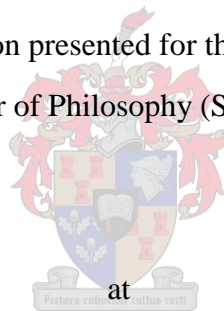# Beta Diversity across the Complementary Zones of the Kogelberg Biosphere Reserve

by

Julia van Schalkwyk

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Department of Conservation Ecology and Entomology, Faculty of AgriSciences

Supervisor: Dr. James S. Pryke

Co-supervisor: Prof. Michael J. Samways

Co-supervisor: Dr. René Gaigher

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Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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General summary

Biodiversity loss is occurring at an alarming rate. Protected areas alone are not sufficient for long-term biodiversity conservation. To address this, conservation efforts need to incorporate the landscape surrounding protected areas. Biosphere reserves (BR) consist of three zones with different (but complementary) functions: a core area (dedicated specifically to long-term biodiversity conservation), an adjoining buffer zone (where activities should be compatible with the objectives of the core), and a flexible transition zone (where sustainable resource use and management is promoted). Zonation will generally match existing land-use patterns, and the buffer forms part of a continuous but increasing gradient of land-use intensity (LUI) as one moves away from the core.

The aim of this study is to assess the success of biodiversity conservation of the different zones of the Kogelberg Biosphere Reserve (KBR) in response to increasing LUI away from the core. I focused on commercial fruit farming, since it is an important economic activity in the study area. I chose objectives that are related to the ecological function of each zone using arthropods as study organisms, and employed principles based on systematic conservation planning (SCP) and landscape ecology. The specific objectives were: 1) to determine whether arthropod diversity tracks plant diversity, 2) assess how well arthropod diversity is represented in the core zone, 3) to determine whether the buffer zone is effective in protecting the core from activities in the transition, 4) to assess whether the buffer zone complements arthropod diversity in the core zone, 5) to assess how orchards influence arthropod diversity in adjacent non-crop habitats, and 6) to determine how LUI at different spatial scales affects arthropod diversity within orchards.

The results showed that arthropod diversity is relatively well-represented within the core zone, but that the buffer has important complementary value by adding ecological environments not present in the core. The buffer also improves the comprehensiveness of the reserve by establishing strong environmental gradients (which are important for congruence in plant and arthropod diversity).

The KBR does not have a continuous buffer surrounding its core area, and this was reflected by the influence of anthropogenic activities (i.e. proximity to deciduous fruit orchards) on diversity in the core zone. This influence reached up to 1 km away from orchards, decreasing the effective conservation area of the core zone where the buffer is absent or not wide enough. Closer investigation showed that the observed edge responses were the result of

differential responses of different arthropod groups, and that they could be predicted by traits related to species habitat specialization (species which prefer natural habitats, species which prefer orchards, and species which occur in either). The results highlighted the variegated nature of the transformed landscapes that is not captured by patch-orientated views of fragmentation. This study also emphasises the importance of management actions within orchards on diversity in adjacent habitats and the associated non-visible heterogeneity.

Arthropod diversity in orchards showed contrasting responses to increasing LUI at different spatial scales. Local LUI (management intensity) had a negative influence on some groups. Landscape scale LUI (in the form of more orchards in the landscape) increased species richness of a subset of species, and contributed to the homogenization of orchard arthropod diversity across the landscape. This highlights the need to consider the influence of LUI on diversity at different spatial scales.

Principles from SCP and landscape ecology are valuable for prioritizing conservation efforts, and for guiding planning and management towards promoting biodiversity across the entire landscape. To enhance arthropod diversity across the KBR, the most important recommendations from this study are to include a range of abiotic variables (especially variables related to climate and geology) in conservation areas. This implies conservation efforts should not be restricted to only the core zone. While LUI was important in determining diversity at the local scale, non-crop habitats are essential for enhancing farmland diversity across the entire BR.

Algemene opsomming

Biodiversiteitsverlies vind plaas teen 'n onrusbarende tempo. Beskermde gebiede alleenlik is nie voldoende vir langtermyn biodiversiteitsbewaring nie. Om dit teen te werk moet bewaringspogings die landskap rondom beskermde gebiede insluit. Biosfeerreservate bestaan uit drie sones met verskillende (maar komplementêre) funksies: 'n kerngebied (spesifiek toegewy aan langtermyn biodiversiteitsbewaring), 'n aangrensende buffersone (waar aktiwiteite verenigbaar moet wees met die doelwitte van kerngebied) en 'n buigsame oorgangsone (waar volhoubare hulpbrongebruik en bestuur bevorder word). Sonering sal oor die algemeen met bestaande grondgebruikspatrone ooreenstem, en die buffersone vorm deel van 'n deurlopende en toenemende gradiënt van grondgebruik intensiteit (GI) met toenemde afstand vanaf die kerngebied.

Die doel van hierdie studie was om die biodiversiteitsbewaringssukses van die verskillende sones van die Kogelberg-biosfeerreservaat te beoordeel in reaksie op toenemende GI weg van kerngebied. Ek het gefokus op kommersiële vrugteboerdery, aangesien dit 'n belangrike ekonomiese aktiwiteit in die studiegebied is. Ek het subvrae ondersoek wat verband hou met die ekologiese funksie van elke sone met behulp van geleedpotiges as studie-organismes en beginsels gebaseer op sistematiese bewaringsbeplanning (SB) en landskapekologie. Die spesifieke doelwitte was: 1) bepaal of plantdiversiteit die diversiteit van geleedpotiges reflekteer, 2) beoordeel hoe goed geleedpotige diversiteit in kerngebiede verteenwoordig word, 3) bepaal of die buffersone effektief is om die kerngebied van aktiwiteite in die oorgangsone te beskerm, 4) assesseer of buffergebiede die geleedpotige diversiteit in die kerngebiede aanvul, 5) beoordeel hoe boorde geleedpotige diversiteit in aangrensende nie-gewas habitatte beïnvloed, en 6) bepaal hoe GI oor verskillende ruimtelike skale die diversiteit van geleedpotiges binne boorde affekteer.

Die resultate het gewys dat geleedpotige diversiteit relatief goed verteenwoordig word in kerngebiede, maar dat die buffersones 'n belangrike aanvullende rol speel deur ekologiese omgewings wat nie in die kerngebiede voorkom nie by te voeg, en ook die volledigheid van die reservaat verbeter deur sterk omgewingsgradiënte te vestig (wat belangrik is vir kongruensie in plant- en geleedpotige diversiteit).

Die Kogelberg-biosfeerreservaat het nie 'n deurlopende buffersone rondom sy kerngebied nie, en dit was weerspieël deur die invloed van menslike aktiwiteite (d.w.s. nabyheid aan vrugteboorde) op diversiteit in kerngebiede. Hierdie invloed het tot 1 km weg van boorde

gestrek, en waar die buffersone afwesig was of nie wyd genoeg was nie het dit gelei tot 'n kleiner effektiewe bewaringsgebied in kerngebiede. Nadere ondersoek het getoon dat die waargenome randreaksies die gevolg was van differensiële reaksies van geleedpotige groepe wat voorspel kon word deur eienskappe wat verband hou met habitat-spesialisasie (spesies wat natuurlike habitatte verkies, spesies wat boorde verkies en spesies wat voorkom in óf natuurlike habitatte of boorde). Die resultate het die gesofistikeerde aard van getransformeerde landskappe beklemtoon wat nie deur lappiesland-georiënteerde sienings van fragmentering vasgevang word nie. Hierdie studie beklemtoon ook die belangrikheid van bestuursaksies binne boorde vir diversiteit in aangrensende natuurlike habitatte en die gepaardgaande verborge heterogeniteit.

Geleedpotige diversiteit in boorde het kontrasterende reaksies op toenemende GI op verskillende ruimtelike skale getoon. Die resultate dui daarop dat plaaslike GI (bestuursintensiteit) 'n negatiewe invloed op sommige groepe het. Landskapskaal GI (in die vorm van meer boorde in die landskap) het die spesiesrykheid van 'n deelversameling spesies verhoog en bygedra tot die homogenisering van geleedpotige diversiteit in boorde oor die landskap. Die resultate beklemtoon dat die invloed van GI op diversiteit op verskillende ruimtelike skale oorweeg moet word.

Beginsels van SB en landskapsekologie is waardevol vir die prioritisering van bewaringspogings en om beplanning en bestuur te rig wat daarop gemik is om biodiversiteit oor die hele landskap te bevorder. Die belangrikste aanbevelings vir die verbetering van geleedpotige diversiteit in die Kogelberg-biosfeerreservaat is om 'n verskeidenheid abiotiese veranderlikes (veral veranderlikes verwant aan klimaat en geologie) in bewaringsgebiede in te sluit. Dit impliseer dat bewaringspogings nie net tot kerngebiede beperk moet word nie. Terwyl GI belangrik was in die bepaling van diversiteit op die plaaslike skaal, is nie-gewas habitatte noodsaaklik om diversiteit in landbougebiede oor die hele biosfeerreservaat te verhoog.

Acknowledgements

Many people have contributed to the completion of this dissertation, to whom I owe an immense amount of gratitude. I would like to thank my supervisors for their knowledge and guidance, for allowing me the autonomy to chart my own path and for supporting me in all my endeavours.

I want thank my family and friends.

Special thanks to my parents, Julia and Louwtjie van Schalkwyk, to whom I dedicate this thesis.

And finally, Theo (my favourite human), thanks for all the free beers.

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Chapter 1 Introduction

1.1 The biodiversity crisis and the development of conservation approaches

Biodiversity loss is occurring at an alarming rate. The main anthropogenic drivers of species extinctions are fast-paced rates of habitat loss and fragmentation as well as large-scale disturbances (e.g. biological invasions and habitat degradation) (Valiente-Banuet et al. 2014). Humans rely on biodiversity for important services, such as clean water, fertile soils for food, recreation or climate regulation (Rodriguez et al. 2006), and our unending manipulation of the environment is affecting nature's ability to provide these services.

A widely accepted and well known strategy for biodiversity conservation is protected areas (Chape et al. 2005). Since the establishment of Yellowstone National Park in the USA in 1872 to the late twentieth century, the most important aim of protected areas have been to protect biodiversity and ecosystems that occur inside them from change that occurs outside (Margules et al. 2002). It soon became clear that these conservation 'islands' were being threatened by transformation outside their borders, which was contributing to their isolation and reducing connectivity with other protected areas (Janzen 1983).

Conservation in the 1990s shifted toward protecting the connections among protected areas and establishing conservation networks. It is also during this phase that systemic conservation planning (SCP) was developed. SCP is aimed at identifying 'priority areas' and separating them from processes that threaten them (Margules and Pressey 2000). SCP is thought of as the most influential paradigm to identify and conserve priority areas (Margules and Pressey 2000; Sarkar et al. 2006; Knight et al. 2010), and has led to the development of several key concepts used in conservation assessments, including 'comprehensiveness', 'representativeness', 'complementarity', and 'efficiency' (Kukkala and Moilanen 2013). Comprehensiveness entails sampling the full variety of biodiversity at multiple levels, including structural, compositional and functional perspectives (Noss 1990). Representativeness is focused on a solution and how well this solution encompasses biodiversity of the region (Kukkala and Moilanen 2013). It led to the concept of complementarity, i.e. the potential of new conservation areas to supplement existing areas by adding biodiversity components (e.g. species) not presently represented (Margules and Pressey 2000; Faith et al. 2003). Since conservation resources (land, money, or

management) are limited, conservation efficiency is realised by maximising complementarity (Williams 2001; Moilanen et al. 2009).

Despite these developments, serious gaps in the protected area network remain. Many protected areas that exist today were set aside for reasons other than biodiversity representation. Instead, the prioritization of these areas were linked to their unique scenic value or because of specific rare species. There are also instances when areas were protected because of their low potential for alternative competing land-uses, such as agricultural production or human habitation, e.g. areas with steeper slopes or that are located far from roads (Margules et al. 2002; Joppa and Pfaff 2009). In addition, protected areas are often defined based on administrative barriers rather than ecological integrity, which can result in the exclusion of areas that are important for maintaining ecological processes (Rouget et al. 2003; Western et al. 2009). Combined with competing land-uses and the general lack of information in the distribution of many species, priority areas will rarely include all natural or semi-natural habitats in a region (Margules et al. 2002). Another important issue is that the establishment of protected areas can lead to conflict between park managers and surrounding people (West et al. 2006).

To address these challenges, it was necessary for conservation approaches to incorporate the landscape around protected areas (IUCN 2005). In addition, protected areas are not closed systems and are affected by land-use change outside their borders, therefore managing these areas in isolation from surrounding semi-natural or production landscapes makes their long-term sustainability uncertain (Vandermeer and Perfecto 2007). The landscape approach involves considering the larger geographical area when addressing sustainability and to consider both social and ecological systems as well as their interactions (Singer 2007; Borrini-Feyerabend et al. 2004). In this regard, landscape ecology has contributed significantly to integrating protected areas with the broader landscape context (Wiens 2009). Landscape ecology views places (or habitats) as part of a larger landscape mosaic and is aimed at using an understanding of landscape patterns and processes to design and manage land that promotes the wellbeing of people and nature (Wiens 2009).

The original idea of protected areas had a strong influence on the development of more modern protected-area models (Palomo et al. 2014) and it is important to note that such areas are required to maintain biodiversity and ecosystem services in the long term, but on their own they are not sufficient. SCP is important in identifying areas to complement existing areas, to

guide land-use planning and to find efficient solutions, while landscape ecology emphasizes that the matrix matters (either increasing or reducing the 'effective area' of a reserve), that land-uses can be arranged along a gradient of intensities and that we need to consider effects at different spatial scales (Wiens 2009).

1.2 Biosphere reserves

1.2.1 Short history

The United Nations Education, Scientific and Cultural Organization's (UNESCOs) Man and the Biosphere (MAB) Programme arose from the 1968 Conference on the Rational Use and Conservation of the Resources of the Biosphere which was aimed at summarising knowledge on sustainable natural resource use and management (Batisse 1986). A chief accomplishment of the MAB Programme around this time was the biosphere reserve (BR) concept (conceptualised in the early 1970's). Since the establishment of the BR concept, BR congresses take place approximately every 12 years and the strategy and focus of BRs are continuously evolving. The first International Biosphere Reserve Congress in Minsk in 1984 produced the 'Action Plan for Biosphere Reserves', which proposed a range of activities for the comprehensive implementation of BRs, which was then defined as (UNESCO 1984):

> "*...protected areas of representative terrestrial and coastal environments which have been internationally recognized under the UNESCO MAB Programme for their value in conservation and providing the scientific knowledge, skills and human values to support sustainable development*"

A particular emphasis at this time was the preservation of a *"representative sample of significant ecosystems, original habitats and remnant populations"* (Batisse 1986). In 1995, two main outputs from the International Conference on Biosphere Reserves in Seville, Spain, the 'Statutory Framework' of the World Network of Biosphere Reserves (WNBRs) and the 'Seville Strategy', have provided a common platform for the development of BRs (UNESCO 1996b; Robertson Vernhes 2007). The third World Congress of Biosphere Reserves was held in 2008 in Madrid, Spain, resulted in the adoption of the 'Madrid Action Plan' (MAP) which expanded on the Seville Strategy. Under the MAP, the new roles of BRs shifted toward "learning sites", with the emphasis on research and continuous action learning for sustainable development. The fourth World Congress of Biosphere Reserves was held in Lima, Peru, in

2016, and endorsed the 'Lima Action Plan' (LAP) which emphasizes the role of BRs as models contributing to sustainable development goals. The new MAB strategy and the LAP encourages countries to use BRs to *"contribute to sustainable, healthy, and equitable societies, economies and thriving human settlements"* (UNESCO 2017). The LAP provides guidance towards ensuring that the WNBRs consists of effectively functioning models of sustainable development and incorporates compliance with the Seville Strategy and the Statutory Framework (UNESCO 2017).

1.2.2 The Biosphere Reserve concept

At the centre of the BR concept are three complementary functions: conservation (from landscapes and habitats to species and genes), sustainable development (ecologically sustainable economic and human development) and logistic support (research, monitoring, education and training) (Box 1; UNESCO 1996a). At the local level, these functions are realised within a defined landscape through a zonation scheme that progresses from preservation to sustainable resource use in the form of one or more core areas (devoted to long term biodiversity conservation), an adjoining buffer zone(s) (where activities should be compatible with the objectives of the core), and a flexible transition zone (where sustainable resource management and development is promoted) (also referred to as the 'egg model', Figure 1.1). The zonation scheme is not necessarily concentric, and in the real world, zonation will generally match existing land-use patterns. Another way of viewing the buffer zone(s) is as one end of an open-ended (and continuous) transition zone (Brunckhorst 2001), with increasing intensity of land-use and management away from the core.

Box 1 Three functions of a biosphere reserve as set out in the Statutory Framework (Article 3) (UNESCO 1996a)

1. Conservation – contribute to the conservation of landscapes, ecosystems, species and genetic variation.

2. Development – foster economic and human development which is socio-culturally and ecologically sustainable.

3. Logistic support – support for demonstration projects, environmental education and training, research and monitoring related to local, regional, national and global issues of conservation and sustainable development.
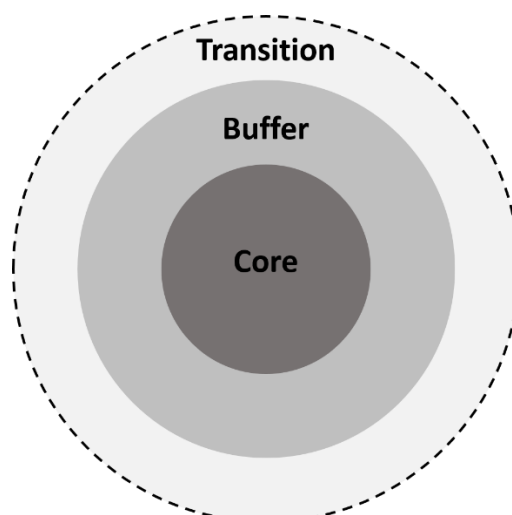
Figure 1.1 The biosphere reserve 'egg model'

Although BRs contain a core area typically protected under national or sub-national legislation, as a whole BRs are regarded as non-conventional protected areas (Price 1996; Batisse 1997) and are not formally recognized as protected areas. BRs are not intended to replace existing conservation actions, but to rather enhance them through improving the relationship between the environment, society and economic development (Coetzer et al. 2013). Since the BR model avoids impacts on the protected areas and acknowledges that the surrounding landscape can be transformed along a gradient of land-use intensity, it is considered one of the better solutions to integrate conservation with the surrounding landscape (Palomo et al. 2014). Where individual BRs consist of more than one core area, regional co-operation in the management of isolated protected areas can translate into a more effective

protected area system (i.e. a regional meta-reserve that includes matrix areas and increases connectivity across the landscape) (Coetzer et al. 2013).

1.3 The Kogelberg Biosphere Reserve

The Kogelberg Biosphere Reserve (KBR) is situated at the south-western tip of South Africa (Figure 1.2). It was registered by UNESCO as a BR in 1998 and is South Africa's oldest BR. The dominant vegetation type in the region is fynbos, a schlerophyllous vegetation type that is adapted to low soil nutrients, winter rainfall and regular fires. The KBR is considered a floral hotspot within a hotspot (the Cape Floristic Region) (Boucher 1982; Rebelo et al. 2006). More than 80% of its terrestrial core and buffer areas are made up of Kogelberg Sandstone Fynbos (KSF) which has exceptional species-level endemism (Rebelo et al. 2006), and the KBR contributes significantly to the conservation of KSF (over 65% of the total distribution of KSF is contained within the borders of the KBR).

The landscape is dominated by high peaks and rugged mountain terrain (Figure 1.3). Protected natural areas (or core zones) are mostly restricted to mountainous parts and make 43% of its approx. 87 000 ha terrestrial component. Agriculture and commercial alien plantations form part of the buffer and transition zones. Most of the land that comprises the buffer zones (approx. 24% of the terrestrial component) is in a natural or near-natural state, while most of the remaining transition area has been converted (Johns et al. 2012; Pool-Stanvliet 2014). Deciduous fruit farming is a major economic activity in the study area as the KBR encompasses part of the Elgin district, South Africa's main pome fruit producing region (Figure 1.4). Approximately 20% of all land transformation bordering core and buffer zones of the KBR is composed of this land use. The KBR does not have a continuous buffer and a significant portion of the KBR buffer zone consists of private small holdings. There is an increasing interest for development (e.g. agriculture or tourists resorts) that is raising concerns regarding the integrity of the buffer zone (Pool-Stanvliet 2014).
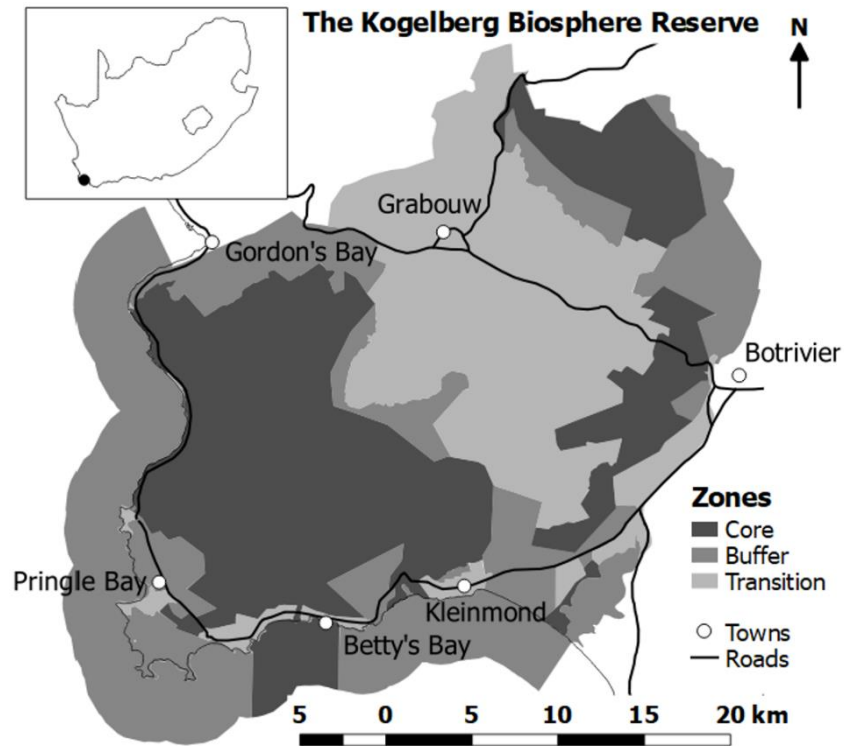
Figure 1.2 Map of Kogelberg Biosphere Reserve, showing both terrestrial and marine
components, major towns and roads

Figure 1.3 Rugged terrain of the Kogelberg Biosphere Reserve

Figure 1.4 View of the Elgin district in the transition zone of the Kogelberg Biosphere Reserve. Background – fruit orchards, foreground - species rich fynbos flora

1.4 Challenges

Sustainable conservation requires a landscape context perspective that incorporates the places where people live and work along with protected areas (Wiens 2009) and BRs can be considered a landscape approach (Axelsson 2009). Core zones (or protected areas) are important for conserving places where biodiversity still retains some element of naturalness, but cannot reduce biodiversity loss on their own. The characteristics of areas surrounding core zones can enhance their conservation value by providing features that complement those within the core, or can contain threats that reduce the effective conservation area. Buffer zones aim to minimize these potential threats by buffering areas in the core from activities in the transition, but can also play an important role in promoting connectivity in a larger spatial framework as they connect biodiversity components within core areas with those in the transition (UNESCO 2008).

