised (often CFR endemic species), there was the likelihood of 1.5 sites being occupied by a widespread species or for every three sites occupied by a widespread species there was the likelihood of localised species occupying two of them. Even with these differences, there was no significant difference in the number of sites occupied by widespread vs. localised species (Z=1.35, P=0.18). The GLMM results also showed that for every single site occupied by a highly mobile species there is the likelihood of a medium mobile species occupying 1.7 sites i.e. highly mobile species occupied 60% of sites occupied by species with medium mobility. There was a significant difference in total number of sites occupied by high and medium mobility species (Z=6.34, P<0.001). Sites occupied by species with low mobility (and often CFR endemics), reduces by a similar margin for every site occupied by highly mobile ones. Sites occupied by highly mobile species and species with low mobility were significantly different (Z=-3.03, P<0.005). The GLMM results further illustrated that abundance of widespread species for each site was more than twice that of localised species, and there was a significant difference between the two distribution types (Z=3.74, P<0.001).

There were also significant differences in abundance of highly mobile species vs. species with medium mobility (Z=13.63, P<0.001) and the highly mobile species vs. species with low mobility (Z=-9.59, P<0.001). Spearman's Rank-Order Correlations tests calculated using the 'cor' function in package 'stats' in R-studio version 3.2.5 (RStudio. 2015) showed that increasing the number of sites occupied by grasshoppers increased their overall abundance (r = 0.77).