BRs hold great potential for developing conservation science but also face a number of challenges (Reed 2016). The growing emphasis on the 'development' function (especially economic development, e.g. Reed (2016)) can be detrimental to the other dimensions of a BR and encouraging unregulated and indiscriminate development in sensitive environments can

have negative impacts on the ecological integrity of the landscape (Coetzer et al. 2013). For example, extraction and transformation in buffer zones can threaten the integrity of core areas, to the point where rezoning has been considered (Ma et al. 2009; Fisher et al. 2011; Radachowsky et al. 2012; Béliveau et al. 2017). Rezoning is not always an option (e.g. lack of funding), and if implemented can lead to conflict between stakeholders, which can result in the withdrawal of a BR from the WNBRs (as was the case for Bayerischer Wald BR in Germany in 2007 (Price et al. 2010)).

The core areas of many BRs were established before the development of key conservation prinicples of SCP and the majority of these principles have been overlooked by the developing BR framework (Possingham et al. 2006; Lourival et al. 2011). Although the idea is that core areas should contain the most diversity and be representative of diversity of the region (Mendez-Larios et al. 2006; Zafra-Calvo et al. 2010), for many established BRs this requires assessment. Although simple in theory, identifying representative communities is not an easy task (Su et al. 2004). The first challenge is that there is too much diversity for us to measure all of it directly. To address this, conservation strategies often make use of 'surrogates' (or 'indicators') that can act as proxies for broader biodiversity value (e.g. Reid et al. 1993).

Core areas should not be considered in isolation from their surroundings and it is important to recognize that a variety of human uses in the landscape can represent a range of potential conservation values. Landscape ecology can be important in helping us understand these values and define which human actions are compatible with biodiversity conservation. Human-modified landscapes are characterised by a dynamic relationship between remaining habitat fragments, edges and transformed areas (Forman and Godron 1981; Tscharntke et al. 2005) and sustainable development will depend on creating multifunctional landscapes that are capable of both maintaining biodiversity and production (Balmford et al. 2012).

Effective conservation across spatial scales will require understanding the relationship between locally collected data and regional diversity dynamics, and the different mechanisms that are driving changes in diversity from local to regional scales (Kraft et al. 2011; Socolar et al. 2016). In response to these questions, there has been renewed interest in understanding the spatial variation in species identities between sites, also referred to as beta (β) diversity (Tuomisto 2010; Anderson et al. 2011; Socolar et al. 2016). Different methods exist to measure β diversity and various definitions have been applied since the concept was first introduced by Whittaker (Whitaker 1960, 1972; for review see Tuomisto 2010). Ultimately, different metrics

measure different aspects of variation in species composition and the choice of measure depends in part on the aspect of interest (Anderson et al. 2011). We can distinguish between two types of β diversity: turnover and variation. The first refers to changes in community structure in reference to a gradient (spatial or environmental). The second refers to differences in the variation in community structure among a set of sampling units within a given spatial extent (Anderson et al. 2011). Dissimilarity between communities can also be separated into replacement and richness or nestedness-resultant components (Harrison et al. 1992; Baselga 2010; 2012). Partitioning these two components can be useful for assessing patterns of variation in species composition, as each can originate from different underlying processes. Species replacement involves the simultaneous loss and gain of species due to environmental filtering, competition, or spatial or historical constraints (Leprieur et al. 2011). Richness difference refers to one community being made up of more species than another. Nestedness is a form of richness difference where the species at a site is a strict subset of species at a richer site (Atmar and Patterson 1993; Baselga 2012). Understanding patterns of beta diversity, the processes that maintain them, and how anthropogenic activities influence these patterns are especially important in understanding the ecological effectiveness of the different zones of a BR, as well as for improving conservation science in general.

The challenges discussed above are especially acute in the context of invertebrate species, which make up the largest proportion of global biodiversity (Mora et al. 2011), but are often neglected in management plans (Samways et al. 2010). In both natural and agricultural landscapes they play integral roles in ecosystem functioning and the delivery of ecosystem services that are essential for agricultural production and maintaining ecological processes for life on Earth (Losey and Vaughan 2006; Lavelle et al. 2006; Payne and Van Itterbeeck 2017). The conservation of invertebrate biodiversity should therefore be an important consideration when planning and managing ecosystems.

1.5 Aim of research

The overall aim of this thesis is to assess the success of the different zones of the KBR with increasing land-use intensity away from the core for arthropod conservation and to provide evidence-based recommendations for management and planning in order to protect and enhance biodiversity across the landscape. Special focus is on the impact of commercial fruit farming, since it is an important economic activity in the study area, but can be detrimental to

arthropod diversity (Adu-Acheampong et al. 2016). The thesis is composed of several complementary studies that investigate sub-questions that are relevant to the ecological functions of the different zones (Table 1.1), and employs quantitative methods used in either SCP or landscape ecology.

Table 1.1 Research questions

Zone	Function	Question	Chapter
Core	Conservation	Does arthropod diversity track plant diversity?	Chapter 2
		How well is arthropod diversity represented in core areas?	Chapter 3
Buffer	Buffer core	Is the buffer zone effective in protecting the core area from activities in the transition?	Chapter 3, 4
	Complementarity	Does the buffer area complement conservation in the core area?	Chapter 3
Transition	Sustainable development	How are fruit orchards influencing diversity in adjacent habitats?	Chapter 3, 4
		How does land-use intensity at different scales affect arthropod diversity across the fruit production landscape?	Chapter 5

The thesis is composed of six chapters. Chapters two to five present the results of the research, written in the form of scientific papers. The results of this research are discussed in Chapter 6 and recommendations are made based on the findings.

1.6 Overview of chapters

Aims and relevance of each chapter:

Chapter 2 – Determine if there is congruence between arthropod and plant diversity in a biodiversity hotspot and identify underlying environmental drivers.

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Vascular plants often form the basis of conservation planning and assessment (Ryti 1992; Myers et al. 2000). I assessed the effectiveness of plant diversity as a surrogate for arthropod diversity in natural areas in the KBR. I explored the influence of arthropod trophic group, habitat association and the spatial scale considered on the relationship between arthropod and plant diversity. I investigated the differential influence of background explanatory variables on plant and arthropod diversity patterns and assessed the surrogacy value of plants relative to that of environmental variables for arthropod diversity.

Chapter 3 - Complementary value of the buffer zone of the Kogelberg Biosphere Reserve for increasing local representativeness of epigaeic arthropods

The main aim of this chapter was to assess the complementary value of the buffer zone for epigaeic arthropod conservation. Information on epigaeic arthropod species turnover and environmental predictors was used in a community level modelling approach to 1) identify important drivers of arthropod turnover (including environmental- and human-influenced factors), 2) assess how well environments present in the buffer zone are represented in the core zone, 3) evaluate gaps in biological survey coverage, 4) quantify the complementarity value of buffer zone in terms of these drivers, and 5) assess whether transformation in the buffer areas has altered this value.

Chapter 4 - Differential influence of orchard edges on the diversity of specialist and generalist epigaeic arthropods in adjacent fynbos habitat

I investigated the influence of commercial fruit orchards on epigaeic arthropod diversity in adjacent natural vegetation. I examined the influence of distance from edge, edge-related changes in local variables, orchard management, orchard age and the presence of windbreaks on epigaeic arthropod species richness and composition. Different groups were assessed based on habitat fidelity, i.e. species associated with the non-crop habitat (stenotopic species), species associated with the crop habitat (cultural species) and species that showed no preference for either crop or non-crop habitats (ubiquitous species).

Chapter 5 - Managing spillover of epigaeic arthropods in perennial crops: the influence of landscape and local scale land-use intensity and permeability on species richness and beta diversity in orchards in a biosphere reserve

I compared different trophic groups of ground dwelling arthropods in pome fruit orchards and adjacent non-crop habitats in terms of species richness, abundance and beta diversity and assessed the influence of local (management) and landscape (proportion of crops in the landscape) scale land-use intensity and proximity to non-crop habitats on species richness, abundance and beta diversity (replacement and nestedness components). I also assess the potential of increasing orchard permeability through reducing orchard contrast.

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Chapter 2 Congruence between arthropod and plant diversity in a biodiversity hotspot largely driven by underlying abiotic factors

Abstract

Plants often form the basis of conservation planning and management. The effectiveness of plant diversity as a surrogate for arthropod diversity was assessed in natural areas in the Kogelberg Biosphere Reserve, a hotspot of floral endemism in the Cape Floristic Region (CFR), South Africa. Arthropods and plants were sampled across 30 topographically heterogeneous sites in a spatially nested design. The relationship between plants and arthropods was quantified in terms of species richness, assemblage variation, and assemblage turnover. The influence of arthropod trophic groups, habitat association, and spatial scale were also explored. Generalized dissimilarity modelling was used to investigate differential influence of groups of explanatory variables (geology, disturbance, local site characteristics, refuge, mesoclimate, terrain) on arthropod and plant turnover. Congruence in assemblage variation was restricted to local scales, and only present between plants and those arthropods associated with the foliar component of the habitat. Weak congruence in species turnover was due to differences in the relative importance of explanatory groups, with different variables within each explanatory group being important, and similar variables predicting different turnover patterns. For both groups, variables related to geology and fire history were important for assemblage turnover. These variables are already incorporated in conservation planning and management for plant diversity across the CFR. Overall plant diversity was a weak surrogate for the arthropod groups included in this study, suggesting that as an alternative, environmental surrogates for arthropod diversity perform better.

Keywords: Surrogate, biodiversity indicator, biodiversity hotspot, alpha diversity, beta diversity, conservation planning, arthropods, plants

2.1 Introduction

Comprehensiveness entails sampling the full variety of biodiversity at multiple levels, including structural, compositional, and functional perspectives (Noss 1990). This in itself poses a problem because there is too much biodiversity for us to measure all of it directly

(Rodrigues and Brooks 2007). To overcome this problem, we regularly make use of surrogates (or biodiversity indicators) that can act as proxies for broader biodiversity value (e.g. Reid et al. 1993). Often the choice of surrogate is influenced by many factors, including the size of the study area (Ferrier 2002), limitations related to data availability (Rondinini et al. 2006), survey costs (Souza et al. 2016) and taxonomic expertise (Sauberer et al. 2004). As a result, the choice of biodiversity surrogate can introduce subjectivity into every conservation planning process (Rondinini et al. 2006) and indicator selection should be well founded and validated (Heink and Kowarik 2010).

One problem that can arise when using surrogates pertains to the level of congruence between the distributional patterns of the surrogate and biodiversity as a whole (Ferrier 2002). To test the effectiveness of one surrogate group in representing overall biodiversity would entail comprehensive knowledge of all biodiversity (which is strictly speaking impossible) (Rodrigues and Brooks 2007; Wilson et al. 2009). Nevertheless, the urgency with which many conservation decisions have to be made requires surrogates that are reasonably good at representing other biodiversity features (Wilson et al. 2009). In this regard, cross-taxon comparisons can be valuable when looking for generalities in the factors that shape biological communities.

Studies have confirmed apparent strong cross-taxa congruence, but the underlying causes remain poorly understood (Lovell et al. 2007; Toranza and Arim 2010; Özkan et al. 2014) and the predictive power of surrogates is still questionable (Lovell et al. 2007). An important factor that influences surrogate effectiveness is spatial scale (Favreau et al. 2006). Congruence between taxa diversity may be stronger at larger spatial and taxonomic scales (e.g. studies comparing grids, regions and countries or families rather than species) (Reid 1998; Lamoreux et al. 2006; McKnight et al. 2007). Although useful for the initial stages of conservation planning, such coarse scales are of limited practical value for real world conservation planning scenarios (e.g. identifying critical habitats within established reserves, informing land-use planning, or efficient expansion through private partnerships) (Reyers et al. 2002; Ricketts et al. 2002; Stork and Habel 2014).

Basic surrogate requirements include 1) response to similar underlying environmental gradients as the group being represented (or the 'target' group) and 2) similar sensitivity to conditions as the target group (Oliver et al. 1998; Pharo et al. 1999; Williams et al. 2000). Weak congruence in biodiversity patterns at finer scales can result from differential responses

of the surrogate and target to local environmental variables (Heino et al. 2009). Using a group of organisms as a surrogate instead of individual species or genera may be more flexible in representing a broader array of species because it is not so dependent on the biological details of the specific species or genera (Wiens et al. 2008). In this case, it would be valuable to understand the environmental factors driving species assemblages among different taxa (Kirkman et al. 2012). Although species rich surrogate groups can also make monitoring more difficult (Gerlach et al. 2013). Some species qualify for special attention in conservation management plans (e.g. contribute to the uniqueness of a conservation area) and it would be useful if such groups could be combined with the surrogate approach.

Another important factor affecting the predictive power and effectiveness of a surrogate involves the measure of diversity used, as well as the associated testing methods (Su et al. 2004, Gioria et al. 2011). Species richness may not be the best indicator of diversity, since using species richness to prioritize areas can result in sites containing similar subsets of species (Mellin et al. 2011). Effective conservation across spatial scales requires an understanding of the relationship between locally collected data and regional diversity dynamics, as well as the mechanisms that are important for changes in diversity from local to regional scales (Kraft et al. 2011). An important question that conservationists face relates to how locally measured changes in biodiversity (alpha diversity) influence regional diversity (gamma diversity) (Socolar et al. 2016). In response to these questions, the past decade has seen a renewed interest in understanding the spatial variation in species composition, otherwise known as beta diversity (Tuomisto 2010; Anderson et al. 2011). For a representative array of biotic communities to contain the majority of species within a given area (i.e. coarse-filter conservation (Hunter 1991, 2001)), tests of cross-taxon congruence should focus on congruency patterns of beta diversity rather than alpha diversity among taxa (Su et al. 2004). At the same time, a comprehensive assessment of cross-taxa relationships should involve multiple approaches and measures (Gioria et al. 2011).

Vascular plants are often used for defining biodiversity hotspots and in the selection of protected areas (Ryti 1992; Myers et al. 2000). The majority of eukaryote terrestrial species on Earth are arthropods (Zhang 2011). The ecology and life history of many arthropods and other invertebrates are unknown, making it often necessary to regard them on the basis of trophic position or morphology (Oliver and Beattie 1996). Considering the large contribution that arthropods make to overall terrestrial diversity and the important roles that insects and other invertebrates play in ecosystem processes (e.g. seed dispersal, predation, decomposition)

(Weisser and Siemann 2007), understanding how plant diversity reflects arthropod diversity is important for conservation that is compositionally and functionally representative.

A region of exceptional botanical diversity is the Cape Floristic Region (CFR), South Africa (Goldblatt and Manning 2002, Rebelo et al. 2006). Covering an area of only 90 000 km^2, the CFR contains more than 9000 plant species, most of which (approx. 69%) are endemic (Rebelo et al. 2006; Allsopp et al. 2014). Conservation planning, management and assessments across different spatial and taxonomic scales in the CFR are largely based on plant data (e.g. Rouget et al. 2003; Cowling et al. 2003; Midgley et al. 2003). Most of the CFR is covered with fynbos, a sclerophyllous shrubland. Local plant diversity of fynbos is high, but it is the high beta diversity (over hundreds of meters to kilometres) that makes the diversity exceptional (Rebelo et al. 2006).

Plant diversity is often a better indicator for primary consumer than secondary consumer diversity (Castagneyrol and Jactel 2012, Stork and Habel 2014), but the sclerophyllous nature of many fynbos plants may limit this to only those groups that are locally host specific (e.g. Wright and Samways 1999; Kemp and Ellis 2017). Previous work across the CFR that has related arthropod diversity to plant diversity has mainly focused on specialized herbivorous groups or groups associated with the foliar component of the habitat. Results suggest a positive relationship (Wright and Samways 1999; Procheş et al. 2009; Kuhlmann 2009; Kemp and Ellis 2017) with arthropod diversity and plant diversity being directly correlated at very local scales (Kemp and Ellis 2017), and underlying abiotic variables becoming more important at broader (inter-biome) scales (Procheş et al. 2009). It is still uncertain whether this relationship will hold when including surface active arthropods or which underlying environmental variables are important for potential congruence at scales corresponding to a defined conservation area. Strong congruence between plant and arthropod diversity would allow us to use plant diversity to predict arthropod diversity (or vice versa). Understanding the relationship between plant and arthropod diversity (and the factors that shape this relationship) would also improve our understanding of the drivers of arthropod diversity (Lewinsohn and Roslin 2008; Pellissier et al. 2013), as well as the factors that are important for promoting representativeness across the study area.

This study investigates the effectiveness of plant diversity as a surrogate for arthropod diversity across topographically heterogeneous sites in the terrestrial component of the Kogelberg Biosphere Reserve, a centre of plant endemism within the CFR. Different measures

are used to assess the relationship between plant and arthropod diversity, including congruence in species richness, beta diversity due to assemblage variation and beta diversity due to assemblage turnover. In addition, the surrogate effectiveness of a subset of plant species that are associated with the study area, the influence of attributes of the target taxa (habitat association and trophic level), and the spatial scale considered are also explored. Finally, I assess explanatory sources important for overall arthropod and plant assemblage turnover, as well as turnover patterns along common environmental gradients. Floristic dissimilarity was also used as a predictor in arthropod turnover to determine which environmental variables are the most important for congruence in turnover patterns and to test for congruence beyond that which can be explained by similar responses to common environmental variables.

2.2 Methods

2.2.1 Study area

The Kogelberg Biosphere Reserve (KBR) is situated at the south-western tip of South Africa. Protected natural areas (or core zones) are mostly restricted to mountainous parts and make 43% of its approx. 87 000 ha terrestrial component. Most of the land that comprises the buffer zones (adjacent areas in private ownership, approx. 24% of the terrestrial component) is in a natural or near-natural state (Pool-Stanvliet 2014). The KBR is considered a floral hotspot within a hotspot and more than 80% of its core and buffer areas are made up of Kogelberg Sandstone Fynbos (KSF) which has exceptional species-level endemism (Rebelo et al. 2006).

2.2.2 Study design

A spatially nested design for site selection was adopted. A five meter resolution digital elevation model and information on fire history were used to incorporate topographic and fire history heterogeneity across the sites. Four locations were selected across the core and buffer areas of the KBR (Figure 2.1). At each location, two sets (or clusters) of sites were situated, one on northerly slopes and the other on southerly slopes. Each cluster consisted of three sites arranged as an equilateral triangle. Distances between three sites in a cluster ranged between 250 m to 475 m. This distance limited sites within each cluster to a 100 m elevation zone.

Northerly and southerly clusters were situated so as to limit differences in elevation between clusters at each location. Minimum distances between clusters at each location ranged from 550 m to 1600 m. This arrangement of sites allowed us to investigate the interrelated influence of topography and local site characteristics as well as include different geographical distances between sites when analysing beta diversity as assemblage turnover. It also allowed the analyses of beta diversity as assemblage variation at three different scales: cluster (between sites in a cluster, $\beta_{v.1}$), location (between sites at a location, $\beta_{v.2}$) and landscape scales (between sites at all locations, $\beta_{v.3}$) (Figure 2.1). During February 2016, six sites (two adjacent clusters of three) burned down and six replacement sites were located nearby. All sites were restricted to natural vegetation and the same vegetation type (KSF). Vegetation age across the study sites ranged between four and >30 years and elevation between 73 and 773 m a.s.l.
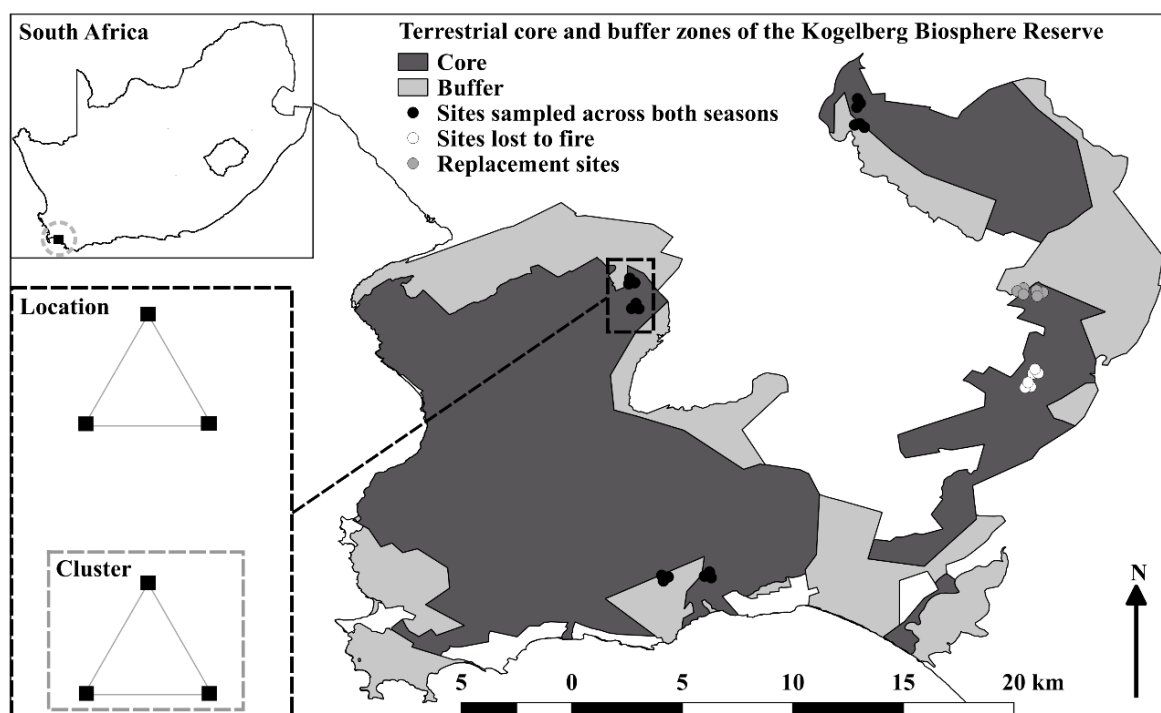
Figure 2.1 Map of study sites. At each location six sites were arranged as two cluster of three sites each, one on northerly slopes, the other on southerly slopes

2.2.3 Biological data

Sampling was carried out during two seasons: summer (October) 2015 and autumn (March) 2016.