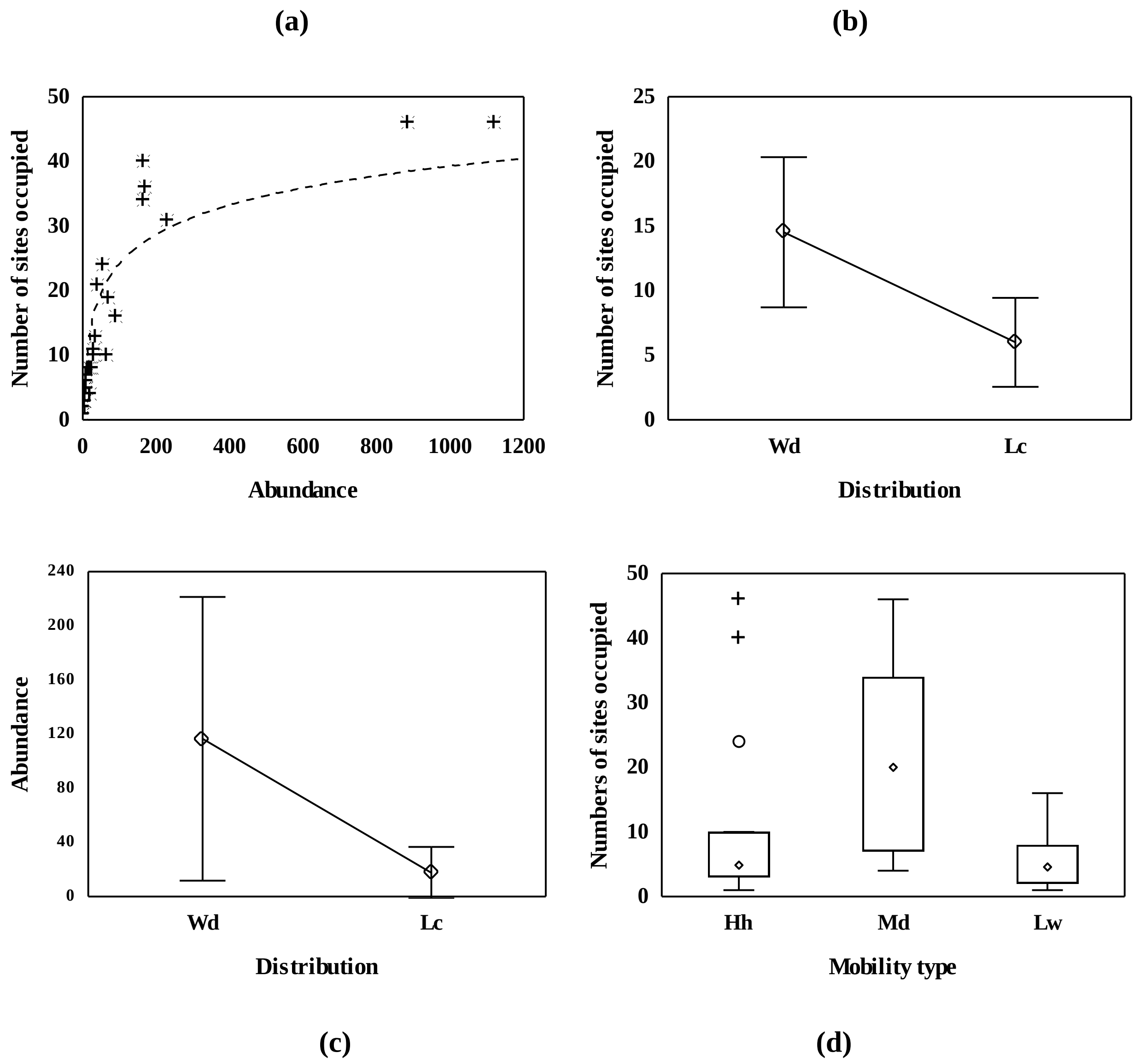

Figure 5.4 Number of sites occupied by grasshoppers vs. abundance **(a).** Number of sites occupied by grasshopper species vs. distribution type **(b),** abundance vs. type of distribution **(c),** and type of mobility **(d).** Wd=Widespread, Lc=localised, Hh=High, Md=Medium and Lw=Low, ○ = outlier, + = extreme values.

The Bray-Curtis dissimilarity based cluster analysis of Table **5.1** showed that all species that occupied >40% of all sampled sites clustered together (Fig. **5.4**). These species also shared <30% dissimilarity in abundance based on land-uses, mobility and number of sites occupied. Species that occupied <20% of sampled sites clustered together sharing <20% dissimilarity (Fig. **5.5**).

Also, winged, flighted and highly mobile species clustered under those that occupied most sampling sites, while wingless and less mobile species clustered under those that were sampled in <20% of the total sampling sites. Acrididae species dominated most sampling sites, and grouped together, indicating high similarity while wingless species also clustered together (Fig. **5.5**).

Table 5.1 A species type of distribution, mobility and total number of sites occupied in fynbos, vineyards and orchards among the grasshopper species sampled here.

Grasshopper species	Type of distribution[a]	Mobility[b]	Number of sites occupied
Anaeolopus dorsalis	Wd	Hh	46
Eyprepocnemis calceata	Wd	Md	46
Aiolopus thalassinus	Wd	Hh	40
Vitticatantops humeralis	Wd	Md	36
Heteropternis couloniana	Wd	Md	34
Calliptamicus semiroseus	Wd	Md	31
Acanthacris ruficornis ruficornis	Wd	Hh	24
Heteropternis pudica	Wd	Md	21
Acrida spp	Wd	Md	19
Euloryma ottei	Lc	Lw	16
Gymnobothrus carinatus	Wd	Md	13
Euloryma umoja	Lc	Lw	11
Acrotylus bilobatus	Wd	Hh	10
Oedaleus nigrofasciatus	Wd	Hh	10
Sphingonotus nigripennis	Wd	Hh	8
Euloryma lapollai	Lc	Lw	8

…cont'

Euloryma larsenorum	Lc	Lw	8
Keya capicola	Wd	Md	7
Morphacris fasciata	Wd	Hh	6
Gymnobothrus linea-alba	Wd	Md	5
Cyrtacanthacris tatarica tatarica	Wd	Hh	5
Devylderia bothai	Lc	Lw	5
Gymnidium cuneatum	Lc	Lw	5
Paragymnobothrus rufipes	Wd	Md	4
Gastrimargus crasicollis	Wd	Hh	4
Gastrimargus determinatus vitripennis	Wd	Hh	4
Dictyophorus spumans	Wd	Lw	4
Thyridota nasuta	Wd	Lw	3
Acrotylus apricarius	Wd	Hh	3
Acrotylus deustus	Wd	Hh	3
Paracinema tricolor	Wd	Hh	3
Cyrtacanthacris aeruginosa aeruginosa	Wd	Hh	2
Euloryma sp.1	Lc	Lw	2
Euloryma cederbergensis	Lc	Lw	2
Devylderia coryphistoides	Lc	Lw	2
Plegmapterus sinuosus	Wd	Hh	1
Gymnidium sp.1	Lc	Lw	1