Each site consisted of a 10 x 10 m plot. Within each plot, arthropods were sampled from the vegetation using a sweep net (100 sweeps per season) and a commercially available vacuum sampler (STIHL BG 56 C, 60 suction samples per season). Both these methods were used to reduce the taxonomic bias which can arise from using only either one (Doxon et al. 2011; Swart et al. 2017). Sweep net sampling was always conducted before using the vacuum sampler, as the latter may disturb arthropods and reduce the effectiveness of the sweep net. Each suction sample consisted of inserting the 30 cm diameter nozzle of the vacuum sampler into the vegetation for at least three seconds. Epigaeic arthropods were sampled using four pitfall traps placed at each corner of the plot (each trap 7 mm in diameter, filled with a 50% ethylene glycol solution, left out for five days per season). Arthropod samples were taken back to the laboratory and sorted to family or superfamily (except mites, the majority of which could only be sorted to order due to the lack of taxonomic resolution) and then to morphospecies and species level where possible. Insects were sorted using the reference guide by Scholtz and Holm (2008), except Formicideae, which were based on Bolton (1994). Acari were sorted with guided input from a specialist. Araneae were sent to specialists (voucher specimens are being held at the South African National Collection of Arachnida). Voucher specimens for the remaining arthropods are being held at the University of Stellenbosch. Functional groups were based on the predominant feeding habit at the family level (or order level for mites), namely predaceous/parasitic, herbivore (which included pollen feeders and wood borers), omnivore, and detritivores (which included saprophages and fungivores). All plants within the 10 x 10 m plot were identified. The majority of plants were identified to genus (>75% to species level, the rest was defined as morphospecies). I refer to 'morphospecies' as 'species' in the rest of the paper.

2.2.4 Environmental predictors

To investigate the influence of environmental predictors on arthropod and floristic turnover, 66 interrelated predictors were compiled into six broad groups: 1) geology, 2) disturbance, 3) local site characteristics, 4) refuge, 5) mesoclimate, and 6) terrain. These variables consisted of both site-measured attributes (measured at the time of sampling) and variables derived from continuous spatial layers. Table S1 lists all candidate environmental variables and their sources.

Bivariate scatter plots of environmental variables were used to view the relationship between pairs of variables. Variables were not considered further if 1) they had a high Pearson correlation (r > 0.8) (in which case only one of the pair were included for further analysis), 2) they were a representative subset of alternative variables (e.g. use minimum and maximum vegetation cover instead of mean), or 3) were similar in function but not directly interchangeable (Williams et al. 2012). After these considerations, 47 variables were retained for analyses.

2.2.5 Analyses

Plant data were further split into those genera which are known to show high diversity and endemism within KSF (referred to here as 'KSF-endemics', see Table S2 in supplementary material for list of genera) (Rebelo et al. 2006). Data on arthropods were split according to functional groups or the habitat association: epigaeic (sampled using pitfalls) and foliar (sweep net and vacuum samples pooled). As ants in fynbos show remarkable resilience to fire (Pryke and Samways 2012) and dominate terrestrial systems, foliar and epigaeic arthropod groups were further split into datasets that exclude ants ('non-ant').

2.2.5.1 Species richness correlates

To measure the effectiveness of sampling effort, species accumulation curves were plotted for plant and arthropod groups weighted by sampling effort (i.e. number of site visits) with the package 'vegan' (Oksanen et al. 2018) in R, version 3.5.0 (R Core Team 2018).

Plant and arthropod species richness were compared using generalized linear models in R. Since sampling effort was different between sites, I used the number of visits to a site as an offset and modelled species richness as rates instead of counts. This was done with plants (all plants or KSF-endemics) as predictors and arthropod groups (all arthropods, all arthropods non-ant, epigaeic, epigaeic non-ant, foliar, foliar non-ant, or arthropod functional groups: herbivores, parasite/predators, omnivores, detritivores) as response variables. Spatial-autocorrelation was assessed with correlograms (Bjørnstad and Falck 2001). With a Poisson distribution, sampling frequency as offset and either all plants or KSF-endemics as a predictor,

none of the arthropod groups showed significant spatial correlation. Predictor significance was assessed using Wald tests.

2.2.5.2 Congruence in beta diversity

Two types of beta diversity were assessed: 1) variation (non-directional, β_v) and 2) turnover (directional, β_t) (Anderson et al. 2011).

Multivariate dispersion was quantified as the mean distance in ordination space between a sampling unit and the regional compositional median (Anderson et al. 2006). This equates to the variation among spatial units as a measure of variation in community structure (β_v), as defined by Anderson et al. (2011). Variation in community structure was calculated for three scales by specifying the compositional median as either each cluster ($\beta_{v.1}$), location ($\beta_{v.2}$), or the entire landscape ($\beta_{v.3}$). Linear models were used to compare β_v between arthropods and plants at each scale. Spatial-autocorrelation was assessed with correlograms (Bjørnstad and Falck 2001). Where spatial-autocorrelation was detected, the introduction of location as a random effect removed spatial correlation in linear mixed-effects models. All models were repeated, weighted by sampling effort (number of site visits). Distance to centroid values were calculated using the 'vegan' package, and models were fitted and predictor significance assessed using the packages 'lme4' (Bates et al. 2015) and 'lmerTest' (Kuznetsova et al. 2017) in R.

Generalized dissimilarity modelling (GDM, Ferrier et al. 2007) was used to evaluate the relative importance of environmental predictors for arthropod and plants species compositional turnover. GDM is a non-linear matrix regression technique that takes into account variation in the rate of compositional turnover at different positions along environmental gradients, as well as the curvilinear relationship between increasing environmental/geographical distance and compositional dissimilarity (Ferrier et al. 2007). Best sets of explanatory variables were selected for each explanatory group separately by permutation-based backward elimination. For each explanatory group, only variables that had significantly higher explained deviance ($p < 0.05$) than that observed after 500 random permutations were retained. To moderate over-fitting of models, a threshold minimum of 0.05 for partial percent explained deviance (ED) for a variable to be retained was used and marginally significant variables removed. As I was only

interested in the extent to which different drivers in community turnover overlap, no secondary backward elimination procedure was used to reduce the number of variables in the initial models (which included all variables that were selected for each explanatory group separately). The Sørensen dissimilarity index was used as dependent variable for all GDM models, and three I-spline basis functions per predictor. All models on arthropods were weighted by sampling frequency (Ferrier et al. 2007). Variance partitioning (Borcard et al. 1992) was used to calculate the unique contribution to ED by each explanatory group when including all other selected variables. The GDM model-fitted transformations of those variables which were selected for both plants and arthropods and for which ED >0.05 when all other variables were include in the model were plotted.

The above procedure was repeated for all arthropods, but here only those variables that were significant after a secondary elimination process were retained (following the process outlined by Williams et al. 2012). The vegetation dissimilarity matrix was then included as a biotic-predictor to test if any additional variation could be explained (which could reflect either common responses to unmeasured variables or biotic interactions) and to investigate which explanatory groups were important for both arthropods and plants (e.g. Jones et al. 2013). This was repeated with a dissimilarity matrix of KSF-endemics as biotic-predictor. Variation partitioning was used (e.g. Blois et al. 2013; Fitzpatrick et al. 2013; Landesman 2014) to calculate the unique and shared contribution to ED by biotic predictors, different explanatory groups (i.e. only those variables retained after secondary backward elimination), and geographical distance. Variation partitioning results are only reported for the biotic predictor (all plants/KSF-endemics) that contribute the most to ED (shared and unique fractions combined). Results from variation partitioning were plotted using area-proportional Euler diagrams. Analyses were done using the R packages 'vegan' and 'gdm' (Manion et al. 2017), and the Euler diagram plotted using the 'eulerr' package (Larsson 2018).

2.3 Results

2.3.1 Characteristics of floral and arthropod data

A total of 201 plant (of which 89 were KSF-endemic) and 522 arthropod species (of which 350 foliar, 279 epigaeic, 209 predaceous/parasitic, 164 herbivore, 73 omnivore, and 76 detritivores) were sampled. The largest plant families were Restionaceae (38 species), Asteraceae (33),

Proteaceae (27) and Ericaceae (21). The sampled arthropod assemblage was dominated by Araneae (106 species), Hemiptera (102) and Coleoptera (101).

2.3.2 Species richness

Species accumulation plots did not reach an asymptote, suggesting more species are present than sampled here (see Appendix 1 for accumulation curves). None of the generalized linear models relating either all plants species richness or KSF-endemic species richness to rates of arthropod species richness were significant (see Table S3).

2.3.3 Assemblage variation

Non-ant foliar arthropod assemblage variation showed a significant positive relationship with that of all plants and KSF-endemics at the local cluster scale (Table 2.1, more information reported in Table S4). Non-ant foliar arthropod assemblage variation also showed a significant positive relationship with KSF-endemic assemblage variation at the landscape scale, but this was only significant when weighted by sampling frequency. None of the other arthropod groups was significantly related in assemblage variation to any of the plant groups at any of the measured scales.

Table 2.1 Summary of linear models and linear mixed-effects models describing the relationships between arthropod and plant assemblage variation (β_v) at the cluster ($\beta_{v.1}$), location ($\beta_{v.2}$) and landscape ($\beta_{v.3}$) scales. Values in parentheses are weighted by sampling frequency (KSF: Kogelberg Sandstone Fynbos; KSFend: plant genera with high richness or endemism in KSF; non-ant: data set excluding ants; foliar: sampled from vegetation; epigaeic: sampled using pitfalls)

	$\beta_{v.1}$		$\beta_{v.2}$		$\beta_{v.3}$	
	All flora	KSFend	All flora	KSFend	All flora	KSFend
All arthropod	-0.01	-0.01	0.01	0.01	-0.11	-0.11
	(0.04)	(-0.01)	(0.01)	(0.01)	(-0.13)	(-0.11)
All arthropod (non-ant)	0.14	0.05	0.03	0.05	-0.05	0.15
	(0.16)	(0.08)	(0.04)	(0.07)	(-0.05)	(0.14)
Strata						
Foliar	0.22.	0.13	0.11	0.10	0.11	0.11
	(0.23.)	(0.12)	(0.06)	(0.08)	(0.09)	(0.09)
Foliar (non-ant)	**0.34****	0.20.	0.18	0.15.	0.14	0.15.
	(**0.37****)	(0.20.)	(0.14)	(0.14.)	(0.13)	(**0.15***)
Epigaeic	-0.22.	-0.10	-0.07	-0.07	0.01	0.08
	(-0.17)	(-0.10)	(-0.07)	(-0.08)	(0.01)	(0.03)
Epigaeic (non-ant)	-0.18	-0.07	-0.09	-0.09	0.21	0.18
	(-0.13)	(-0.06)	(-0.05)	(-0.06)	(0.18)	(0.16)
Functional groups						
Herbivores	0.10	-0.05	0.17	0.17.	0.17	0.13
	(0.19)	(-0.01)	(0.10)	(0.14)	(0.12)	(0.11)
Predators	0.07	0.06	-0.14	-0.02	-0.14	0.01
	(0.12)	(0.07)	(-0.07)	(-0.02)	(-0.05)	(0.09)
Omnivores	-0.32.	-0.23	-0.02	-0.02	-0.11	-0.20
	(-0.27)	(-0.23)	(-0.07)	(-0.06)	(-0.24)	(-0.29.)
Detritivores	0.18	0.23	0.08	0.07	0.09	0.07
	(0.11)	(0.17)	(0.12)	(0.09)	(0.08)	(0.05)

Values indicate estimates.
.$p<0.1$, *$p<0.05$, **$p<0.01$

2.3.5 Assemblage turnover

2.3.5.1 Initial models

When including all variables selected for each explanatory group the total explained deviance (ED) in arthropod species turnover was 50.73% and the corresponding value in plants was 54.04% (Figure 2.2). ED for each explanatory group ranged between 9.50% and 43.24% in arthropods and 0% and 32.40% in plants.

Variables related to geology explained the highest total ED in arthropod and plant turnover (43.23% and 32.40% respectively). For arthropod turnover, the best geology related variables included (in order of importance) average soil clay content, distance to nearest shale band, and distance to edaphic interface, while for plants they included distance to nearest shale band, distance to edaphic interface and average soil clay content. For both arthropods and plants, these predictors explained the second highest unique fraction in ED (2.37% and 5.81% respectively).

Predictors related to local site characteristics explained the greatest independent fraction of ED in plant turnover (16.51%) and arthropod turnover (3.29%). For plants these predictors included NDVI (normalized difference vegetation index) of August 2015, maximum vegetation density, and maximum soil moisture (total ED 31.74%) and for arthropods maximum vegetation height and maximum soil moisture (total ED 19.66%).

Fire frequency in the past five years was the only important disturbance predictor for both arthropod and plant turnover (total ED 23.17% and 9.97% respectively), and explained a higher independent fraction of ED in arthropod turnover (1.79% compared to only 0.39% for plants). Geographical distance explained more deviance in plant species turnover (total ED 16.61%, unique fraction1.14%) compared to arthropod species turnover (total ED 11.62%, unique fraction 0.00%). Terrain variables explained more of the deviance in arthropod turnover (total ED 11.12%, unique fraction 0.95%) than plant turnover (none of the terrain variables were significant for plant turnover), and included elevation, topographic wetness and aspect for arthropods.

Among the refuge variables, distance to nearest riparian vegetation and distance to nearest wetland were important predictors of arthropod turnover (total ED 12.13%, unique fraction 1.22%) while distance to nearest permanent wetlands and reservoirs were important predictors for plant species turnover (15.87%, 0.48%). Standard deviation of mean monthly maximum temperature throughout the year was the only important mesoclimate variable for arthropods (total ED of 9.50% and unique ED of 0.92%), while none of the mesoclimate variables was important for plant species turnover.

Of the 10 variables selected for plants and 13 variables selected for arthropods in these initial models, six were similar (of which five were derived from spatial layers and only one was site measured). These included three variables related to geology (distance to edaphic interface, average soil clay content, and distance to nearest shale band), one disturbance

variable (fire frequency in the past 5 years), one site characteristic variable (maximum soil moisture (site measured)) and geographical distance between sites (Figure 2.3a-f).

Arthropod and plant species turnover patterns showed different responses to some of the selected variables. Plants showed more rapid species turnover at shorter geographical distances (especially below c. 1.3 km), while arthropod species turnover increased more steadily with geographical distance. Arthropods, but especially plants, showed greatest compositional turnover closer to edaphic interface areas (< 2 km). Both groups showed high turnover rates at distances close to shale bands (< 1 km) and showed steady increase in turnover at low soil clay content. Both arthropod and plant species turnover increased with fire frequency in five years. Plants showed higher turnover rates than arthropods with increasing soil moisture.
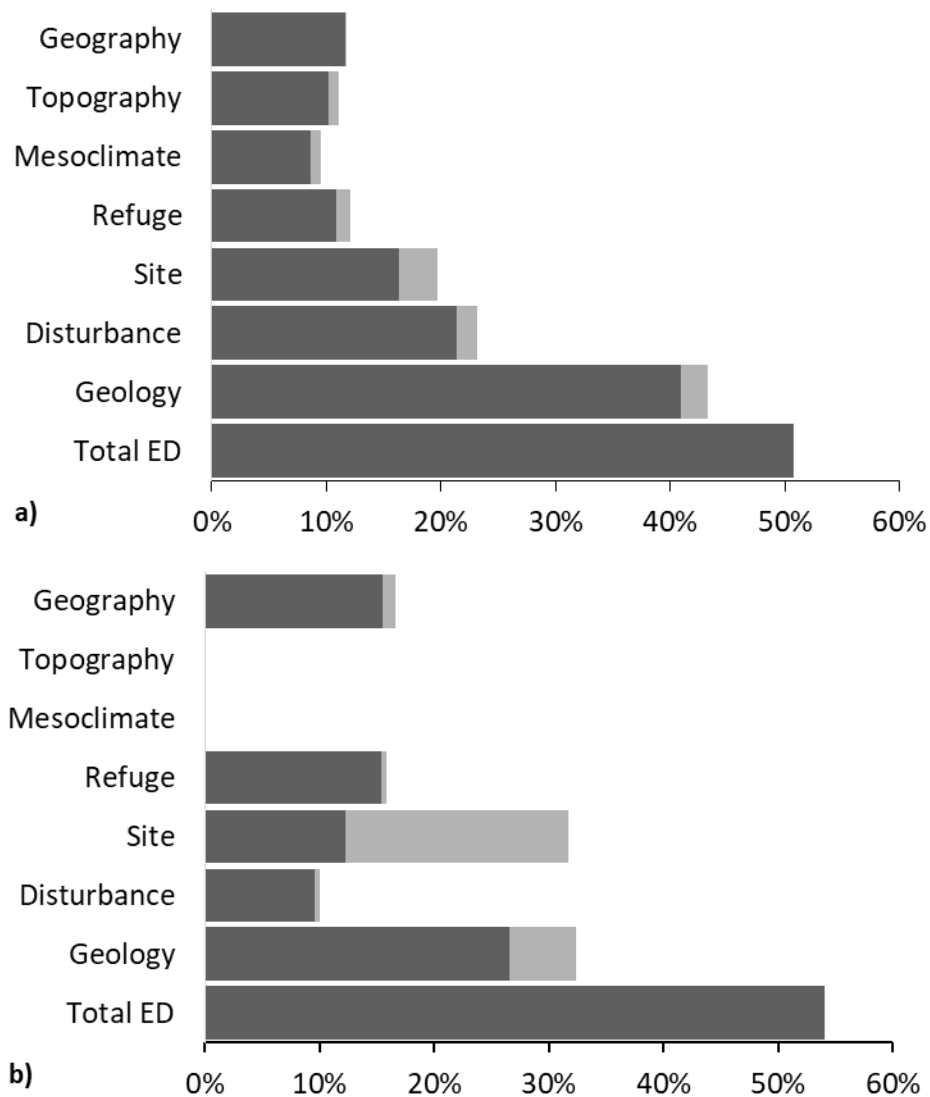
Figure 2.2 Total model explained deviance (ED) for each explanatory group for unrefined models of a) arthropod and b) plant species turnover. Light grey indicates unique ED when all selected variables are considered
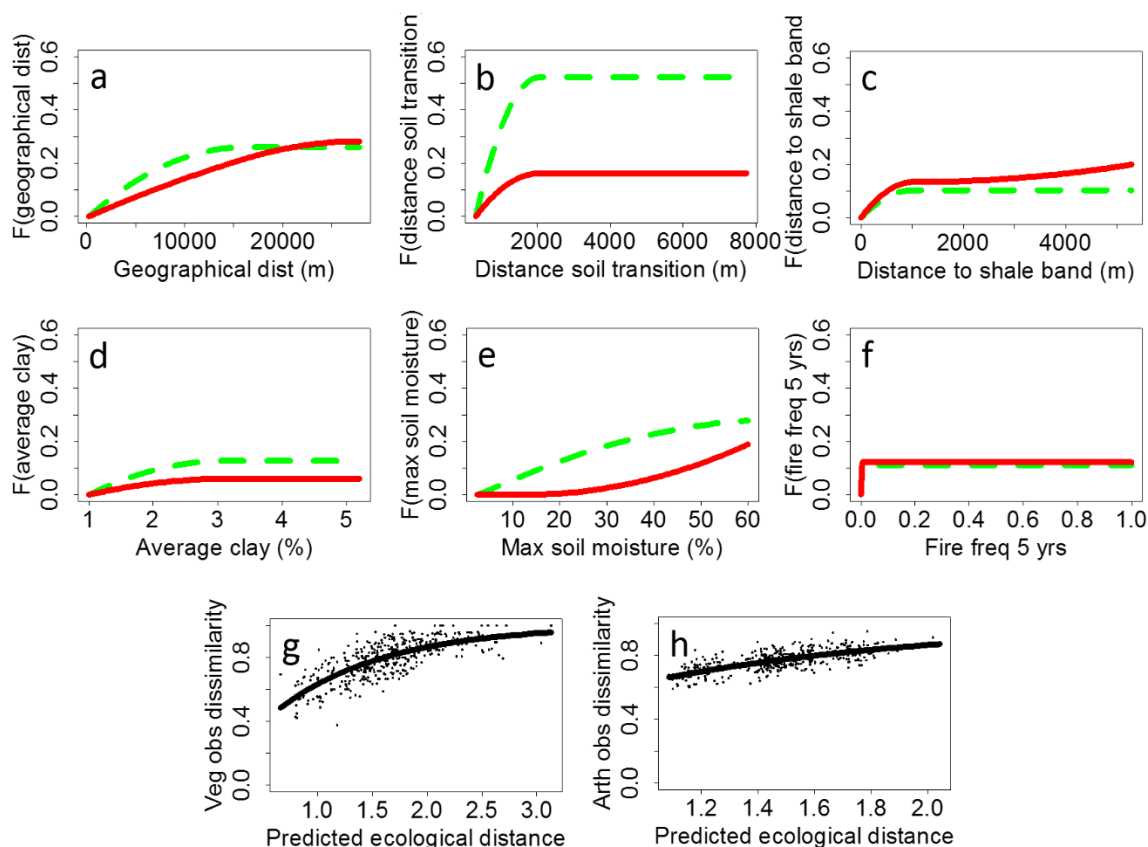
Figure 2.3 Generalised dissimilarity model (GDM)-fitted transformations of geographical distance (a) and environmental variables (b-f) that were selected as predictors for both arthropod (red solid line) and vegetation (green dashed line) species turnover during the initial variables selection procedure. The maximum height of each curve represents the total amount of turnover explained by the environmental gradient while holding all other selected variables constant. The last two panels show the relationship between observed vegetation (g) and arthropod (h) compositional dissimilarity and the predicted ecological distance

2.3.5.2 Refined arthropod models

The refined model of arthropod species turnover explained 46.83% and consisted of five environmental variables (both site measured and spatial variables) related to geology (total ED 30.92% and unique ED 8.15%), disturbance (23.17% and 7.24%) and site characteristics (19.66% and 6.60%). Geographical distance was also significant (total ED 11.62% and unique ED 0.00%). Four of the five environmental variables corresponded with those variables selected by the unrefined models for plant species turnover, namely distance to edaphic interface, average soil clay content, fire frequency in five years, and maximum soil moisture.