[a] Abbreviations: Lc, localised; Wd, widespread [b]. [b]Abbreviations: Lw, low; Md, medium; Hh, high

5.4 Discussion

Rank abundance curves are one of the most useful and statistically relevant ways of estimating differences in terrestrial invertebrate assemblage structures between sites. Here, rank abundance curves were used to differentiate grasshopper species richness and evenness under three land uses (vineyards, orchards and fynbos). Two species, *E. calceata* and *A. dorsalis*, dominated the entire sample, as well dominating each land use. Despite this dominance by the two species, richness was high under all land uses, with fynbos the highest, followed by vineyards, and then orchards. This indicates that *E. calceata* and *A. dorsalis* are highly tolerant of landscape change and habitat transformation, typical of generalist species. Indeed, overall the CFR agro-natural landscape is dominated by the Acridinae but with other groups, especially the lentulids, showing a distinct preference for natural fynbos (Matenaar *et al*. 2015). Domination by Acridinae species and only a few species from other groups is indicative of high levels of fragmentation in the CFR as elsewhere (Joern & Gaines 1990; Marvier *et al*. 2004; Pawson *et al*. 2009). Nevertheless, the genrally high species richness indicates a diverse insect group in a biodiversity hotspot. Overall, there were many species in low abundance and only a few others in great abundance, suggesting that cultural practices or landscape changes that are taking place in the CFR favour the few and disfavouring the majority.