Deviance explained by the vegetation dissimilarity matrices was 10.43% for all plants and 10.40% for KSF endemics. Only results for inclusion of the dissimilarity matrix of all plants are reported here. Inclusion of the plant species dissimilarity matrix as biotic predictor in the model increased total ED by only 0.13% and there was substantial covariance between the total deviance explained by the biotic predictor and the other explanatory groups (Figure 2.4). Highest shared explained deviance between the biotic predictor and the environmental variables was with those variables related to geology, disturbance, and geographical distance (6.97%), while no deviance was shared with local site variables alone.
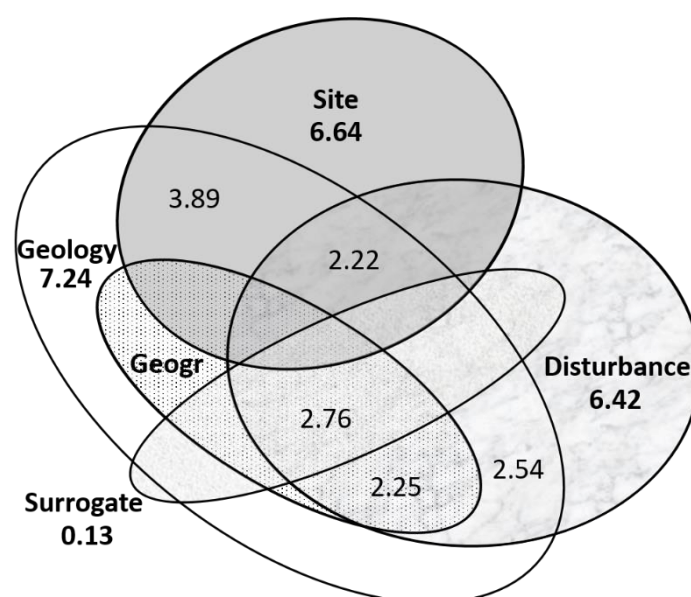
Figure 2.4 Variance partitioning of arthropod species turnover among the selected explanatory groups using generalised dissimilarity modelling. Values represent fractions of total percent deviance explained. Shaded areas represent fractions explained by selected explanatory data sets (geol – geology, dist – disturbance, site – site characteristics, surrogate – dissimilarity matrix of vegetation composition, geogr – geographical distance). Values in bold represent unique fractions. Only shared fractions > 2% are shown

2.4 Discussion

A large proportion of the world's terrestrial species (>80%) remain undescribed (Mora et al. 2011), making it necessary to rely on surrogate species or groups of species that can effectively describe broader biodiversity patterns. Attempts to identify and test surrogate measures of biodiversity have been criticized for being inconsistent with ecological theory and congruence

may be limited to groups with direct functional links (Stork and Habel 2014; Castagneyrol and Jactel 2012), comparisons across broad spatial scales (Lewandowski et al. 2010), and limited to areas with strong and persistent environmental gradients (Sætersdal and Gjerde 2011). Here we found little evidence that plant data alone are a good surrogate for arthropod diversity. Congruence between arthropods and plants was determined by the habitat association of the target group, limited to very local scales, and influenced by differential responses of plants and arthropods to underlying environmental gradients.

One mechanism which may explain the proposed positive relationship between the diversity of plant species and that of associated consumer species is related to productivity. Diverse plant communities are often more productive compared to simple plant communities (e.g. Tilman et al. 2001), and the higher amount of resources associated with higher above ground primary productivity should support more herbivore individuals, and therefore more consumer species (Srivastava and Lawton 1998). The results do not indicate a stronger relationship between primary arthropod consumer and plant diversity than other trophic groups. Procheş et al. (2009) found functional groups other than herbivores (i.e. detritivores) to show a stronger relationship with fynbos plant species richness. Sclerification can limit the feeding of sucking and chewing insects (Hoffman and McEvoy 1986; Scheirs et al.1997) and the physical limitations imposed on herbivores can directly curtail abundance (Peeters 2002). The sclerophyllous nature of fynbos vegetation may therefore limit strong herbivore plant diversity relationships to host specific primary consumers (e.g. Wright and Samways 1999; Kemp and Ellis 2017).

Congruence in plant and arthropod diversity measured as assemblage variation was in part determined by the habitat association of arthropods. Previous work that has reported positive congruence in species diversity of plants and arthropods in the Cape Floristic Region (CFR) has focused on those groups sampled from the foliar component of the habitat. These results have been inconsistent in terms of scale, with positive correlations either restricted to very local scales (<10 x 10 m) (Kemp and Ellis 2017) or present for up to 1 km (Procheş et al 2009). Here, strong congruence in assemblage variation was restricted to local scales (250 to 475 m) and only present between the entire plant assemblage and arthropods sampled from the vegetation when ants were removed. Within the fire prone fynbos, ants show great resilience to fire (Donnelly and Giliomee 1985; Pryke and Samways 2011, 2012), which could explain why their exclusion can improve congruence between plant and foliar arthropod assemblage variation at local scales. Non-ant foliar arthropod assemblage variation also showed a

significant relationship with that of KSF-endemics at the landscape scale, but this relationship was not very strong and only present when the analysis was weighted by sampling frequency. The scale dependency of cross taxon congruence indicates that it is not advisable to use plants as a surrogate for foliar arthropod diversity beyond local scales (Schuldt et al. 2015).

Part of the challenge in identifying effective surrogate groups stems from different taxonomic groups showing differential responses to environmental variables (Heino et al. 2009). Including the plant dissimilarity matrix as a predictor in arthropod species turnover explained (relative to environmental predictors) little of the total deviation in arthropod species turnover. This is partly due to 1) differences in deviance explained by each of the explanatory groups (e.g. local site variables were much more important for plant turnover, while geology was more important for arthropods), 2) different variables being the most important for turnover within each explanatory group (e.g. average soil clay content was more important for arthropod turnover, while distance to shale band intrusions was more important for plant species turnover), 3) different predicted turnover patterns along common environmental gradients (plant species turnover increased more rapidly with maximum soil moisture than arthropod turnover), and 4) common variables predicting similar turnover patterns explaining relatively little of the overall deviance in species turnover.

Congruence in species turnover was due to similar arthropod and plant turnover patterns along variables related to geology, fire history and geographical distance. Both arthropods and plants showed high turnover rates close to edaphic interfaces (up to 2 km) and shale band intrusions (up to 1 km). Edaphic interfaces, specifically composed of juxtaposed acidic and alkaline parent materials, are believed to drive ecological plant diversification (Bakker et al. 1999; Reeves et al. 2001). Previous work in the CFR has recognized these interfaces as spatially fixed components important for maintaining and generating biodiversity (Rouget et al. 2003, 2003b), and have incorporated these into conservation planning aimed at achieving conservation targets and maintaining processes that support diversity across the CFR (Cowling et al. 2003). Although it is unclear whether the high turnover rates observed for arthropods and plants here are due to spatially dependent spillover from these habitats or due to nutrient input, the results support the importance of strong environmental gradients for surrogate effectiveness (Sætersdal and Gjerde 2011), and the role of edaphic heterogeneity for plant turnover and representativeness at finer scales (within a single reserve).

Plant structural diversity has been cited as a potentially important indirect driver of congruence in fynbos plant and arthropod diversity (Procheş and Cowling 2006; Procheş et al. 2009). The structural components that were important for turnover in the entire arthropod dataset here (namely vegetation height) were not the same as those structural variables that were important for plant turnover (vegetation density). This does not mean indirect drivers of congruence can be ruled out, e.g. different structural attributes important for arthropod and plant turnover can be determined by the fire regime (Vlok and Yeaton 1999; Kim and Holt 2012). These results suggest that management aimed at promoting local heterogeneity in habitat structure will promote plant and arthropod diversity, as has been suggested for invertebrates and plants in other Mediterranean systems (e.g. Bonari et al. 2017).

Most of the turnover in arthropod and plant species related to disturbance could be explained by the number of fires in the past five years. For plants, part of this turnover can be explained by high temporal turnover which has been associated with the fire regime at local scales (Thuiller et al. 2007). Many fynbos plants however, require more time to fully recover. Repeated short 4-5 year intervals result in a reduction of dominant reseeding shrubs and an increase in re-sprouting species (Vlok and Yeaton 1999). If reseeding species do not have enough time between fires to mature and set seed again, repeated short term fires can have a negative impact on these species (van Wilgen and Forsyth 1992). For arthropods, these results should be interpreted with caution as there is still a great lack in research on proper implementation of the fire regime (frequency, intensity, season, and size) on fauna (particularly arthropods) in South Africa (Parr and Chown 2003, but see Pryke and Samways 2012, Yekwayo et al. 2018).

The surrogate value of plants as assessed here involves only one goal of conservation planning - representation. As mentioned elsewhere (Ferrier 2002; Rodrigues and Brooks 2007) surrogates can also be assessed in terms of biodiversity persistence by including a temporal dimension (e.g. Lopes et al. 2011; Mackey et al. 2012). An important limitation of the present study is its limited temporal dimension. Another problem is that species accumulation curves did not reach asymptotes for many groups, probably due to many rare species not being sampled in this area of extremely high species richness. Ecologists often make use of standardized sampling to compare incomplete inventories (Cardoso et al. 2009). Here, sampling effort among all sites was not similar, due to factors related to the nature of the study system (i.e. lost to a fire). Although this was taken into account in analyses of the data, the results may still be confounded by differences in sampling effort. Surrogate effectiveness has

been found to be context specific (i.e. determined by the study region (Grantham et al. 2010)), and therefore generalizations to other fynbos vegetation types would require further research. The results are also not representative of specific highly mobile groups (such as Diptera or Lepidoptera). There is also the possibility that plant genera could be a better predictor than plant species, which the present study did not assess (Procheş et al (2009).

Using different approaches and measurements of diversity can elucidate congruence in diversity patterns that may otherwise not be detected, especially in studies restricted to finer scales (Gioria et al. 2011). While some authors argue that different taxa will show highly independent responses to environmental gradients (Beck et al. 2013, Guareschi et al 2015) and others link cross-taxon congruence to common responses (Jetz et al. 2009, Axmacher et al 2009), a combination of these two extremes influencing congruence in arthropod and plant species turnover occurs. Low congruence between plant and arthropod diversity was due to the influence of habitat association of the target group, spatial scale, and differential turnover patterns along environmental variables. Despite differences in turnover patterns in relation to environmental variables, specific variables (geology and fire frequency) did predict similar turnover patterns. These variables are already incorporated in present conservation planning and management of reserve systems across the CFR. Future work should investigate factors important for plant and arthropod congruence in other fynbos vegetation types. Overall plants explained very little additional variation in arthropod turnover. Furthermore, at the spatial scale studied here, conserving arthropod diversity would be more effective if based on environmental surrogates rather than plant diversity.

Areas identified as important for conservation at the global or continental scale need finer-scale assessments to guide conservation action at the local scale (Cowling et al. 2004). Information on environmental surrogates are generally more available than biodiversity data, especially in species rich but poorly explored developing countries (Ferrier 2002). Abiotic surrogates have been incorporated in conservation planning at different resolutions, with goals ranging from designing conservation corridors (Brost and Beier 2012) to addressing modern climate change (Shoo et al. 2011; Olson et al. 2012; Lawler et al. 2015). Our work highlights the importance of including a range of abiotic conditions in the conservation-planning process at the scale of a single reserve for conserving both plant and arthropod diversity.

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Chapter 3 Complementary value of the buffer zone of the Kogelberg Biosphere Reserve for increasing local representativeness of epigaeic arthropods

Abstract

Biosphere reserves (BRs) are areas of high biodiversity value that promote conservation and sustainable development. BRs consist of core, buffer and transition zones. Buffer zones are where human and ecological activities overlap and are key functional spaces in BRs that can have important value in terms of complementarity. I use generalized dissimilarity modelling to describe the compositional dissimilarity of epigaeic arthropod assemblages as a function of environmental drivers between pairs of survey sites, and use the transformed spatial predictors as surrogates for biodiversity to assess complementarity using the Environmental Diversity approach. Important drivers of epigaeic arthropod species turnover were related to mesoclimate, fire history and geology. Buffer areas had important complementary value (including or excluding disturbance variables). Current habitat transformation across core and buffer zones does not change this, as the results were the same when removing all transformed areas from the analyses. Important areas in buffer zones that increased local representativeness coincided with areas of increased temperature variability across the year. Orchards in transformed areas also influenced arthropod diversity in adjacent natural vegetation by up to 1 km from orchard edges. This edge effect influenced both core and buffer sites due to the lack of a continuous buffer. Thus where present, the buffer zone plays an important role in buffering the core. As fire management is an important driver of epigaeic arthropod turnover, the complementary value of the buffer zone can have a strong temporal dimension. Overall the buffer zone had high complementary value. When the aim is to maximize local representativeness, it is important that conservation management should not be restricted to core areas only.

Keywords: Compositional turnover, representativeness, complementarity, epigaeic arthropods, biosphere reserve, fynbos

3.1 Introduction

The United Nations Educational, Scientific and Cultural Organisation's (UNESCO) Man and the Biosphere (MAB) Programme is an international initiative aimed at recognising areas with important biodiversity value that exhibit and promote a balanced relationship between conservation and sustainable development (UNESCO MAB 1996). Biosphere reserves (BRs) have three main functions: conservation, sustainable development and logistic support. At the local level, these functions are implemented through a zonation scheme that consists of one or more core areas that focus on biodiversity conservation, a buffer zone where activities should be compatible with the objectives of the core, and a transition zone where sustainable resource management and development is promoted.

Although the idea of a buffer surrounding protected areas has been around since 1933 (Shafer 1999), the establishment of the MAB programme had a profound influence as reflected by various types of national parks increasingly incorporating a buffer zone. The benefits of buffer zones are still being debated, partly due to a lack of agreement on the role of buffer zones and an associated lack of clear goals and measurable objectives (see Diego 2001). Biosphere Reserve buffer zones are key functional spaces (Pool-Stanvliet 2018). These areas surround, or are contiguous to, core areas and not only contribute to their protection and management by providing a buffering function, but can also have their own inherent value for maintaining diversity, and when regarded from a larger spatial framework, they can connect biodiversity components of core and transition areas (UNESCO 2017). Buffer zones can therefore have important value in terms of complementarity.

The concept of complementarity is closely linked to that of representativeness (Kukkala and Moilanen 2013). Representativeness refers to the need for reserves to represent the full variety of biodiversity (Margules and Pressey 2000). It can be seen as a part of a solution (i.e. conservation area network) and a simple measure can be the number of surrogate features represented (or included) at least somewhere in the reserve system (Ferrier and Wintle 2009).

Whittaker (1972) related diversity to geographical scale by introducing the concepts of alpha, beta and gamma diversity. Representativeness has been linked to gamma diversity (Smith and Theberge 1986, Whittaker 1972) and is influenced by the geographical scale of assessment (Mackey et al. 1989). Since biotic variation can be examined at different resolutions, representativeness can be examined in terms of the biophysical characteristics

found on the globe (Ferrier et al. 2004), continent (Williams et al. 2016), region (Gibson et al. 2015) or in the surrounding locality (Wessels et al. 1999; Kati et al. 2004; Mackey et al. 1989).

Complementarity refers to the contribution of an area or set of areas to unrepresented features in an existing area or set of areas (Margules and Pressey 2000), and is influenced by gamma and beta diversity combined (or spatial turnover) (Sarkar et al. 2006). The complementarity of areas surrounding reserves can be important for increasing local representativeness, especially where *ad hoc* criteria such as relative lack of commercial value, scenic value, or water supply have driven conservation decisions (Pressey et al. 1993; Pressey 1994). In the context of BRs, the complementary value of the buffer zone will be determined by the extent to which it differs from core zones in terms of the biological entities it contains, which in turn, can be the product of differences in local ecological environments, as well as the influence of activities in the transition area.

Conservation planning and assessment require information on the spatial distribution of species (Margules and Pressey 2000). The time, expense and taxonomic expertise required for thorough biodiversity inventories means that there is relatively little information available regarding the spatial distribution of biodiversity at fine-scales (Ferrier et al. 2004, Laidlaw et al. 2015). Biosphere reserves are assumed to be well-known in terms of their biodiversity, but this is not necessarily the case, even for relatively well known groups such as vertebrates (e.g. Pino-Del-Carpio et al. 2014). This problem is especially acute in countries where government funding for BRs are virtually non-existent. To deal with data limitations, many conservation ecologists have used a mixture of biodiversity surrogates (Pressey 2004). With recent advances in availability and resolution of remotely sensed abiotic environmental spatial layers, an approach growing in popularity is to use environmental variables in conjunction with species distribution data to model how species distributions relate to environmental variables.

Species-level surrogates require detailed information about the species of interest, and are therefore better suited to well-known iconic species rather than organisms for which less detailed information is available (e.g. invertebrates, a group which is often neglected in conservation studies and policies) (Ferrier et al. 1999; Moritz et al. 2001; Zamin et al. 2010; Cardoso et al. 2011; D'Amen et al. 2013). An alternative is community-level surrogates that incorporate information on biodiversity as a whole. Advantages of this approach include the modelling of rare species (which would otherwise be excluded from conservation assessments) and that community-level surrogates may reflect emergent assemblage properties not contained

in the species level approach (Hortal and Lobo 2006). Community-level modelling which, if linked to continuous environmental space, can be used to select sites to maximize representation (Arponen et al. 2008). The continuous form of the community-level surrogate approach also avoids the need to select arbitrary cut-offs in defining community classes.

The Environmental Diversity (ED) strategy uses continuous environmental data as surrogates for biodiversity to select or prioritize sites for conservation (Faith and Walker 1996; Faith et al 2004). The approach is an example of a general pattern framework where 'objects' of interest form a pattern that allows inferences to be made about some lower level of 'features'. For the ED strategy, sites or geographical places are the objects and the pattern-relationships among these sites are assumed to indicate underlying features relating to species or similar units (Faith et al. 2004). The ED strategy can be based on environmental data alone or a combination of environmental and available biotic data (e.g. through generalized dissimilarity modelling; GDM, Ferrier et al. 2007) (Faith 2011). Evaluation of the ED approach has delivered mixed results due to the suboptimal forms of the ED procedure used (Araújo et al. 2001; Hortal et al. 2009; Beier et al 2015, Faith 2011). The ED strategy, and its variants, have been used to quantify gaps in conservation representation (Ferrier et al. 2004; Overton et al. 2009) and biodiversity surveys (Hortal and Lobo 2005; Bell et al. 2014), as well as incorporating biodiversity and opportunity costs in sustainability analyses (Faith 1995; Faith and Walker 2002).

The Kogelberg Biosphere Reserve (KBR) is situated at the south western tip of South Africa. It is considered to be the heart of the Cape Floristic Region (CFR), a global biodiversity hotspot (Boucher 1982) and more than 80% of its terrestrial core and buffer areas are comprised of Kogelberg Sandstone Fynbos, a fire prone vegetation type which has exceptional species-level endemism (Rebelo et al. 2006). The KBR does not have a continuous buffer. A significant portion of the KBR buffer zone consists of private small holdings, and there is an increasing interest in development (e.g. agriculture or tourists resorts) that is raising concerns regarding the integrity of the buffer zone (Pool-Stanvliet 2014).

My aim here is to assess the complementary value of the buffer zone of the KBR for epigaeic arthropod conservation. Despite the importance of the KBR for plant conservation, at the landscape scale, environmental surrogates may be a better indicator of arthropod diversity than plant diversity (see Chapter 2). Information on epigaeic arthropod species turnover and environmental predictors were used in a community level modelling approach to 1) identify

important drivers of arthropod turnover (including environmental- and human-influenced factors), 2) assess how well environments present in the buffer zone are represented in the core zone, 3) evaluate gaps in biological survey coverage, 4) quantify the complementarity value of buffer zone in terms of these drivers, and 5) assess whether transformation in the buffer areas has altered this value. This was done by treating each geographical location across the study area (i.e. every grid cell) as a separate entity and viewing biological composition as sitting within a continuum of variation (Ferrier et al. 2009). Understanding the influence of transformation in the transition areas at a landscape scale is important for understanding the value of the buffer zone. Here I expect the buffer zone to contribute to local representativeness when it includes ecological environments not well represented in core areas.

3.2 Methods

3.2.1 Study area

The KBR has several core zones that make up 43% of its approx. 87 000 ha terrestrial component and are mostly in natural, state owned land restricted to mountainous areas. Most of the land that comprises the buffer zone (approx. 24% of the terrestrial component, either state owned or in private ownership) is in a natural or near-natural state, while most of the remaining transition area has been converted (mainly to agriculture or commercial alien plantations) (Johns et al. 2012; Pool-Stanvliet 2014).

3.2.2 Study design

A total of 65 sites were selected across the study region (Figure 3.1). Forty five of the sites were located in core and buffer zones in natural or near-natural fynbos. Site placement in these areas was aimed at including both fine and broad scale spatial patterns, limit collinearity between elevation and geographical distance, and incorporate topographic and fire history heterogeneity. An additional twenty sites were also included here to assess the influence of habitat transformation (especially deciduous fruit farming, the most important agricultural activity in the area) on species turnover in adjacent fynbos habitat, as well as including more geological heterogeneity (as important edaphic interfaces are present at lower elevations). Turnover patterns directly adjacent to orchard edges may reflect responses related to specific

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management practices within orchards (see Chapter 4), and my interest here lay in broad landscape scale influences, and so sites adjacent to orchards were placed about 80 m from the orchard edge. Many potential site locations in the buffer zone and adjacent farms were on private property and site placement was also influenced by access. The majority of sites were in a natural state. Due to a wildfire in February 2016, 18 sites received less intense sampling than the remaining sites. This was taken into account in the analyses.
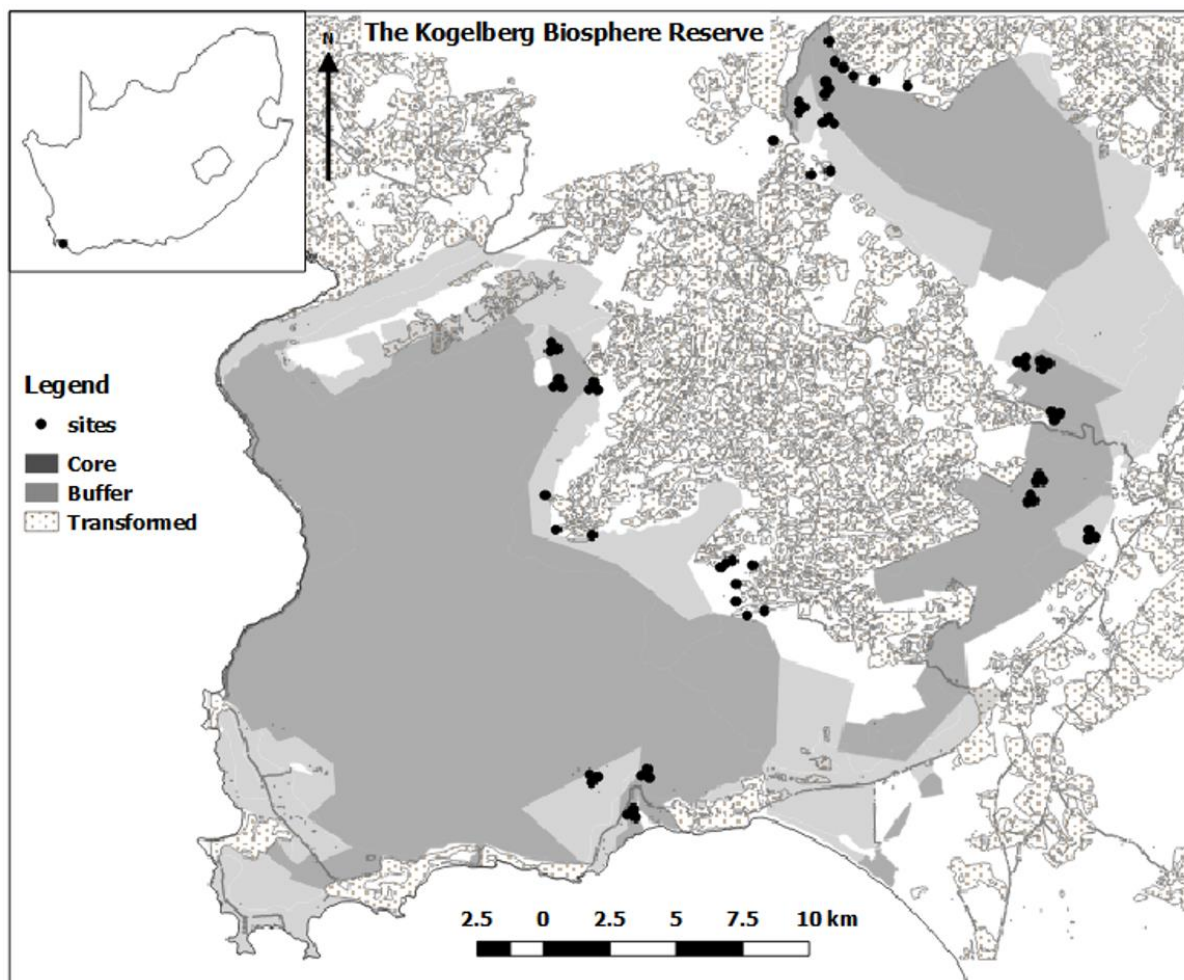
Figure 3.1 Map of study sites. Only terrestrial component of core and buffer zones are shown

3.2.3 Sampling

Epigaeic arthropod sampling occurred across two seasons: summer (October) 2015 and autumn (March) 2016. Each site consisted of 4 pitfall traps arranged as a 10 x 10 m square. Each trap was 7 mm in diameter, filled with a 50% ethylene glycol solution and left out for five days per season (10 days in total). Arthropods were taken back to the lab and sorted to genus, family or superfamily (except mites, the majority of which could only be sorted to order due to lack of taxonomic resolution), and then to morphospecies (called 'species' here) where possible. Insects were sorted using the reference guide by Scholtz and Holm (2008), except Formicideae, which were based on Bolton (1994). Acari were sorted with guided input from a specialist. Araneae were sent to specialists (voucher specimens are being held at the South African

National Collection of Arachnida). Voucher specimens for the remaining arthropods are being held at the University of Stellenbosch. Species presence-absence data were pooled across both sampling seasons.

3.2.4 Environmental predictors

To investigate the influence of environmental predictors on arthropod turnover, 66 interrelated predictors were compiled into seven broad groups: 1) geology, 2) disturbance related to fire history, 3) disturbance related to habitat transformation 4) local site characteristics, 5) refuge, 6) mesoclimate, and 7) terrain. These variables consisted of both site-measured attributes (measured at the time of sampling) and variables derived from continuous spatial layers. All spatial layers were resampled to 30 m resolution (Table S1).

The model assumes that terrestrial biodiversity may respond to both physical and biological environmental components. Physical components may be described directly (e.g. terrain, geology) while biological components may be described directly or indirectly by physical environmental correlates (e.g. Normalized Difference Vegetation Index (NDVI) can describe vegetation productivity (Wang et al. 2004)). Geographical distance between sites was included as a variable, as it may reflect either unmeasured environmental variables or dispersal processes.

I distinguish between two measures of habitat condition: one due to fire history and the other from anthropogenic land transformation (agriculture, plantation forestry, invasive alien plants etc.). Fire history variables were derived from spatial layers and included mean vegetation age (within a buffer of 15 m from the central point of each plot), fire frequency (in five, ten and twenty years) and the standard deviation of vegetation age. These variables were averaged for sites visited in both sampling seasons. Habitat condition variables related to habitat transformation included both local site measured variables and variables derived from spatial layers. Distance to nearest transformed area (developed areas (including agriculture and built up areas), orchards, and alien tree plantations) were derived from a 30 m resolution land classification map. Site measured variables included an estimate of site condition based on the proportion of native vegetation replaced by invasive alien species (*Pinus* and *Acacia* spp.). Table S1 lists all candidate environmental variables and their sources, and Appendix 2 includes more details on the explanatory groups and variable measurement.

Bivariate scatter plots of environmental variables were used to view the relationship between pairs of variables. Variables were not considered further if 1) they had a high Pearson correlation (r > 0.8) (in which case only one of the pair were included for further analysis), 2) they were a representative subset of alternative variables (e.g. use minimum and maximum vegetation cover instead of mean), or 3) were similar in function but not directly interchangeable (Williams et al. 2012).

3.2.5 Conservation assessment

Analyses were not aimed at quantifying total diversity of the area (for which information on biodiversity of each land-use would be required (Ferrier et al. 2004)). Analyses were restricted to natural or near natural habitat, but no spatial information regarding habitat quality was available. An important assumption is that most of the terrestrial habitat is in a good state, which applies to large areas of the terrestrial core and buffer zones of the KBR but not to the transition area. Therefore analyses were based on terrestrial spatial layers restricted to the core and buffer boundaries of the KBR (i.e. large water bodies were removed).

3.2.5.1 Drivers of arthropod turnover

Generalized dissimilarity modelling (GDM, Ferrier et al. 2007) was used to evaluate the relative importance of environmental predictors for epigaeic arthropod species turnover. GDM is a non-linear matrix regression technique that takes into account variation in the rate of compositional turnover at different positions along environmental gradients, as well as the curvilinear relationship between increasing environmental/geographical distance and compositional dissimilarity (Ferrier et al. 2007).

Epigaeic arthropod species composition (presence/absence) at each site was used to calculate the Sørensen dissimilarity between pairs of locations. Best sets of explanatory variables were selected for each explanatory group separately by permutation-based backward elimination. For each explanatory group, only variables that had significantly higher explained deviance ($p < 0.05$) than that observed after 500 random permutations were retained. To moderate over-fitting of models, a threshold minimum of 0.05 for partial percent explained

deviance for a variable to be retained was used and marginally significant variables removed. Significant variables selected in this initial selection process were subjected to a secondary elimination process (following the process outlined by Williams et al. 2012). Exploratory analyses of explanatory groups guided the order of variable inclusion in the secondary elimination process. Geographical distance was included in the refined models, followed by disturbance related variables (which if selected were also subjected to backward elimination) (Pennifold et al. 2017). These analyses were conducted using the package 'gdm' (Manion et al. 2017) in R, version 3.5.0 (R Core Team 2018).

The above procedure was repeated including both spatial and site measured variable (model 1) and including only spatial variables (model 2). Variation partitioning was used (e.g. Blois et al. 2013; Fitzpatrick et al. 2013; Landesman 2014) to calculate the unique and shared contribution to explained deviance by explanatory groups (irrespective of whether site measured or derived from spatial layers). Following Pennifold et al. (2017), to quantify the reduction in model performance from only using spatial predictors, variation partitioning was repeated to evaluate the unique and shared contribution to explain deviance by site measured variables and variables derived from spatial layers.

3.2.5.2 Assessing complementarity

I use two approaches to identify areas in the buffer zone important for local representativeness and estimate the complementary value of the buffer in terms of different drivers of species turnover. In the first approach, species-based dissimilarities among areas are modelled using GDM, and the predicted dissimilarities across core and buffer areas are used to assess how well ecological environments important for epigaeic arthropods present in the buffer are represented in the core (Ferrier et al. 2004). In the second approach, GDM weighted and scaled environmental spatial layers are used in the ED procedure (Faith and Walker 1996).

3.2.5.2.1 Representativeness

GDM model 2 was used to transform selected spatial environmental predictors into one common unit for use in the conservation assessment (using the 'gdm' package). The first approach is similar to the basic principle of estimating and mapping the proportional coverage

of habitat types in protected areas, but instead, every grid cell is seen as sitting within a continuum of environmental variation. A continuous metric of representativeness was derived following the approach first described by Ferrier et al. (2004) and subsequently has been applied in various conservation assessments (e.g. Allnutt et al. 2008, Gibson et al. 2015; Pennifold et al. 2017). The assessment here does not assess representativeness of core areas in terms of regional diversity, for which information on turnover patterns at a broader scale would be required. Since the analyses are restricted to the core and buffer areas of the KBR, the value of each grid cell can be interpreted as the mean proportional protection in the core of the ecological environment associated with a given grid cell in the buffer.

Compositional dissimilarity (dij, estimated as if both cells were in a natural state) was predicted across all n cells of the core and buffer areas (Ferrier et al. 2007). To simplify interpretation, dissimilarity was converted to similarity ($s_{ij} = 1 - d_{ij}$). For each cell i (across core and buffer areas) the proportion of habitat protected in core areas (p_i) was calculated as:

$$p_i = \left. \sum_j^n s_{ij} h_j \middle/ \sum_j^n s_{ij} \right.$$

Where h is the habitat state as either protected in core areas (h = 1) or in buffer areas (h= 0). This was repeated for two scenarios: 1) Environmental variables excluding disturbance related variables, 2) all environmental variables. These analyses were conducted using a Python3 script, which implemented the GDAL and Numpy Python libraries.

3.2.5.2.3 Survey coverage

Similar to the approach above, representativeness of survey sites was evaluated as a continuous fraction of the KBR total area (scaled by GDM model predictions) (Gibson et al. 2015; Pennifold et al. 2017). The analysis produced an estimate of survey density for the ecological environment associated with every grid cell. This was used to show spatial uncertainty in the fitted GDM (or those areas where estimates of representation will be the least reliable). The following equation was applied:

$$s_i = \frac{A^{survey}}{A^{total}} = \left. \sum_j^n s_{ij} h_j \middle/ \sum_j^n s_{ij} \right.$$

Where S_i, the proportional sampling of ecological environments to cell i similar to the 65 survey sites, is given by A^{survey}, the area in survey sites, which is calculated as the sum of similarities (s_{ij}) multiplied by a binary index h_j (0 non-survey, 1 surveyed), divided by A^{total}, calculated as the sum of similarities (s_{ij}) for all n cells in the study region.

3.2.5.2.4 Complementarity

Gaps in environmental space can be quantified in several ways. The p-median criterion (Faith and Walker 1996; Faith 2003) is based on methods from operations research where it is used to define the optimal locations of a set of facilities to supply a demand from a set of users (Reese 2006, Mladenović et al. 2007). The criterion seeks to minimize distance from each 'demand point' (e.g. houses) to its nearest 'supply point' (e.g. fire station, schools, etc.). Sites for facilities are selected from a number of potential supply points in a way that minimizes travel distance (or connection cost) of any user to the nearest facility. For the ED strategy, geographical distances are replaced with environmental distances in ordination space. The relative distribution of sites to each other in environmental space can affect the p-median procedure in such a way that more sites will be selected in regions with greater demand point densities (Faith and Walker 1996). For this reason the modified 'continuous' form of the p-median model (in which case demand points are hypothetical points distributed uniformly across environmental space) is considered superior to the 'discrete' form (Faith 2003; Faith 2011; Beier and Albuquerque 2015).

The environmental/ordination space is well represented if it produces a small sum, over all demand points, of the distance from each point to its nearest selected area. The ED complementarity of site to any given set of sites (Faith et al. 2004) is indicated by how much its addition reduces the value of the p-median (overall ED values). Expected complementary value, 'C', of an area can be indicated by how much the addition of that area to a partial-set reduces the sum of distances, or minimises "forgone biodiversity" (Faith 1995).

Output from GDM model 2 (transformed and weighted environmental predictors) was used in the ED procedure. Due to computational limitations, this assessment was based on 10 repeated random samples of 4000 sites each across the study area (core and buffer zones of KBR). Hybrid multidimensional scaling (HMDS, Faith et al. 1987) with 1000 iterations and 10 random starts was used to create a two-dimensional ordination space where intersite distance

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reflect (Manhattan) dissimilarities in environmental variables between sites. For each random sample a convex hull was created to define the polytope space (Faith and Walker 1994) within which 4000 continuous demand points were placed. These analyses were conducted in R using various utility packages. For each random sample, the hybrid heuristic p-median procedure in POPSTAR (Resende and Werneck 2003) with 32 random starts was used to identify the solution that best spanned the ordination space. Solutions were obtained for sites representing 5% to 95% of the 4000 randomly selected sites. By removing or retaining sites from input for the selection procedure in POPSTAR, the analyses were repeated for all core sites only, all core and buffer sites combined, intact core sites only (all transformed areas in core and buffer areas removed), and intact core and buffer sites combined.

For each of above scenarios, the procedure was repeated based on:

1) Environmental variables excluding disturbance variables
2) Environmental variables with disturbance related to habitat transformation
3) All variables (environmental variables, habitat transformation, fire history)

The resulting ED values were plotted against the percentage of selected sites.

3.3 Results

I sampled 20 463 arthropod individuals from 425 species, with the most dominant taxa being Formicidae, Acari, Coleoptera and Hemiptera.

3.3.1 Drivers of arthropod turnover

3.3.1.1 Model 1 – site measured and spatial variables

Refined model 1 consisted of 10 variables (including geographical distance), and explained 25.19% of epigaeic arthropod turnover with an intercept of 1.01 (Table S5). The environmental variables selected in Model 1 were related to geology (total explained deviance 10.26%, unique deviance 4.51%), fire related disturbance (total explained deviance 6.27%, unique deviance 3.36%), site characteristics (total explained deviance 6.55%, unique deviance 3.08%), climate (total explained deviance 6.08%, unique deviance 3.91%) and disturbance related to habitat

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transformation (total explained deviance 1.67%, unique deviance 1.09%). None of the variables related to refuge or terrain were significant for epigaeic arthropod species turnover.

Important geological variables included average soil clay content and distance to shale band intrusions (Figure 3.2). Only one climate related variable was selected, namely standard deviation of average monthly minimum temperature across the year. Variables related to local site characteristics included average vegetation height and minimum soil moisture. Fire related variables included fire frequency in the past 5 years, fire frequency in the past 10 years and standard deviation of vegetation age. Distance to nearest orchard was the only important variable related to habitat transformation.

Geological variables explained the largest independent fraction and geographical distance contributed the least to the model (0.35%). The largest proportion of shared explained deviance was between variables related to climate and geology (2.96%), followed by fire history and site characteristics (2.33%) and geology and site characteristics (1.16%) (Figure 3.3).
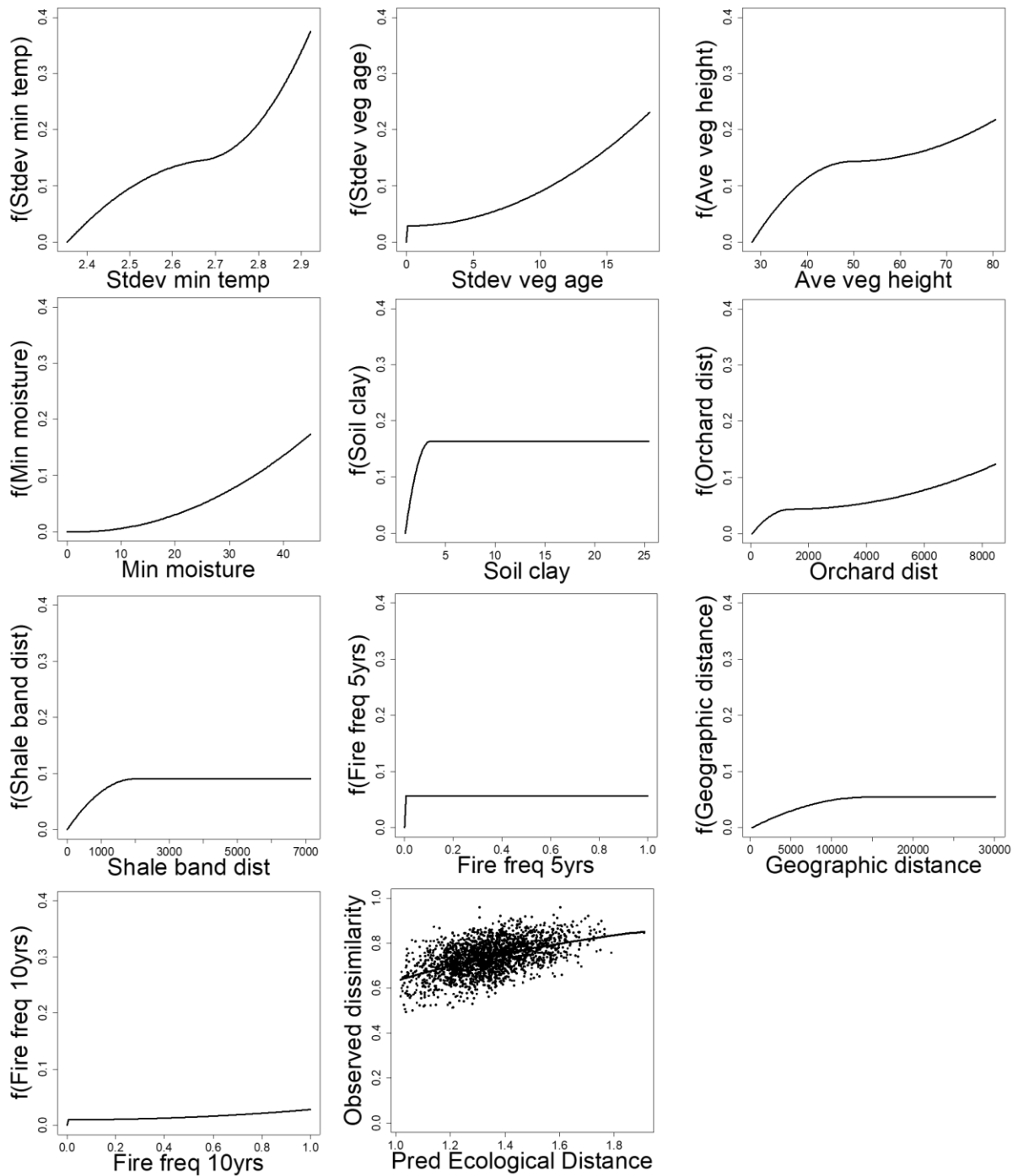
Figure 3.2 Generalised dissimilarity model-fitted transformations of geographical distance and environmental variables that were selected as predictors for epigaeic arthropod species turnover. The maximum height of each curve represents the total amount of turnover explained by the environmental gradient while holding all other selected variables constant. The last panel shows the relationship between observed arthropod compositional dissimilarity and the predicted ecological distance
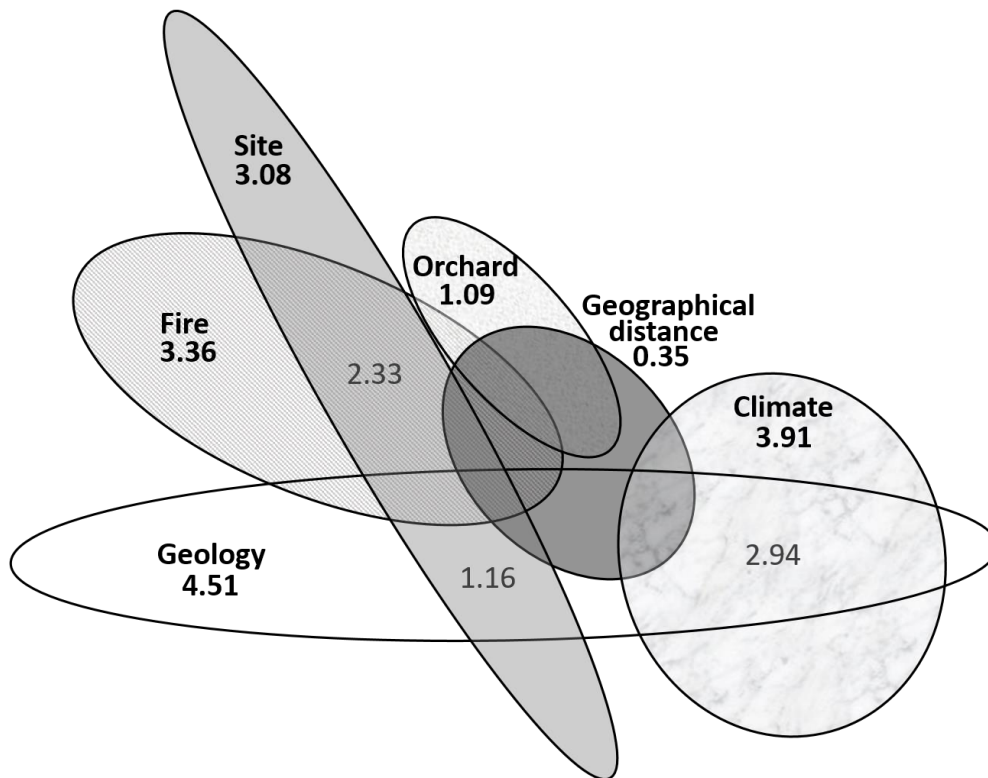
Figure 3.3 Variance partitioning of epigaeic arthropod species turnover among the selected explanatory groups using GDM model 1. Values represent fractions of total percentage deviance explained. Shaded areas represent fractions explained by selected explanatory data sets. Values in bold indicate fractions of unique deviance explained by the specific explanatory group. Shared deviance of less than 1% is not shown

3.3.1.2 Model 2 – spatial variables

Model 2 explained 22.12% of the deviance in arthropod turnover, and consisted of 7 variables (including geographical distance) with an intercept of 1.04 (Table S6). The selected spatial variables were all similar to those selected by Model 1. The only site measured variables that were not included in Model 2 were related to local site characteristics (namely average vegetation height and minimum soil moisture). Spatial variables explained a greater proportion of the explained deviance (unique deviance 15.09%) than site measured variables (3.08%) and also shared more of the deviance explained by geographical distance (Appendix 3).

3.3.2 Representativeness

Given the small effect that including geographical distance between sites had on model performance (< 1% improvement in ED), the following assessments were based on an environmental response model only. Ecological environments that exclude disturbance related variables in the KBR buffer areas have representation levels in core areas varying between 66.76% and 69.44% (Figure 3.4). Inclusion of the influence of proximity to transformed areas (distance to orchards) changed this value slightly (66.42% to 69.84%, map not shown). The range of representation levels increased more when also including fire related disturbance variables (66.22% to 70.33%) (Figure 3.5).