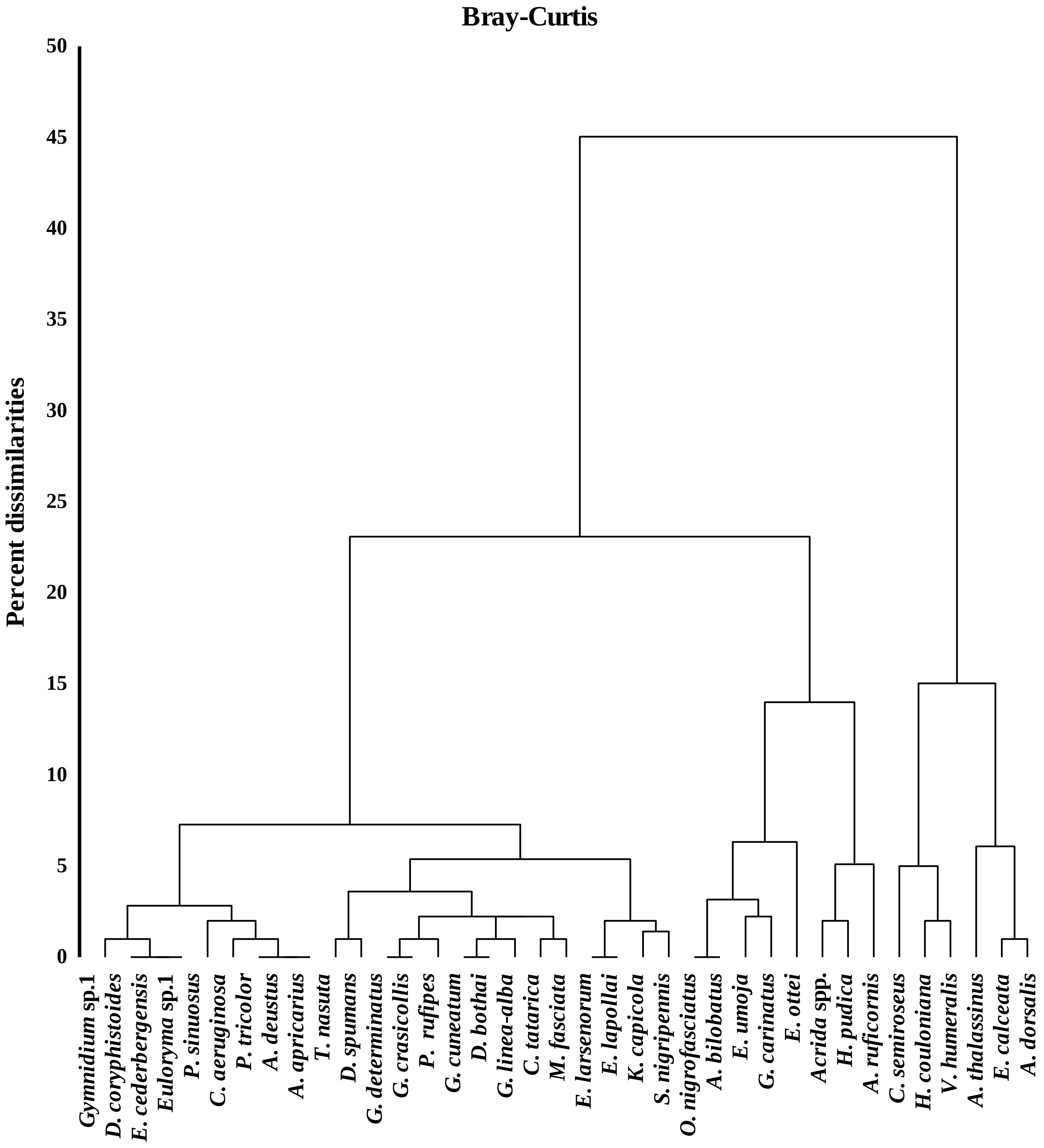

Figure 5.5 A Bray-Curtis dissimilarity tree showing clusters of grasshopper species based on a combination of abundance, type of mobility, and number of sites they occupied.

Those most affected by land transformation are likely to be specialists which are localised. My results suggest 73% of the grasshopper species here have been impacted negatively as evidenced from the recorded abundances. The most affected of all are the low mobility species that are mostly wingless, and confined to South Africa or endemic to the CFR. These species are mostly specialist feeders and with transformation of the landscape destroying their food resources or habitats (Kassen 2002; Brouat *et al*. 2004). In contrast, only ten species, about 27% of the total, benefitted from the landscape transformation here. Interestingly, all of these that benefitted from anthropogenic activities were acridids, which are known often to withstand highly impacted environmental conditions (Uvarov 1966; Peveling 2001). The most notable acridids that responded positively to this land transformation in the CFR were *E. calceata* and *A. dorsalis*, which benefitted in particular from the open spaces associated with vineyards, and made up 77% of all indivuduals, even though the agricultural environment in the CFR can be detrimental to grasshopper development (Adu-Acheampong *et al*. 2016). Surprisingly, *E. ottei* is the only wingless and flightless species that was dominant in both natural vegetation and vineyards, yet not recorded in the highly impacted orchard environment.

The general theme arising from my research is that for this grasshopper there is a tendency to taxonomic and functional homogenization, which would be exacerbated given further landscape transformation, and even possible local extinction (Devictor *et al*. 2008a and b; Clavel *et al*. 2011). In effect, they could replace localised and specialist CFR endemics like *Devylderia* spp. and *Euloryma* spp. Such great changes in the grasshopper assemblages could also have long term effects and cause non-reversible ecosystem function change (Díaz *et al*. 2006), which will also be synergistic with global climate change (McKinney & Lockwood 1999; Warren *et al*. 2001; Sodhi *et al.* 2009), with reduced evolutionary opportunities (Futuyma &Moreno 1988; Kassen 2002; Brouat *et al*. 2004). My results from this biodiversity hotspot confirm a worldwide trend of declining specialists across all taxa (Steffan-Dewenter & Tscharntke 2000; Kotze & O'Hara 2003; Krauss *et al*. 2003; Devictor *et al*. 2008a and b). The magnitude of the situation in the CFR is emphasized by almost 30 of species being recorded as <100 individuals in 184 sampling events at 46 sites across a 90 km transect.

I also found that the higher the individual counts or abundance of a species, the higher the number of sites it occupies, with a high and near perfect correlation between abundance and number of sites occupied by species. Obviously, very rare species would not be able to occupy all or even many of the sites, but still abundant species were the most widespread ones. Furthermore, all species that were sampled in >50% of the total number of sites were either high or medium in mobility, which points to site occupation and mobility going largely hand in hand, which in turn is largely the widespsread species.

5.4.1 Conclusions and conservation recommendations

Grasshopper species assemblages in agro-natural landscape of CFR are dominated by species of Acrididae family, especially *E. calceata* and *A. dorsalis*. Most acridid species, including these two, are dominant across the land uses investigated here. These species are also largely generalists, in contrast to the flightless/low mobility specialists which are mostly CFR endemics with particular natural habitat requirements. There is taxonomic replacement of specialists by generalists with an overall drift towards homogenization across the local area. I recommend development of a biotic index using generalist/high mobility species vs. specialist/low mobility species for keeping track of the extent and degree of homogenization taking place in the CFR as has been developed elsewhere in Germany (Poniatowski & Fartmann 2008).

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CHAPTER 6: General conclusions and conservation recommendations

Agricultural production is one of the main drivers of the on-going biodiversity crisis in the world. As a result, research in this area has increased over time, especially on larger animals e.g. birds and mammals. Studies on arthropods and especially insects are relatively small. More often, findings from such studies (mostly larger animals) show trends of decline with respect to agricultural production compared to natural areas. Nevertheless, there are few exceptions, with some positive contributions from agricultural production on biodiversity when the production methods are eco-friendly.

Although insects constitute more than 75% of all animals and are also major contributors of ecosystem functions in the terrestrial world (Samways 2005), relatively little (compared to mammals) is known about the impact of agriculture on them. This is especially true for grasshoppers that are reported to show high sensitivity to changes in vegetation type and structure. There is therefore the need for concerted efforts to document the impact of agriculture on insects (and other arthropods), especially grasshoppers, on both negative and positive contributions for well-informed conservation actions to be taken in agro-natural landscapes. This is even more important in a biodiversity hotspot which is also known for intensive agricultural production such as the Cape Floristic Region (CFR). To date, there are a few reported cases of the impact of agriculture on different insect taxa except grasshoppers in the CFR (Gaigher & Samways 2010; Kehinde & Samways 2012; Magoba 7 Samways 2011; Vrdoljak & Samways, 2014).

Grasshoppers are an important insect group that can be studied towards conservation under heterogeneous landscapes e.g. agro-natural mosaics with the potential of success, because of their generally wide-ranging sensitivity to land-use change. In view of that, I used grasshoppers here as keystone organisms to further increase our understanding on the importance of agricultural production on biodiversity in the CFR. I set to accomplish this task through four main studies. I first quantified the contribution of two types of agricultural production systems towards supporting local biodiversity compared to the dominant natural vegetation in the CFR (fynbos). This study measured the relative contributions of different agricultural systems towards biodiversity conservation especially on insects using grasshoppers as keystone species (Chapter 2). Secondly, I went on to study the level at which various patches (agriculture vs. natural vegetation) in an agro-natural landscape are utilised by grasshopper species as a function of their inherited traits through changing seasons. This study also shows how the agriculture environment can contribute to local diversity of an insect group in terms of providing support for species that require heterogeneous habitats for their persistence on the landscape (Chapter 3). Thirdly, I developed species distribution models for four CFR endemic, flightless grasshoppers based on their association with either natural vegetation only (two species) or both natural and agriculture (two species) in order to identify the most important environmental variables that account for their distribution in the CFR. This study compared important variables for the distribution of these flightless groups between those associated with natural vegetation only, and those associated with both natural and agricultural production sites, to draw conclusions on the importance of agriculture on species distribution. (Chapter 4). Finally, I studied grasshopper species assemblage composition as a key indicator of landscape change. Here, I also quantify the observation that grasshopper generalist species occupy more habitats and patches in heterogeneous landscapes compared to specialist species (Chapter 5).

My findings from the first study (Chapter 2) show that although agriculture has a negative impact on grasshopper diversity, species overlap between agricultural production areas and the dominant natural vegetation (fynbos) is high in the CFR. Half of the species found only in fynbos were flightless CFR endemics, while those dominating the agricultural patches were winged, strong flyers and mostly more widespread species. This shows that the agricultural environment is a more degraded habitat compared to natural patches, especially for the endemic, narrow range, highly sensitive species. On the other hand, the agricultural environment was the more preferred of the two broad land-use classifications by highly mobile, generalist, and widespread species. This is a positive contribution of agricultural production towards the conservation of local biodiversity in the CFR. Furthermore, these dissimilarities in grasshopper assemblages also varied according to crop type and production practices, with the greater the divergence of the crop from the natural fynbos (the greater the filter) the lower the species richness of grasshoppers in that crop. I arrived at this conclusion based on evidence from vineyards because it provided more opportunities for improving the land sharing approach for grasshopper conservation. Vineyards were less divergent from natural fynbos compared to orchards which were also in the agricultural environment studied. This is mainly because the vineyard floor has high insolation, as with fynbos. Furthermore, vineyard management practices usually involve the planting of cover crops, mostly legumes, rye grasses and oats, to preserve soil structure and conserve water. This favours grasshoppers, especially the widespread, flighted ones, at the expense of flightless, narrow range endemics. Perhaps it will also favour the endemic species if alien cover crops were replaced by fynbos vegetation. Deciduous fruit orchards on the other hand provided less opportunity than vineyards for land sharing, mostly because it has dense canopy that shades the ground making it unfavourable for grasshopper-friendly vegetation and for grasshoppers themselves. Management practices in orchards, especially high levels of irrigation as well as pesticide applications, may have compounded the situation. These conclusions, especially for vineyards, show that the agricultural environment is very important for a number of grasshoppers especially generalist, wide spread and strong flyers. Nevertheless, natural and protected areas are still important for conserving the diversity of a variety of insect taxa as has been shown for butterflies (Krämer *et al*. 2012)