3.3.3 Survey coverage

Evaluation of survey coverage showed that ecological environments across buffer areas related to geology, fire history, and distance from orchards were relatively well represented by the study sites, while terrestrial environments at very high elevations were not well represented (see Appendix 4).
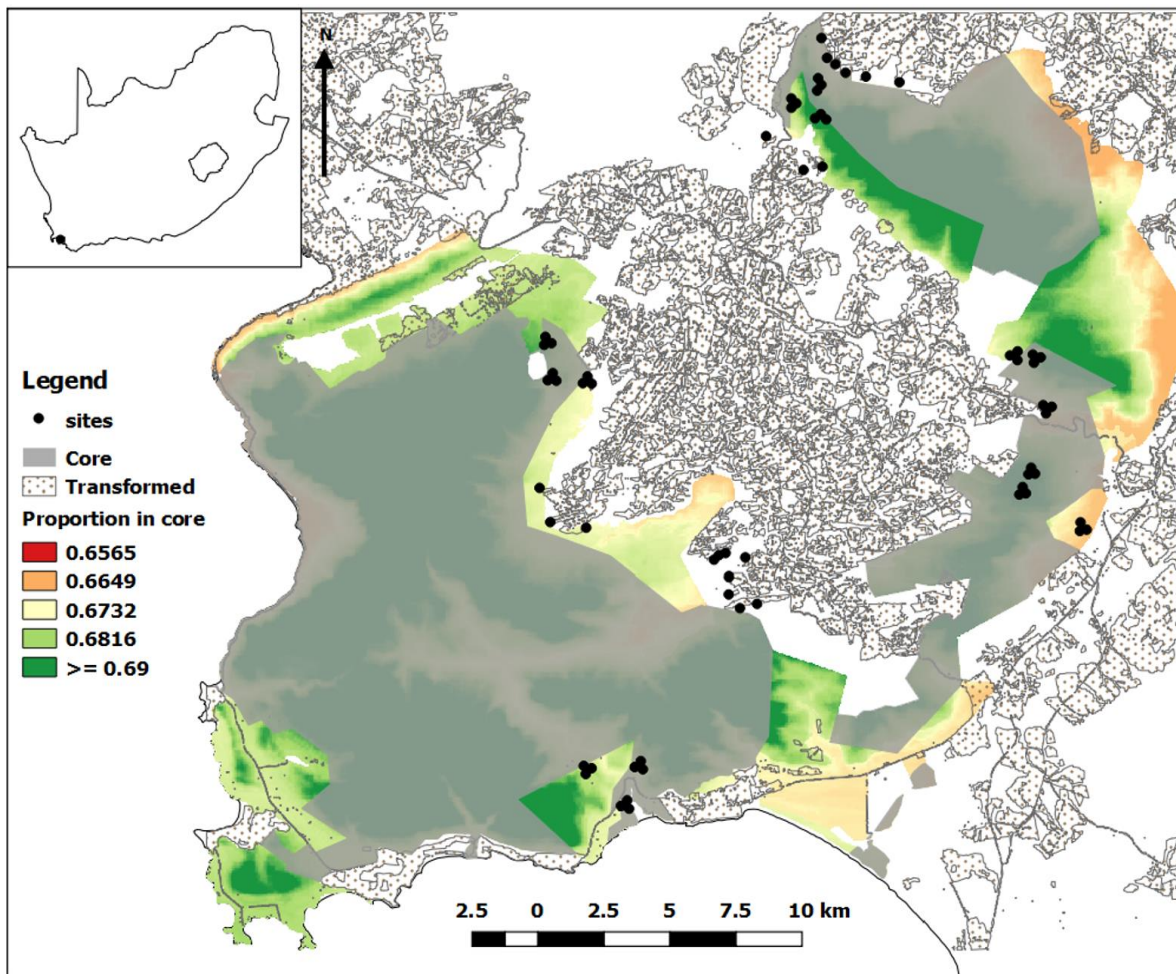
Figure 3.4 Proportion of ecological environments (excluding disturbance variables) present in buffer that is represented in the core of the Kogelberg Biosphere Reserve
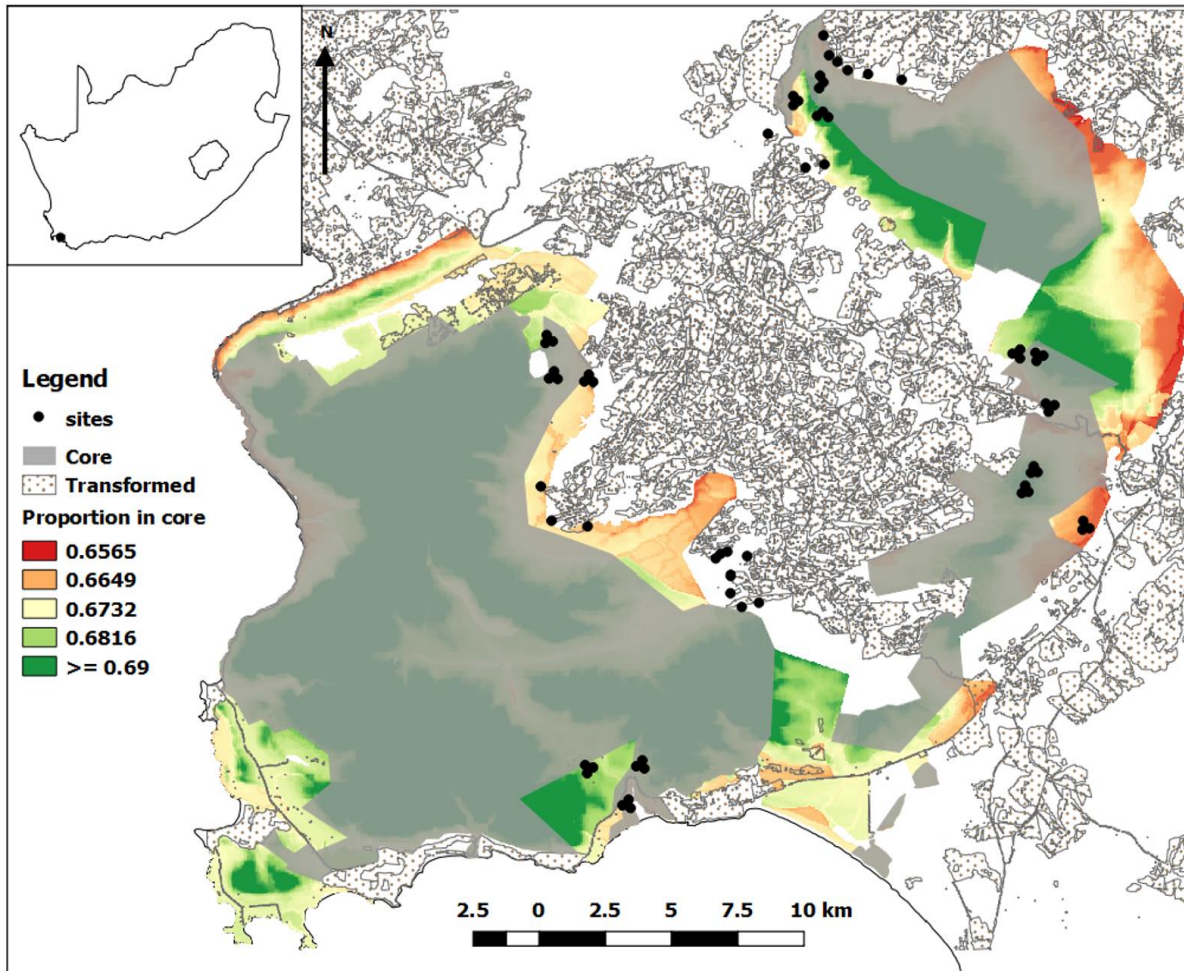
Figure 3.5 Proportion of ecological environments (including all disturbance variables, fire related and distance to orchards) present in buffer zone that is represented in the core of the Kogelberg Biosphere Reserve

3.3.4 Complementarity

Figure 3.6 shows the curve tracing successive increases in expected species representation, corresponding to decrease in ED's p-median value, as more sites were selected. In all cases, the inclusion of buffer sites significantly reduced the ED value. Limiting the analyses to intact sites only gave very similar results. Including distance to orchard as a variable increased the reduction in ED for both selections based on only core sites and core and buffer sites combined. The inclusion of all disturbance variables reduced the reduction in ED values. All HMDS plots had acceptable levels of stress. The highest stress values were for plots with all variables (maximum stress of 0.20) and the lowest for plots excluding all disturbance related variables (maximum stress of 0.09). Table S7 includes information on all HMDS stress values
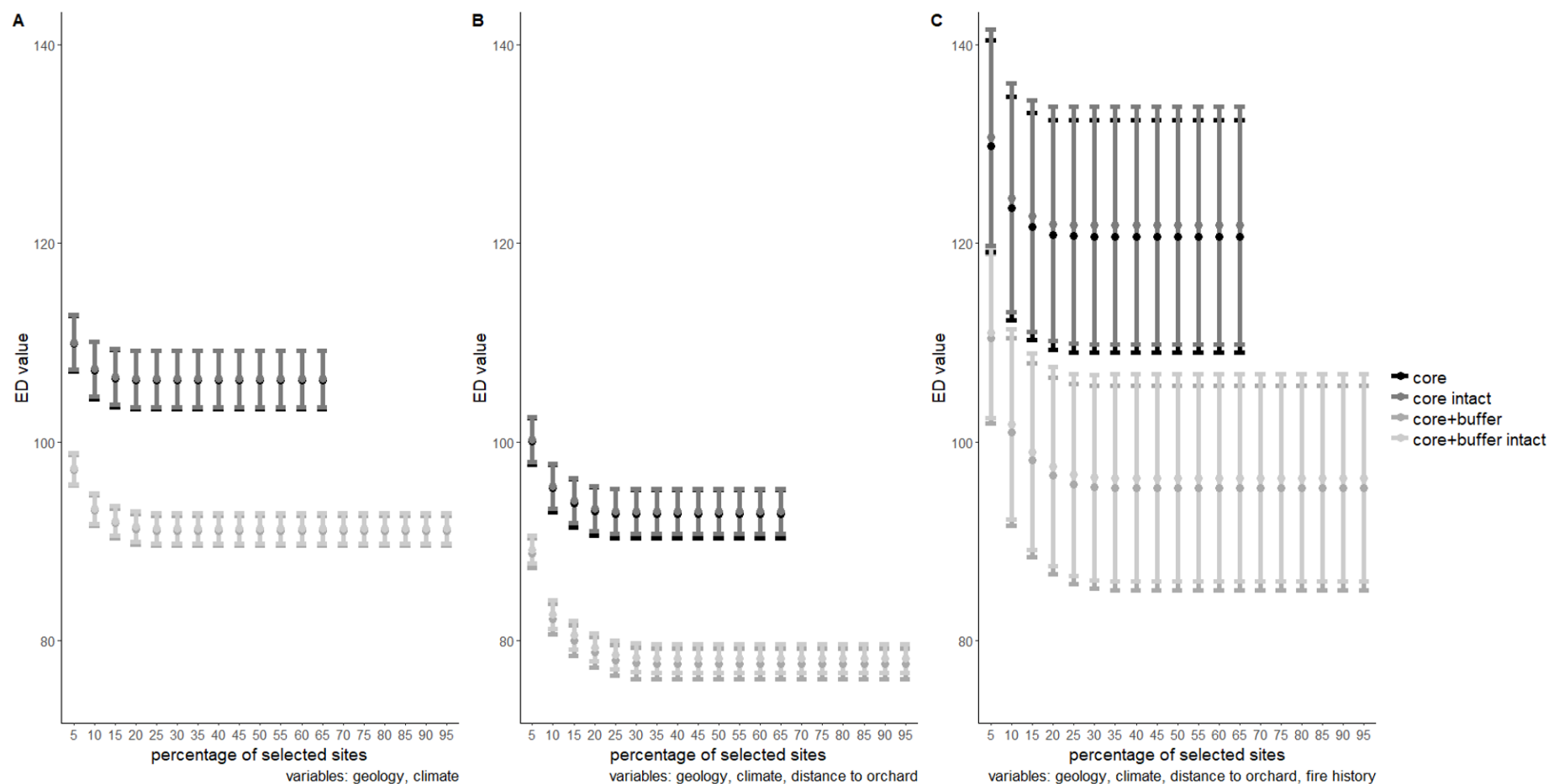
Figure 3.6 The x axis indicates the percentage of sites selected by ED, and the y axis is the corresponding ED value. The curve shows the gain in representation, corresponding to a decrease in ED value as additional sites are selected for A) environmental variables excluding all disturbance (i.e. related to climate and geology), B) all variables excluding fire management related disturbance variables (distance from nearest orchard included) and C) all variables (fire management related variables added). Intact sites exclude all transformed areas from site selection (i.e. orchard, built up areas, plantations). Bars represent 95% confidence intervals

3.4 Discussion

My aim was to assess the complementary value of the buffer zone of the Kogelberg Biosphere Reserve (KBR) for epigaeic arthropod conservation. Advances in community-level modelling approaches and the growing accessibility of spatial data have improved the ability to assess biodiversity patterns across large geographic areas. I have made use of recent developments, specifically generalised dissimilarity modelling (GDM), to relate changes in epigaeic arthropod composition (or turnover) to environmental gradients across the core and buffer zones of the KBR. Identifying important drivers of arthropod turnover allowed me to assess the representativeness of core areas, as well as the complementary value of the buffer. In addition, including anthropogenic land transformation as a predictor allowed me to assess the capacity of the buffer zone to protect the core from activities in the transition.

Important environmental drivers for epigaeic arthropod turnover patterns that were used in this assessment included (in order of importance): Variability in monthly minimum temperature across the year, standard deviation in vegetation age, average soil clay content, shale band intrusions, fire frequency in the past five years, and fire frequency in the past ten years. The importance of these variables for arthropod turnover reflects results from other studies in South Africa and across the world (e.g. Botes et al. 2006; Andersen et al. 2009; Illán et al. 2010; Munyai and Foord 2011; Gollan et al. 2015).

I also found an increase in epigaeic arthropod turnover < 1 km from orchard edges. Numerous studies have reported an increase in arthropod diversity near agricultural edges (e.g. Haynes and Cronin 2003; Clough et al. 2005; Villada-Bedoya et al. 2017), and this has also been reported for work in fynbos habitats edges (Magoba 2010; Theron 2017). Underlying mechanisms include increased proximity to important alternative resources, especially for natural enemies (e.g. over-wintering sites, alternative host species, and alternative energy sources) (Landis et al. 2000; Tylianakis et al. 2004). Spillover edge effects are expected to be greater when there is a steep gradient in annual primary productivity between two adjacent biotope types (Rand et al. 2006). This can be influenced by the characteristics of the cropping system (e.g. irrigation and fertilizer application) and the surrounding locality. Gradients in productivity are magnified when considering that habitat loss is often non-random with relatively fertile lowlands being more rapidly selected for conversion to agricultural uses (Saebloom et al. 2002), which is the case for the CFR. Additional factors can influence edge effects by impeding movement, e.g. edge contrast (Collinger and Palmer 2002; Wratten et al.

2003) or habitat permeability (Haynes and Cronin 2003). Perennial crops such as orchards are intensively managed to produce standardized 'zero damage' fruits (Parisi et al. 2014). The absence of ground cover in many orchards and their closed canopy can make this land-use less hospitable for endemic fynbos arthropod assemblages compared to other land-uses, e.g. vineyards (Adu-Acheampong et al. 2016). Although the present study did include edge related predictors of other land-uses, site placement focused strongly on orchards (a major economic activity within the study area) and are therefore better representative of the influence of the effects of this land-use. Differences in local management practices can also influence edge effects and were not considered here (but see Chapter 4).

Approximately 66% to 70% of ecological environments in the buffer zone are represented in the core zone. The approach used to calculate p may overestimate representativeness (see Faith 2016), but this relatively high figure is to be expected considering the local scale of assessment and the topographic heterogeneity of the core zone. Areas that were the most unrepresented overlapped with lower elevation sites (especially areas away from the coast) that coincided with greater changes in minimum temperatures throughout the year. The lower elevation of many of these sites puts them in close proximity to present developed areas and makes them more vulnerable to edge related influences, future transformation and associated invasive species. An important threat in the area is from invasive alien plants (specifically *Pinus* and *Acacia* spp.) and therefore the present results should be interpreted as potential added benefit of buffer habitat, and can be used to identify priority areas for restoration and management. Although habitat condition measured as percentage native vegetation displaced by alien tree species was included in the model, it was not found to be significant. This should be interpreted with caution as the majority of sites included here were in a natural state, and the level of habitat condition of invaded sites were not exceptionally low (<30% of native vegetation displaced by invasive species). Other work has found a strong influence of invasive alien tree species on local epigaeic arthropod species composition in fynbos habitats (French 2001; Schoeman and Samways 2011; Liu et al. 2012; Magoba and Samways 2012). What is promising is that clearing of alien trees in the CFR can result in the recovery of native arthropod species richness and turnover patterns (Samways and Sharratt 2010; Magoba and Samways 2012; Maoela et al. 2016).

Previous work in the study area that has compared the different zones has focused on dragonflies and riverine habitats (Grant and Samways 2011). Grant and Samways (2011) found buffer and transition areas provided additional habitat for dragonfly species that would

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otherwise have been excluded. Here I found a significant reduction in ED values when including buffer sites in the site selection procedure. This was true for both analyses that excluded all disturbance related variables (including only geology and climate variables) and including disturbance variables. Limiting site selection to only intact sites gave similar results. Orchard related edge effects reduced ED values even more, likely because of increased heterogeneity in ecological environments and the influence of orchards being the strongest at lower elevation sites (areas that already have highly complementary value). This was the case for both analyses that included only core sites and those for core and buffer sites combined, which is due to the lack of a continuous buffer surrounding core areas. Where present, the buffer zone is crucial for limiting edge related influences of land transformation in the transition area on habitat in the core. The inclusion of fire related variables increased the variability in ED values, which could be related to the relatively fine scale environmental heterogeneity associated with standard deviation in vegetation age, as well as the increase in HMDS stress values. Overall, the inclusion of fire related variables limited the reduction in ED values for both analyses which focused on core sites, and those which included core and buffer sites combined. An important point is that the biodiversity patterns used to estimate the complementary value of the buffer area describe only the current (or recent historical) state. Differences in fire management can alter diversity patterns and the complementary value of the buffer zone.

Fire management in the CFR that is focused on maintaining floral diversity aims at a minimum fire return interval of between 12 and 20 years (Altwegg et al. 2015; CapeNature 2016). A fixed return interval is, however, not the norm, and variation in fire return interval, intensity and season at the same site is ecologically important (Vlok and Yeaton 1999; Thuiller et al. 2007). Four years post-fire, the amount of fuel load has built up enough to support a spreading fire and fire occurrence is no longer restricted by fuel availability (van Wilgen et al. 2016). Both lightning and (increasingly) human ignition sources are important sources of fire (Kraaij et al. 2013; Pooley 2014). Fire frequency will also be influenced by climate change (Southey et al. 2009; Wilson et al. 2010). Using prescribed burning to manage the vegetation of the CFR may not be appropriate in many areas (van Wilgen et al. 2010) and the greatest challenge at the moment is to protect fynbos from too frequent fires (CapeNature 2016). Compared to fynbos flora, relatively little work has been done on proper fire management aimed at maintaining arthropod diversity. Work done to date however, suggests that there is considerable variation between arthropod functional and taxonomic groups in resilience to fire,

and that long term recovery is important for overall diversity (Pryke and Samways 2012; Yekwayo et al. 2018).

The reliability of any biodiversity assessment will be influenced by the predictive link between environmental data and species turnover (Faith and Ferrier 2002). Here, models explained around 22% of the turnover in epigaeic arthropods. Larger plots will sample more species, but can become impractical. The large amount of unexplained variation can be due to limitations related to the modelling procedure or important environmental factors missing from these models. Small-scale processes are expected to obscure patterns of community variation at more local scales (Prendergast et al. 1999). Factors related to metacommunity processes are difficult to represent with available spatial layers (e.g. McKenzie and Bullen 2012). Different taxonomic groups can also show considerable differences in relation to the same variables (Beck et al. 2013). Another important factor could be a mismatch between predictor resolution and the actual processes that affect turnover patterns locally. Including site measured variables on those factors, which were found to be the most important, could improve our understanding of how data sources provide complementary information (Gibson et al. 2015). The inclusion of site measured variables (namely average vegetation height and minimum soil moisture) improved the model only slightly, and more than half of the deviance explained by average vegetation height was shared with that explained by fire related disturbance variables. Other site measured variables that were related to important spatial predictors, but not selected by the selection procedure, were site measured temperature. This was measured only for the time of sampling and does not reflect the long term pattern of changes in temperature throughout the year, which was found to be important. The inclusion of higher resolution information regarding regolith (through radiometric or gamma-ray spectrometry, e.g. Gibson et al. 2015) could also greatly increase the predictive power of abiotic environmental data. This study also used simple Euclidean distance to assess geographical turnover. Other measures (such as least cost pathways (Drielsma et al. 2007)) may be a more realistic approach. In the present study. Here, sampling effort among all sites was not similar due to factors related to the nature of the study system (i.e. lost to a fire). Although this was taken into account in analyses of the data, the results may still be confounded by differences in sampling effort. Lastly, I should acknowledge the influence of taxonomic resolution on the results. Arthropods were identified to the lowest possible taxonomic units which was in some cases limited by the lack of taxonomic knowledge (e.g. epigaeic Acari, a group rarely included in ecological studies).

This assessment only looked at the complementary value of buffer areas for increasing local representativeness of epigaeic arthropods. Effective conservation also requires considering factors related to changes in threat intensity (e.g. habitat alteration or climate change), population viability analysis, as well as ecological and evolutionary processes (e.g. Araújo et al. 2002; Harwood et al. 2016). It is possible to incorporate this information if it becomes available (see Ferrier and Drielsma 2010). Where possible, field-based monitoring should be used to test predictions and refine models further (e.g. McCarthy and Possingham 2007). This is a major challenge because funding has not kept pace with protected area expansion, and research in the CFR has moved away from long-term research embedded in management agencies in favour of shorter term research conducted mostly by tertiary institutions (van Wilgen et al. 2016). Secondary biological data sources could become a valuable solution to part of this problem (e.g. Sevilha 2016).

Maximizing environmental diversity within conservation networks should guarantee representation of a diversity of species (Faith and Walker 1996). This should also ensure long term persistence by allowing adaptive responses to occur (Smith et al. 2001). Enduring features (e.g. geophysical features such as elevation and soil properties) have been proposed to prioritize sites in the face of climate change (Hunter et al. 1988). This coarse filter strategy is referred to as conserving nature's stage (Beier et al. 2015). While regional conservation goals should be large-scale, finer resolution data can be used to identify important areas at smaller spatial scales (Hortal and Lobo 2006). Abiotic surrogates can identify areas that will support the processes that generate and maintain biodiversity (e.g. edaphic interfaces (Cowling et al. 2003; Rouget et al 2003)). The geological characteristics identified as important here were proximity to shale band intrusions and average soil clay content. Turnover increased rapidly < 1.5 km from shale band intrusions. These intrusions are well represented in core areas. Turnover was also higher in soils of low clay content, which are also well represented in core areas. An important contribution that lower lying buffer areas make in local representativeness of epigaeic arthropods is increasing climatic heterogeneity.