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My second study (Chapter 3) provided more evidence to suggest that certain aspects of the agricultural environment is required if the landscape is to support a higher density of grasshopper species than would be the case naturally. I show that highly mobile, widely distributed and mostly grass to mixed feeders utilise more than one patch for their life history activities on the landscape. They characteristically establish in good quality habitat (vineyard) for a short time during favourable conditions, but later, decrease there greatly during unfavourable conditions (see Figs. **3.3** and **3.4.**). This could be as a result of their life history traits of overwintering as eggs, hatching as nymphs during spring, and reaching adulthood in a different habitat. Other species, especially the wingless, localised endemics that display little to medium mobility, and that eat mostly forbs or are mixed feeders, utilised a small variety of patches. This was determined through their being encountered on a few occasions or not at all in vineyards across the changing seasons. Agro-natural landscapes in the CFR provide the perfect heterogeneous environment for diverse grasshopper assemblages to persist.

My third study (Chapter 4) further suggested that agricultural production is an important factor to consider when conserving narrow range endemic CFR species (*Euloryma* species). Environmental factors accounted most for *Euloryma* species distribution patterns in the CFR. These were mainly vegetation and soil characteristics, with altitude a secondary contributor. Vegetation type was also important. The distribution models also showed that these endemic species have very narrow ranges of predicted habitat suitability. My results also suggest that although all species in *Euloryma* have narrow geographical ranges, species associated with only fynbos should be a higher conservation priority than those associated with both agriculture and fynbos, because of their high sensitivity to land-use change and hence are more vulnerable to habitat transformation.

My last study (Chapter 5) also showed that, although agriculture is important for providing a heterogeneous environment for maintaining high diversity of grasshoppers, it also reduces evenness on the landscape. Here, I show that the Acrididae family, especially *E. calceata* and *A. dorsalis*, dominate the entire assemblage composition, and that most acridid species, including these two, are dominant across the land-uses investigated here. These species are also largely generalists, in contrast to the flightless/low mobility specialists which are mostly CFR endemics with particular natural habitat requirements. With agricultural conversion there is taxonomic replacement of specialists by generalists with an overall drift towards homogenization across the local area.

Conservation recommendation from this thesis

- The distinctive species composition associated with the various land-uses substantiates that grasshoppers can potentially be used for monitoring qualitative changes in production patches in the CFR towards or away from the historic fynbos condition.
- Land sparing in both vineyards and orchards, will be an important management intervention to conserve endemic species in particular. Therefore, some degree of land sparing on farms in the form of remnant patches are likely to be positive for grasshoppers.
- Grasshopper species in an agro-natural mosaic in the CFR can potentially be used as bio-indicators of habitat quality. For instance, the dynamics of hemiacridines could be used for fynbos quality surveillance.
- A biodiversity conservationist could use the life history traits of a particular grasshopper species to help design conservation schemes in agro-natural landscapes. E.g.
    - *Euloryma* species can possibly also be used as surrogate group for designing conservation schemes for species with similar life history traits in the CFR.
    - *Euloryma* species-groups can also be used as bioindicators for measuring type of soil and/or, most importantly, its quality in the CFR.
- These species could be used to determine the quality and the quantity of fynbos/forb vegetation in and around vineyards to see whether these are sufficient to maintain population levels without any ecological relaxation.