Effective conservation planning consists of considering the many complicated biological, social and economic factors that impact the ecological integrity of a site, and to then focus limited conservation resources on those actions which have the greatest impact on ecological structure and function (Sanderson et al. 2002). Conserving maximum biodiversity and the processes that maintain it, will not be achieved by restricting conservation efforts to core areas only. When the BR model was conceived, the important principles of systematic conservation

planning were not yet established. As with many other protected areas, many BR core zones were assigned ad hoc. This has implications for the conservation of both geodiversity and climatic diversity. Genuine collaboration between stakeholders and managers will be essential to realise the co-existence between land-use and conservation in buffer zones so as to increase local representativeness and the processes that maintain biodiversity across the KBR.

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Chapter 4 Differential influence of orchard edges on the diversity of specialist and generalist epigaeic arthropods in adjacent fynbos habitat

Abstract

Clearing and fragmentation of natural vegetation and the establishment of crops has resulted in large parts of human-modified landscapes consisting of boundaries between various landscape features. This study investigates the influence of commercial fruit orchards on epigaeic arthropod diversity in the adjacent natural vegetation of the Kogelberg Biosphere Reserve, South Africa. I sampled epigaeic arthropods and environmental variables along transects that were perpendicular to orchard edges and assessed the influence of distance from edge boundary, orchard management (insecticide and cover crop management), permeability (orchard age and windbreaks) and edge-associated changes in local environmental variables on species richness and composition of arthropods in adjacent non-crop habitats. Different groups were assessed based on habitat fidelity, i.e. species associated with the non-crop habitat (stenotopic species), species associated with the crop habitat (cultural species) and species that showed no preference for either crop or non-crop habitats (ubiquitous species). I used mixed models to assess edge influences on species richness and redundancy analyses to assess edge influences on species composition. Cultural species richness decreased with increasing distance from orchard edge, but did not result in higher overall species richness near edges. Higher species richness of most species was related to edge related changes in local environmental variables. Habitat permeability was more important for stenotopic species composition while management was more important for cultural and ubiquitous species composition. The results highlight that local management within these orchards can influence the region's biodiversity in adjacent non-crop habitat and that habitat fidelity can be an important determinant of edge effects. Farmers who wish to reduce the influence of spillover from cultural species on sensitive natural habitats on farms, should maintain a buffer strip of at least 80 m. To enhance the diversity of arthropods which occur in both orchards and fynbos habitats, vegetation within this strip can be manipulated to maintain heterogenous structure over short distances (e.g. through maintaining fire breaks or alien clearing).

Keywords: edge effect, spillover, orchard, epigaeic arthropods, biosphere reserve, fynbos

4.1 Introduction

The clearing and fragmentation of natural vegetation and the establishment of crops have led to large parts of human-modified landscapes consisting of boundaries between distinct vegetation cover classes (often broadly referred to as 'habitat types') that have been superimposed on pre-existing patterns of environmental heterogeneity (Tscharntke et al. 2012; Haddad et al. 2015).

Island biogeography theory was developed to explain the regulation of species richness on islands (MacArthur and Wilson 1963, 1967). It stipulates that islands have an equilibrium number of species, and that species richness increases as island size increases and isolation to similar habitats decreases. Similarities between MacArthur and Wilson's theory and fragmented continental habitats have triggered its use in conservation science, e.g. protected area design and the estimation of species extinctions in fragmented landscapes (Diamond and May 1976; Margules et al. 1982).

Island biogeography theory reduces landscapes to patches of habitat and non-habitat. This can provide an oversimplified view of the dynamic relationship between remaining habitat fragments, edges and transformed areas (Forman and Godron 1981; Tscharntke et al. 2005). A key aspect of habitat edges is their capacity to influence the flow of energy and materials. Edges can be viewed as semi-permeable boundaries that allow certain materials or organisms to flow freely, while restricting others (Laurance et al. 2001, Harper et al. 2005). Similarly, cross-system fluxes of organisms occur across natural-anthropogenic habitat interfaces, and are an important mechanism by which habitat fragmentation may influence ecological dynamics within remaining habitats (Tscharntke et al. 2005).

When different habitats are suitable for species occupation (i.e. contain usable resources), transformed areas may not only act as a resource base for species that thrive in these habitats, but can also have the potential to influence populations in remaining adjacent habitats (Tscharntke et al. 2005; Pawson et al. 2008, Driscoll et al. 2013). A species' ability to utilize resources within transformed areas will be influenced by its degree of habitat specialization (Ewers and Didham 2006). For example, specialist butterfly species are less likely to move into transformed areas than generalist species (Ries and Debinksi 2001). Based on the spatial distribution of species at the interface of crop and non-crop habitats, we can distinguish between at least three different groups: 'stenotopic species' specialise on non-crop habitats and are rarely found to be associated with crops, 'cultural species' have a preference for crop

habitats, while 'ubiquitous species' occur in both habitat types, and show no preference for either (Duelli and Obrist 2003). When there is sufficient movement between habitat types, the quality of transformed habitats can have a strong impact on species composition in remaining non-crop habitats (Perfecto and Vandermeer 2002). Local management practices within cropping systems can influence the availability of alternative resources (Driscoll et al. 2013), and habitat fidelity can influence an organism's exposure to different management practices within crop habitats (EFSA PPR 2015). Edge permeability can also influence cross-edge spillover (Rand et al. 2006) and is a function of edge contrast (Holmquist 1998). For example, edge contrast can influence the movement of ground-dwelling and flying insects (Collinge and Palmer 2002; Harper et al. 2005; Barnes et al. 2014).

Edges can also cause variation in the spatial distribution of biologically important variables and influence ecological response variables through indirect pathways mediated by local conditions (Ruffel and Didham 2016). There is strong evidence from various systems that distance from edge influences habitat structure (Murcia 1995; Ruffel et al. 2014; Mairota et al. 2015). Unique species composition near edges can result from unique local conditions that are due to the blending of juxtaposed habitat conditions (Laurance et al. 2001) or resources occurring at edges that are relatively rare in the interiors of either habitat types (van Halder et al. 2011). In agricultural systems, changes in local conditions are not necessarily directly related to conditions in croplands but can also be influenced by management interventions, e.g. maintaining firebreaks or the establishment of windbreaks.

Several studies have demonstrated that the structure and diversity of invertebrate assemblages show characteristic changes near biotope edges and that species richness typically increases with decreasing distance to edge (Ewers and Didham 2006). The most common explanation for this pattern is that there is a mixing of matrix and non-matrix species near edges, resulting in a zone of overlap with higher overall species richness, also termed 'spillover' or 'mass effect' (Kotze and Samways 2001, Rand et al. 2006). This pattern is by no means universal, e.g. some species avoid edges and fauna associated with transformed habitats may not be enough to compensate for the loss of species near edges (Ewers and Didham 2006). Another way in which edges can influence species diversity is through differential influences on species' mortality and the resulting changes in the outcome of interspecific interactions (Fagan et al. 1999). This is conceptually related to disturbance-mediated coexistence (Fagan et al. 1999), e.g. the intermediate disturbance hypothesis (IDH, Connell 1978) which has been

used to explain higher species richness near habitat edges (e.g. Baker et al. 2006; Pankiw 2011; Delgado et al. 2013; Rotholz and Mandelik 2013).

Orchard systems consist of perennial multi-strata designs that may provide rich resources and habitats to living communities (Simon et al. 2010). However, these systems are intensively managed to produce standardized 'zero damage' fruits (Parisi et al. 2014). The use of broad spectrum insecticides can have adverse effects on arthropod abundance and species richness (Cárcamo et al. 1995; Epstein et al. 2000) and their reduction is an indicator of improved sustainability in pest management and considered a priority in intensively sprayed systems such as orchards (Wearing 1997; Simon et al. 2010). Maintaining cover crops (usually a grassy strip) in orchard alleys can shelter an abundant arthropod community that can consist of both beneficial organisms and pests (Vogt et al. 1998; Simon et al. 2010). Orchard-age can have a strong influence on habitat contrast and related permeability, since light availability strongly decreases as the orchard matures. The perennial nature of the system combined with the fact that fruits are delicate high value products, often promote the establishment of windbreaks in windy regions (Prokopy 1994). Wind breaks can act as a barrier to some arthropods (Ries and Debinksi 2001) or result in an accumulation of organisms by altering wind conditions (Corbett and Rosenheim 1996; Lewis and Stephenson 1966, Nguyen and Nansen 2018).

Much of the research on organism movement in agricultural systems has focused on movement from adjacent non-crop habitats into crop habitats (e.g. Norris and Kogan 2000; Sackett et al. 2009) rather than vice versa (Rand et al. 2006; Blitzer et al. 2012). There has also been a strong focus on particular taxonomic groups that have specific functional implications, e.g. beneficial organisms (Labrie et al. 2003) or pests (Sétemou and Bartels 2015). Knowledge of how ecological patterns near habitat edges change is essential for understanding the impact of land-use change and associated fragmentation dynamics at the landscape-level (Laurance et al. 2001; Ries et al. 2004; Ewers and Didham 2006; Ruffel and Didham 2016). Changes in species richness and composition can also significantly influence ecosystem functioning (Cardinal et al. 2006; Hillebrand et al. 2008). These impacts can be especially important when conservation areas are nested within human-dominated landscapes, as the context of conservation areas can have an important effect on what goes on inside a reserve (Schonewald-Cox and Bayless 1986; Wiens 2002). Beta diversity (the change in species composition) provides a direct link between biodiversity at local scales (i.e. species richness or alpha diversity) and broader spatial scales (Anderson et al. 2010). Investigating edge related changes in beta diversity can shed light on how land-use change influences landscape-scale diversity in

remaining habitats (Marsh et al. 2018). Species composition may also indicate effects that are not apparent when only examining changes in species richness (e.g. Clough et al. 2007).

Biosphere reserves (BRs) consist of three zones: core areas that focus on biodiversity conservation, a buffer zone where activities should be compatible with the objectives of the core, and a transition zone where sustainable resource management and development is promoted. Previous work has found higher species turnover near orchard edges (Chapter 3), and here I investigate the underlying causes. The present study investigates the mechanisms by which orchard edges differentially influence stenotopic, ubiquitous and cultural epigaeic arthropods in non-crop habitats adjacent to deciduous fruit orchards in the Kogelberg Biosphere Reserve (KBR), South Africa. I sampled epigaeic arthropods and environmental variables along transects that were perpendicular to orchard edges and assessed the influence of orchards on arthropod diversity regarding orchard edge permeability, orchard management and edge induced changes in local environmental conditions. Based on previous research in the area, I expect that species richness will be lower in the orchard habitat than adjacent fynbos habitat (Witt and Samways 2004). I hypothesize that edge-effects will be different for each of the distributional groups (stenotopic, cultural and ubiquitous) and that overall species richness will show a negative relationship with distance to orchard edge (higher species richness near edges), but that this relationship will be either neutral or positive when excluding cultural species. This would highlight the importance of spillover of cultural species for arthropod species richness patterns near orchard edges. Alternatively, higher species richness near orchard edges will be a consequence of changes in local abiotic conditions. Because cultural and ubiquitous species do not avoid orchards and are more exposed to management practices within orchards, I expect that orchard management will have a stronger influence on these groups than stenotopic species. High contrast edges are expected to generate stronger edge effects due to the associated lower permeability, especially for specialist species (Ries and Debinski 2001; Ewers and Didham 2006; Peyras et al. 2013) and I expect variables related to habitat permeability to be more important for stenotopic species than either ubiquitous or cultural species.

4.2. Methods

4.2.1 Study area

The KBR is situated at the southwestern tip of South Africa. The dominant vegetation type in the region is fynbos, a schlerophyllous vegetation type that is adapted to low soil nutrients, winter rainfall and fires. Most of the land that comprises the terrestrial parts of core and buffer zones of the KBR are in a natural or near-natural state. Deciduous fruit farming is a major economic activity in the study area. Approximately 20% of all land transformation bordering core and buffer zones of the KBR are composed of this land use (Figure 4.1).

Figure 4.1 The orchard-fynbos interface

4.2.2 Study design

Twenty sites were selected across the KBR (Figure 4.2). Orchard blocks were selected to represent the interface between orchards and natural fynbos, and to characterize the different management types present in the study area. Farmers and managers were interviewed, noting the application of insecticides around the time of sampling. All orchards received a mixture of organic and conventional (i.e. integrated) management, but it is difficult to give absolute

differences between management practices. However, interviews showed that there are two key management practices that differ between farms in the study area. These differ mainly in whether cover crops (mostly Fescue grass) are planted and maintained in the orchard alley (between trees) and whether broad spectrum insecticides are applied throughout the growing season or restricted to early in the growing season. Ten of the selected sites applied broad-spectrum insecticide throughout the growing season and the remaining ten relied more on selective insecticides later in the growing season (Table S8 lists all insecticides used). Orchard ages ranged between four and 37 years. Distances between sites ranged from 300 m to 21 km.
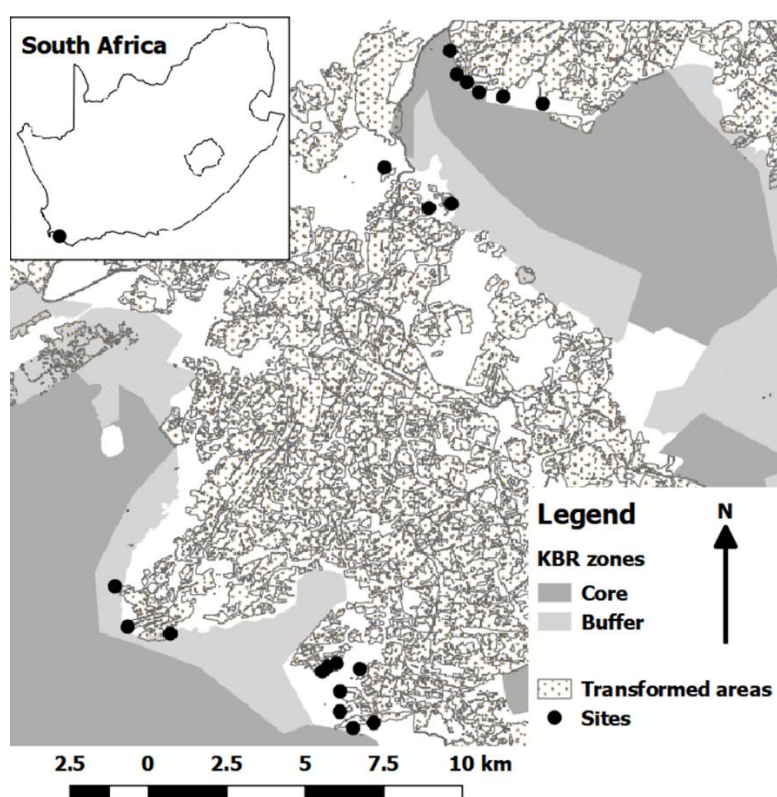
Figure 4.2 Map of study sites across the Kogelberg Biosphere Reserve (KBR)

4.2.3 Sampling

Epigaeic arthropods were sampled over two seasons: summer (October) 2015 and autumn (March) 2016. These periods coincide with flowering and fruiting stages of the pome fruit orchards. Each site consisted of a transect composed of three plots (each consisting of 4 pitfall traps arranged as a 10 x 10 m square) positioned in fynbos habitat adjacent to orchards at 15

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m, 45 m and 85 m (= central position) from the orchard edge. Plots near the orchard edge were placed closer together since it is assumed that changes in species diversity will occur more rapidly near habitat edges (Ewers et al 2007). An additional two plots were placed in adjacent orchard blocks at 15 m and 45 m from the edge (with traps positioned in orchard alleys). For most orchard blocks, 45 m was the maximum possible distance, as the size of blocks limited greater distances.

Each pitfall trap was 7 mm in diameter, filled with a 50% ethylene glycol solution and left out for five days per season (10 days in total). Arthropods were taken back to the laboratory and sorted to genus, family or superfamily (except mites, the majority of which could only be sorted to order due to lack of taxonomic resolution), and then to morpho-species where possible. Insects were sorted using the reference guide by Scholtz and Holm (2008), except Formicideae, which were based on Bolton (1994). Acari were sorted with guided input from a specialist. Araneae were sent to specialists (voucher specimens are being held at the South African National Collection of Arachnida). Voucher specimens for the remaining arthropods are being held at the University of Stellenbosch. Morpho-species are referred to as species in the rest of the chapter. Species data were pooled across both sampling seasons.

4.2.4 Environmental variables

4.2.4.1 Edge related variables

Local environmental variables for each plot consisted of habitat structure measurements and soil moisture content. Habitat structure was measured in terms of vertical and horizontal vegetation characteristics using similar methods as Parr et al. (2004) and Munyai and Foord (2012). At each pitfall trap (i.e. each corner of the 10 x 10 m plot) vertical vegetation height profiles were measured at four points located at 90 degrees apart in a 1.5 m radius centred on each trap. At each point, a 1.5 m pole (1 cm diameter) was held vertically and the total times vegetation came into contact with the pole was noted at 25 cm intervals. Horizontal structure was measured by placing a 1 m^2 quadrat over each trap and visually estimating the percentage of vegetation cover. Visual estimations were also made of percentage bare ground and litter cover around each trap. To keep visual estimates consistent across sites, photos of quadrats were taken and all estimates were done by the same person with the aid of a visual estimation guide as reference. Measurements of vegetation structure taken at each trap was averaged to

obtain a single measure per plot. At each plot, four soil moisture measurements were taken using a soil moisture meter (ZD-05 pH and Moisture Meter). These measurements were averaged for each plot.

To reduce the number of environmental variables, I used Principal Component Analysis (PCA) to construct new synthetic variables that are linear combinations of the raw variables (i.e. proportion cover of litter, vegetation and bare ground, vegetation height, vertical density, complexity and soil moisture). To obtain a measure of environmental variability in adjacent orchard sites, measurements of local environmental variables were averaged across all orchard plots and site scores were extracted from the first PCA axis (which described around 80 % of variance in environmental variables).

Applied to local environmental variables across fynbos plots, PCA would summarize overall variability among all plots. This would not necessarily illustrate differences in between-group variability at different distance classes, especially considering the different fire histories between sites. To obtain a measure of change in local environmental variables associated with edge effects for each plot in fynbos habitat, I used Discriminant Analysis of Principal Components (DAPC) to describe the diversity in environmental variables of predefined groups (in this case each of the distance categories) and then used the principal component of DAPC which showed the strongest discrimination between distance classes to describe edge related changes in local environmental variables. The component showed positive correlation with distance from orchard edge ($r < 0.55$). Other edge related variables recorded for each plot in fynbos were distance to orchard edge, insecticide management of adjacent orchard (broad spectrum pesticide sprayed throughout the growing season or only early), the presence of a tree line (wind break), and orchard age. Table 4.1 summarizes measured variables.

Table 4.1 Edge related variables included in the analyses. PCA - Principal Component Analysis; DAPC - Discriminant Analysis of Principal Components

Variable class	Parameter	Description
Distance from edge	Distance from edge	Distance from edge boundary in meters
Orchard management	Insecticide management	Two classes: broad-spectrum insecticide sprayed throughout or only early in the growing season
	Cover crop management	Variability in local environmental conditions in adjacent orchard block measured as first PCA axis
Permeability	Orchard age	Age of adjacent orchard block in years
	Wind break	Presence or absence of windbreak
Indirect edge effect	Change in local environmental conditions	Variability in local environmental conditions related to edge effects measured as the principal component of DAPC

4.2.4.2 Background environmental heterogeneity

Variables describing background environmental heterogeneity were selected based on previous exploratory analyses (Chapter 3). These consisted of both site measured variables and variables derived from spatial layers and included information on burn history, geology, mesoclimate and specific local habitat variables (see Table S9 for details).

4.2.5 Data analyses

To measure the effectiveness of sampling effort, species accumulation curves were plotted for fynbos and orchard plots respectively and species richness was estimated using the Chao estimator (Chao 1987). These analyses were conducted with the package 'vegan' (Oksanen et al. 2018) in R, version 3.5.0 (R Core Team 2018).

4.2.5.1 Species classification

Species were classified as either stenotopic, cultural, or ubiquitous species based on whether they showed any habitat preference (fynbos vs. orchard) or showed no preference (Duelli and Obrist 2003). Habitat fidelity was calculated using Pearson's phi coefficient of association using the package 'indicspecies' (De Cáceres and Legendre 2009) in R. Species classified as habitat specialists when the probability of association was <0.05, after correcting for unequal sample sizes (Tichý and Chytrý 2006). Species that did not show a strong association with either fynbos or orchard habitats, were assigned as ubiquitous. Since it is impossible to determine the habitat preference of singleton species, all subsequent analyses were repeated with singletons removed.

4.2.5.2 Species richness

All analyses were conducted on observed species richness. I used regression models to examine the influence of orchard edge-effects on species richness in natural fynbos at each station (15, 45, and 85 m from orchard edge, n = 60). Explanatory variables included in the models were distance to orchard edge, insecticide management, cover crop management (PCA scores), edge

related change in local environmental variables (DAPC scores), windbreak presence and orchard age.

Spatial-autocorrelation was assessed with correlograms (Bjørnstad and Falck 2001). Pearson residuals of a logistic regression model containing all explanatory variables (using a Poisson distribution) showed significant positive spatial correlation at short lag distances. Introducing site as a random effect removed spatial correlation. I used generalized linear mixed-effects models (GLMMs) with a Poisson distribution and with site as a random effect (i.e. grouping variable) to evaluate the variables of interest (fixed effects). Interaction terms were not included as it made the model too complex considering the sample size. I used adaptive Gauss-Hermite quadrature to estimate GLMM parameters. The data did not exhibit overdispersion, and significance of fixed effects were based on Type II Wald chisquare tests. The above procedure was repeated for all species, all species with cultural species excluded, stenotopic, cultural and ubiquitous species, as well as for all groups with singletons removed. GLMMs were performed with the package 'lme4' (Bates et al. 2015) in R.

4.2.5.3 Beta diversity

To reduce the influence of very abundant species (especially the social ants) on results, all analyses on beta diversity were conducted on presence-absence data. I investigated how beta diversity (as differences in group homogeneities) changed with proximity to the orchard edge. This was done by creating a distance matrix between all sampling points for each distance category (15 m, 45 m, and 85 m). Using a subset of contrasting dissimilarity measures can help reveal the nature of changes in ecological communities, and including joint-absences can be useful when the goal is to evaluate total changes in community (Anderson et al. 2011; Blanchet et al. 2014). I measured beta diversity using the Sørensen dissimilarity (excludes joint absences) and the simple matching coefficient (includes joint absences, Sokal & Michener 1958) (Anderson et al. 2011). I tested the null hypothesis of homogeneity of multivariate dispersions using a permutation based test using the 'betadisper' function in the package 'vegan' in R (Anderson et al. 2006). The above procedure was repeated for all species, all species with cultural species removed, stenotopic, cultural, and ubiquitous species.