- My study also shows that although agricultural land is of high importance for the persistence of certain species, especially those that are generalist, widespread and mobile. Under large-scale expansion of agriculture into natural vegetation, low mobility habitat specialists will be at risk of extinction, because of their limited ability to move between optimal patches to escape harsh conditions.
- I recommend development of a biotic index using generalist/high mobility species vs. specialist/low mobility species for keeping track of the extent and degree of homogenization taking place in the CFR.
- I suggest that further studies be conducted to ascertain whether soil conditions affect *Euloryma* species directly through breeding sites or indirectly through host plant regulation.

6.1 References

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Appendix

Location of sampling sites in Somerset West, Stellenbosch, Paardebeg and Grabouw including and indication of land-use type in the CFR

Sampling area	Land-use	Latitude	Longitude
Somerset West	Natural	S34°03'42.8"	E018°52'16.7"
Somerset West	Natural	S34°03'42.5"	E018°52'28.8"
Somerset West	Natural	S34°03'54.6"	E018°52'28.5"
Somerset West	Natural	S34°03'54.6"	E018°52'15.8"
Somerset West	Vineyard	S34°04'12.4"	E018°53'55.4"
Somerset West	Vineyard	S34°04'18.2"	E018°53'44.1"
Somerset West	Vineyard	S34°04'59.9"	E018°54'08.1"
Somerset West	Vineyard	S34°04'56.4"	E018°54'02.9"
Somerset West	Orchard	S34°04'48.1"	E018°53'33.7"
Somerset West	Orchard	S34°04'11.2"	E018°53'55.4"
Somerset West	Orchard	S34°04'17.2"	E018°53'44.7"
Somerset West	Orchard	S34°04'48.1"	E018°54'05.3"
Stellenbosch	Natural	S33°58'29.7"	E018°56'19.3"
Stellenbosch	Natural	S33°58'52.8"	E018°56'45.0"
Stellenbosch	Natural	S33°59'20.4"	E018°57'59.5"
Stellenbosch	Natural	S33°58'39.1"	E018°56'35.1"
Stellenbosch	Vineyard	S33°52'26.6"	E018°53'26.5"
Stellenbosch	Vineyard	S33°52'14.4"	E018°53'14.8"

…cont’

Stellenbosch	Vineyard	S33°50'46.3"	E018°51'20.6"
Stellenbosch	Vineyard	S33°50'52.9"	E018°51'04.8"
Stellenbosch	Orchard	S33°54'15.0"	E018°52'21.5"
Stellenbosch	Orchard	S33°54'16.3"	E018°52'08.9"
Stellenbosch	Orchard	S33°54'23.8"	E018°51'38.6"
Stellenbosch	Orchard	S33°54'10.3"	E018°51'43.8"
Paardebeg	Natural	S33°35'38.0"	E018°50'34.5"
Paardebeg	Natural	S33°35'39.2"	E018°50'29.2"
Paardebeg	Natural	S33°37'15.8"	E018°49'03.2"
Paardebeg	Natural	S33°37'15.3"	E018°49'06.2"
Paardebeg	Vineyard	S33°37'24.2"	E018°49'06.4"
Paardebeg	Vineyard	S33°37'44.0"	E018°49'11.4"
Paardebeg	Vineyard	S33°35'44.3"	E018°50'35.3"
Paardebeg	Vineyard	S33°35'48.6"	E018°51'00.8"
Paardebeg	Orchard	S33°38'15.2"	E018°51'0.07"
Paardebeg	Orchard	S33°37'43.1"	E018°49'26.2"
Grabouw	Natural	S34°04'05.7"	E019°03'16.6"
Grabouw	Natural	S34°03'57.6"	E019°02'44.9"
Grabouw	Natural	S34°04'09.3"	E019°03'0.06"
Grabouw	Natural	S34°04'09.2"	E019°03'08.7"
Grabouw	Vineyard	S34°09'26.8"	E019°06'32.6"
Grabouw	Vineyard	S34°04'45.7"	E018°54'05.6"

…cont'

Grabouw	Vineyard	S34°05'0.04"	E018°54'07.6"
Grabouw	Vineyard	S34°09'36.4"	E019°06'23.4"
Grabouw	Orchard	S34°10'24.48"	E019°05'04.80"
Grabouw	Orchard	S34°10'05.52"	E019°04'53.63"
Grabouw	Orchard	S34°09'49.8"	E019°05'15.0"
Grabouw	Orchard	S34°10'13.8"	E019°05'06.8"