To relate community patterns to edge influences, I used canonical ordination. Interest here lay in estimating how much of the variation in community composition among fynbos plots

could be explained by the different edge-related variables after accounting for background environmental heterogeneity and residual spatial autocorrelation. I used transformation based RDA, and selected Hellinger transformation, as it yielded the highest fraction of explained variance (Legendre and Gallagher 2001). To partition the variation in community structure among different sources I used partial RDA (Davies and Tso 1982; Legendre and Legendre 2012). Previous analyses suggest the importance of climate, fire history, and geological variables for epigaeic arthropod diversity, and these variables were included here as representative of background environmental heterogeneity. I used a global test of significance, and only submitted the variables representing background environmental heterogeneity to forward selection, when this was significant. I used Moran's eigenvector maps (MEMs) to describe spatial structures (Dray et al. 2006). To detect spatial patterns in the residuals once the effect of environmental predictors had been removed, I used the residuals of the model fitted with edge variables (and variables representing background heterogeneity if significant), and used forward selection with double stopping criterion to select significant MEM variables (Blanchet et al. 2008; Bauman et al. 2018). This was repeated for several candidate spatial weighting matrices (Bauman et al. 2018). In the final partial RDA, I partitioned out variance due to background environmental heterogeneity and spatial structures to quantify the variation explained by distance to edge, orchard management, permeability, and edge-induced changes in local environmental variables. For each RDA model, I performed permutation tests for the spatial independence of residuals to check for significant spatial autocorrelation at short lag distances (Wagner 2004). I performed separate significance tests for each marginal term in the model with all other terms and used partial RDA to isolate the effect of each explanatory variable. The above procedure was repeated for all, all minus cultural, stenotopic, cultural, and ubiquitous species as well as for all groups with singletons removed. Partial RDAs were performed using the 'vegan' package and MEMs constructed and selected using the 'adespatial' package (Dray et al. 2018) in R.

4.3 Results

4.3.1. Species richness

Overall, I sampled 20 573 individuals of 434 species. Species accumulation curves did not reach asymptotes (see Appendix 5 for accumulation curves) and the Chao-estimated total species richness was 636.57 (± 43.75) species. The most species rich groups across both habitat

types were Coleoptera (102 species), Acari (84 species) and Araneae (74 species). The most species rich groups in fynbos habitat were also Coleoptera (83 species), Acari (72 species) and Araneae (69 species). Species diversity was higher in natural fynbos than orchards. In the fynbos, most of the species consisted of ubiquitous species (297 species, 135 excluding singletons), followed by stenotopic species (60 species, 58 excluding singletons) and cultural species (32 species, 27 excluding singletons).

Results from GLMMs revealed that edge-associated changes in local environmental variables were important for all, all species with cultural species removed, and ubiquitous species richness (Table 4.2, Figure 4.3a-c). The measure of edge-associated change in local conditions was positively correlated with distance to edge, and the results indicate higher species richness associated with change in local environmental conditions closer to orchard edge. None of the measured predictors were important for stenotopic species. Distance to edge was the only important predictor for cultural species richness, and showed a negative relationship with cultural species richness (Figure 4.3d). All results were similar when singletons were removed.
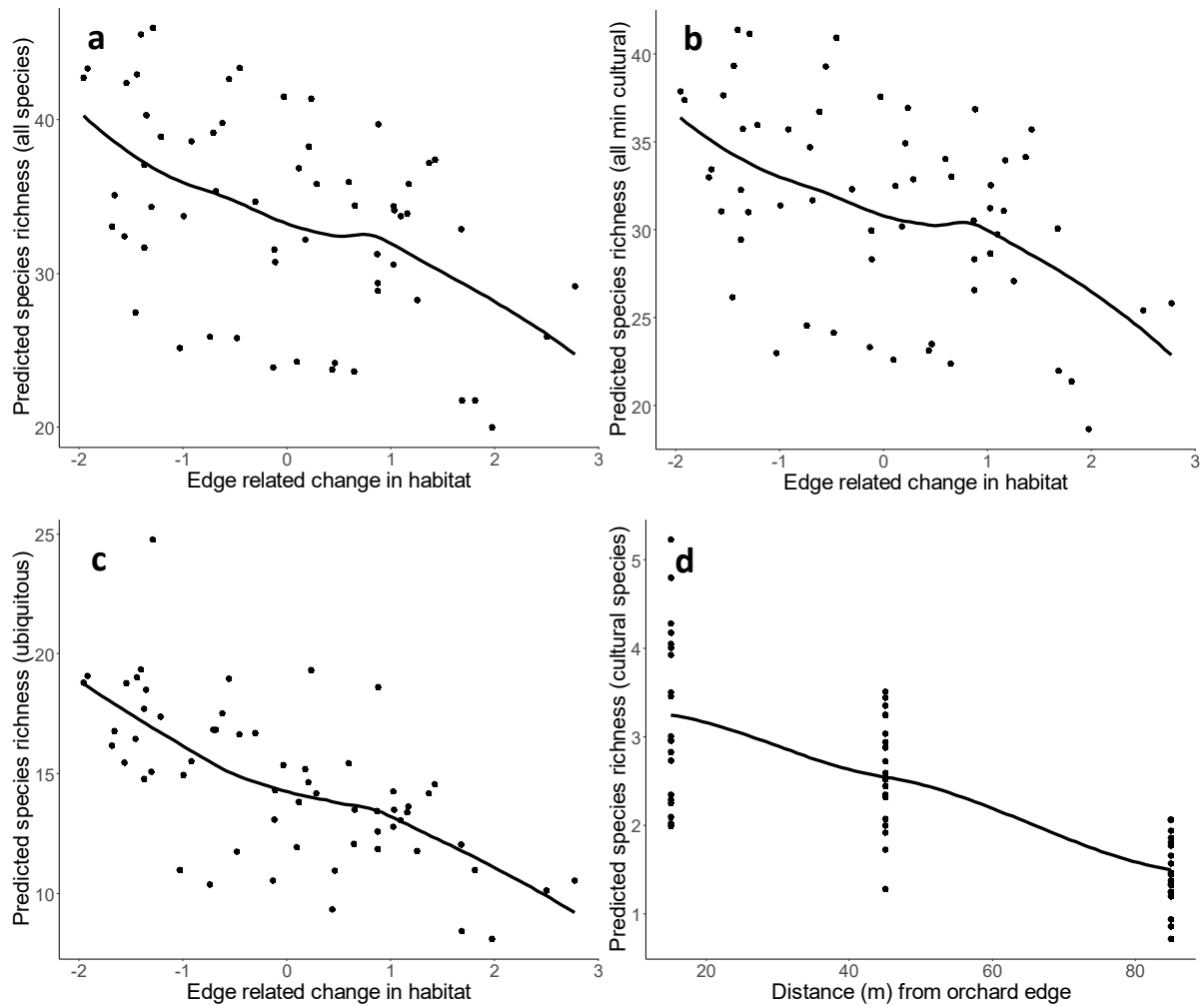
Figure 4.3 Generalized linear mixed model relating predicted species richness of a) all, b) all species with cultural species removed and c) ubiquitous species to edge related changes in local environmental variables (principal component of DAPC) as well as d) cultural species and distance from orchard edge

Table 4.2 Results of generalized linear mixed-effects models showing the effects of distance from edge, management, permeability, and edge associated changes in local environmental variables on species richness of all, all species with cultural species removed, stenotopic, cultural, and ubiquitous species. Site was included as a random variable in all models. Values represent Wald-chi squared values. Significant results ($p < 0.05$) are shown in bold. Values in brackets are for analyses excluding singletons. Manage – management, Permeab – permeability, Indirect – Indirect edge effect, Distance edge – distance from orchard edge, Insecticide – insecticide management, Cov.crop – cover crop management, Orch.age – orchard age, Windbreak – presence of windbreak, Edge.env – edge-associated change in local environmental variables

	Parameter	All species	All min cultural	Stenotopic	Cultural	Ubiquitous
Edge	Distance edge	0.05	1.45	1.14	**7.54***	0.23
		(0.08)	(1.07)	(1.67)	**(5.22*)**	(0.17)
Manage	Insecticide	1.67	1.37	0.51	2.09	1.86
		(1.63)	(1.40)	(1.01)	(1.69)	(1.68)
	Cov.crop	1.38	1.10	0.08	2.50	2.41
		(1.06)	(0.68)	(0.20)	(3.36)	(1.06)
Permeab	Orch.age	1.09	1.17	1.48	0.10	0.32
		(1.05)	(1.13)	(0.82)	(0.04)	(0.94)
	Windbreak	0.01	0.06	0.17	1.72	0.81
		(0.15)	(0.01)	(0.02)	(1.56)	(0.25)
Indirect	Edge. env	**5.46***	**5.63***	1.52	0.50	**4.86***
		(6.03*)	**(5.69*)**	(1.59)	(0.97)	**(4.81*)**

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

4.3.2 Beta diversity

Group homogeneities across the different distance classes showed no difference when using the Sørensen dissimilarity (Table 4.3). Only cultural species group homogeneities showed a significant decrease at increasing distance from orchard edge when using simple matching.

Variables related to background environmental heterogeneity were important for all groups except cultural species (see Table S10 for a list of selected variables). When including selected background environmental variables along with edge related variables, none of the model

residuals showed significant spatial patterns, and this was confirmed by the test for residual autocorrelation across distance classes. None of the partial RDA therefore contained MEMs as spatial predictors. The final partial RDAs indicated that edge-related variables explained 12.51% of the variation in all species composition, 12.85% of the variation in species composition when cultural species were removed, 14.59% of the variation in stenotopic species composition, 13.79% of the variation in cultural species composition, and 11.88% of the variation in ubiquitous species composition (Table 4.4). Similar values were obtained when excluding singletons from analyses. For all species, insecticide management and orchard age were significant components. When excluding singletons from all species, cover crop management and edge-related changes in local environmental variables were also significant. When excluding cultural species from the assemblage, insecticide management, cover crop management, orchard age and edge-related changes in local environmental conditions explained significant components of variation. When excluding singletons from the assemblage without cultural species, cover crop management was no longer significant. For stenotopic species composition insecticide management and orchard age explained significant components. When excluding singletons from the stenotopic species assemblage distance from orchard edge was also significant. Only insecticide management explained a significant component of the variation in cultural species composition. These results were similar when excluding singletons from the cultural species assemblage. Both insecticide management and cover crop management explained significant components of variation in ubiquitous species composition. When excluding singleton from the ubiquitous species assemblage, edge related changes in local environmental conditions were also significant.

Table 4.3 Results for the analyses of multivariate homogeneity of group dispersion based on Sørensen dissimilarity and simple matching coefficient for all, all species with cultural species removed, stenotopic, cultural and ubiquitous species. Significant results ($p < 0.05$) are shown in bold

Multivariate measure		15 m	45 m	85 m	p	Pairwise results
Sørensen	All species	0.48	0.50	0.47	0.19	-
	All min cultural	0.47	0.49	0.46	0.17	-
	Stenotopic	0.38	0.41	0.37	0.18	-
	Cultural	0.59	0.55	0.61	0.49	**-**
	Ubiquitous	0.57	0.59	0.57	0.33	-
Simple matching	All species	4.83	4.73	4.52	0.26	-
	All min cultural	4.53	4.52	4.36	0.55	-
	Stenotopic	2.85	2.98	2.93	0.37	-
	Cultural	**1.61**	**1.31**	**1.09**	**0.01***	85m < (15 m, 45 m)
	Ubiquitous	3.50	3.38	3.21	0.18	-

Values represent average distance to median, $* p < 0.05$, $** p < 0.01$, $*** p < 0.001$
Permutations: 999

Table 4.4 Permutation test for partial RDA under the reduced model. Significance of terms was assessed as marginal effects. Values in brackets indicate results for analyses with singletons removed. Manage – management, Permeab – permeability, Indirect – Indirect edge effects, Distance edge – distance from orchard edge, Insecticide – insecticide management, Cov.crop – cover crop management, Orch.age – orchard age, Windbreak – presence of windbreak, Edge.env – edge-associated change in local environmental variables

		All species	All min cultural	Stenotopic	Cultural	Ubiquitous
Full model						
	Conditional	7.39%	7.4%	9.2%	-%	2.29%
		(7.68%)	(7.75%)	(9.33%)	(-%)	(2.48%)
	Constrained	**12.51%***	**12.85%***	**14.59%***	**13.79%**	**11.88%***
	(edge variables)	**(13.15%***)**	**(13.26%***)**	**(14.86%***)**	**(13.85%**)**	**(12.39%***)**
Marginal effects						
Edge	Distance edge	1.90%	1.90%	2.10%	1.13%	1.79%
		(1.91%)	(1.94%)	**(2.20%*)**	(1.18%)	(1.72%)
Manage	Insecticide	**2.11%***	**1.98%***	**2.39%***	**4.09%***	**2.13%***
		(2.12%*)	**(2.02%)***	**(2.39%*)**	**(4.17%**)**	**(2.39%**)**
	Cov.crop	1.56%	**1.68%***	1.51%	1.66%	**2.02%***
		(1.62%*)	(1.67%)	(1.49%)	(1.66%)	**(2.16%)***
Permeab	Orch.age	**2.03%***	**2.01%***	**2.31%***	2.15%	1.87%
		(2.04%*)	**(2.06%*)**	**(2.38%**)**	(2.17%)	(1.86%)
	Windbreak	1.79%	1.74%	1.94%	2.23%	1.67%
		(1.71%)	(1.75%)	(1.94%)	(2.27 %)	(1.68%)
Indirect	Edge.env	1.86%	**2.48%***	1.85%	1.49%	2.00%
		(2.52%*)**	**(2.57%)***	(1.84%)	(1.46%)	**(2.07%*)**

Values indicate proportion of variance explained (full model) and partial fraction of the variation accounted for by each explanatory term (marginal effects). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

4.4 Discussion

More arthropod species were found in fynbos habitat than orchards, which supports previous work in this area (Witt and Samways 2004; Adu-Achaempong et al. 2016), as well as other studies that have compared natural habitats with managed orchard systems (Scalercio et al.

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2007). Most species were ubiquitous. This relatively high number of ubiquitous epigaeic arthropods supports other fragmentation studies in South Africa (Ingham and Samways 1996), but should also be interpreted with caution. Numerous species can be classified as ubiquitous if they are passive dispersers over large areas (Tscharntke et al. 2005). This is partly supported by the fact that a large number of ubiquitous species were also singletons, and evidence suggests that many rare species can be accidentally sampled transient species (Sgarbi and Melo 2017).

Overall species richness did not show a negative relationship with distance to orchard edge as hypothesized. This contrasts with other studies that found higher arthropod species richness at the interface of crop and non-crop biotopes (Kammerer et al. 2016). The removal of cultural species did not change this relationship. Cultural species richness did however show a negative relationship with distance to orchard edge. This was reflected by changes in cultural species beta diversity (measured as differences in group homogeneities), and which showed significantly lower variability farther away from the edge when including joint absences. None of the locally measured environmental variables (edge related or background environmental heterogeneity) were important for cultural species composition. These results indicate that mass effects are important for cultural species diversity near orchard edges, but that this does not result in an increase in overall species richness near edges. This could be because orchards do not contain enough species to compensate for species loss, or that the spillover of cultural species is not high enough to result in higher overall species richness near the orchard edge at the distances studied here.

Ecotonal studies suggest that edge-biased distribution of species can be explained by differences in vegetation structure and microclimate between edge and interior locations (Magura 2002; Kautz et al. 2013). Edge induced changes in local conditions were related to higher species richness of all species, all species without cultural species, and ubiquitous arthropod species near edges. Edge-induced changes in local conditions also explained significant components of variation in the species composition of these groups when excluding singletons. Evidence suggests that species which tend to avoid transformed areas are more vulnerable to the negative effects of fragmentation, while those that are able to exploit transformed habitats remain stable or increase (Gascon et al. 1999). This could explain why stenotopic species did not show the same response as ubiquitous species to changes in local environmental conditions.

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Edge-associated changes in local environmental variables was mostly driven by changes in litter cover (higher litter cover near edges) and in vegetation structure (less vegetation cover and lower vegetation height near edges). Some orchard blocks were bordered by firebreaks of various ages that consisted of more open habitat compared to neighbouring fynbos habitat farther away, as well as windbreaks that resulted in higher litter cover near edges. Artificial windbreaks have also been shown to create a surrounding quiet zone where higher densities of airborne arthropods are located (Lewis 1965; Samways and Manicom 1983). Although this study focused on epigaeic arthropods, this includes organisms that use non-directed, passive dispersal by wind (e.g. ballooning spiders). Higher species richness near edges could be a response to unique local environmental conditions related to these management interventions, or result from inherent biases associated with pitfall trapping which is a function of a species population size, activity and ease of capture (Greenslade 1964). Since catchability can be influenced by habitat structure (Melbourne 1999, Koivula et al. 2003), my measure of edge effects could be compromised by associated changes in vegetation structure.

Structural edge contrast is an important extrinsic factor determining edge responses (Ries et al. 2004), and several studies have found edge contrast to be important for determining edge effects on organisms in remaining natural habitats (Peyras et al. 2013; Chabrerie et al. 2013; Gieselman et al. 2013; Aragón et al. 2015). Species specialization has been proposed as an important factor explaining the differential response of species to edge effects, with specialist species showing stronger edge responses than generalist species (Peyras et al. 2013). As predicted, permeability (measured as orchard age) was more important for stenotopic species than either ubiquitous or cultural species. This was only apparent when examining changes in species composition. Biodiversity loss can take many years to unfold (Essl et al. 2015) and care should be taken when analysing data collected over short time durations (Gonzalez et al. 2016). As the measure of edge contrast here was orchard age, the results can also reflect a temporal change in species composition since edge establishment (Chabrerie et al. 2013). Further investigation is required to investigate how edge contrast influences orchard permeability (see Chapter 5).

Numerous studies have found an influence of broad-spectrum vs. selective insecticide treatment on arthropod diversity and abundance (Epstein et al. 2000; Markó and Kádár 2005; Balog and Markó 2007; Markó et al. 2009). Here, I found this influence to be evident for epigaeic arthropods in adjacent non-crop habitats. Agroecosystems are characterised by organisms dispersing and foraging between crop and non-crop habitats (Tscharntke et al. 2005)

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and differences in vulnerability of off-crop and in-crop species to management within crop habitats can be explained by differences in exposure (de Lange et al. 2012). The prediction that management related variables will be more important for ubiquitous and cultural species than stenotopic species was upheld by the results. Compared to stenotopic species, management related variables explained around twice as much of the variation in cultural and ubiquitous species composition. Insecticide management was the only important management variable for cultural species composition, while both insecticide and cover crop management was important for ubiquitous species composition. The maintenance of cover crops have been found to have a positive influence on arthropod diversity within orchards (Carpio et al. 2018), but here differences in cover crop management did not influence arthropod species richness in adjacent non-crop habitats. Insecticide management influenced species composition, but not species richness. Why this is the case is unclear. One reason could be the differential response of different taxonomic groups to broad-spectrum insecticides (Mansfield et al. 2006) and associated changes through tropic cascades (Fountain et al. 2007).

This study analysed the role of orchard permeability, management and edge related changes in local environmental conditions for epigaeic arthropod assemblages in adjacent non-crop habitats. I found that the edge-mediated effects were by no means mutually exclusive and depended on both extrinsic edge characteristics and intrinsic characteristics related species habitat specialisation (Fagan et al. 1999). This supports other work that has examined the role of species specialization in determining differential species responses to habitat edges (Peyras et al. 2013). The results also highlight the role that "hidden heterogeneity" (Chloé et al. 2013) of agricultural systems plays in determining edge effects on epigaeic arthropods in adjacent non-crop habitats. Even though I did not compare highly contrasting management types (e.g. organic vs. conventional), insecticide management was important for all groups, and it is important to recognize that local differences in orchard management can determine the region's biodiversity in adjacent non-crop habitats. There is also potential for interactions among the different edge variables that were not considered here, and which might further promote heterogeneity. For example, the development of the phytophagous arthropod community in the first five years since orchard establishment is influenced by management (Brown and Welker 1992), and insecticide use can be a dominant factor limiting the development of otherwise distinct communities (Brown and Puterka 1997). Orchard cover crop management can influence re-colonization from adjacent non-crop habitats following insecticide applications (Markó and Kádár 2005). Orchard age and windbreaks can influence the amount of insecticide

drift to adjacent non-crop habitats (Nuyttens et al. 2010; Zaady et al. 2018), and the vegetation characteristics in adjacent non-crop habitat can influence the route of exposure (de Lange et al. 2012; EFSA PPR 2015).

Patch-orientated measures of fragmentation are easy to implement with modern geospatial tools (i.e. geographical information systems) and valuable for conservation planning and assessment, but this remnant-based perspective does not capture how processes in the matrix contribute to changes in ecological patterns across the modified landscape as a whole (Kupfer et al. 2006). The results support conceptual landscapes that rely less on human-defined landcover and emphasizes that the variegated nature of transformed landscapes can contribute to various degrees to overall biodiversity (McIntyre and Barrett 1992; Ingham and Samways 1996). Managed systems are often highly productive and can provide a wealth of resources that can be used by non-agricultural species (Westphal et al. 2003). Cross-edge spillover of agriculturally subsidised species are expected to be most likely under conditions where there is a strong gradient in productivity (Tscharntke et al. 2005; Rand et al. 2006). Such edge effects can have important conservation implications, as they can lead to significant changes in ecosystems function (Blitzer et al. 2012; Rand et al. 2006; Ries and Sisk 2004). Transformed habitats can also affect the spread of invasive species and the susceptibility of communities to invasions (With 2002). These impacts are likely to increase as humans continue to modify natural systems (Blitzer et al. 2012).

Edge influences from surrounding land-uses can be extensive, and ultimately determine the response of communities to fragmentation and therefore a comprehensive strategy for biodiversity conservation requires more than reserve-areas where human disruption is minimized (Franklin 1993; Öckinger et al. 2012). Previous work in this area has found edge induced changes in epigaeic arthropod species composition up to 1 km from orchard edges (Chapter 3). At the distances studied here (15m, 45m and 85 m from edge), none of the groups showed higher dispersion (when excluding joint absences). Except for stenotopic species (excluding singletons), distance from edge did not explain any unique variation in species composition when also considering the influence of other edge related variables. For the majority of species, the results are in contrast to other studies that have found community composition to be more variable near habitat edges (Clough et al. 2007; Filgueiras et al. 2016) but coincides with work that has observed changes to be only apparent at larger spatial scales (Marsh et al. 2018). Buffer zones with limited or restricted intensive land-use is one possible solution that can reduce the influence of surrounding land-use activities on remaining diversity

in protected areas (Schonewald-Cox and Bayless 1986). The KBR does not have a continuous buffer zone, but where present, wide enough and properly managed, the buffer is necessary for supporting conservation of epigaeic arthropod diversity within core areas by limiting the influence of agricultural practices associated with orchard systems in the transition zone. To reduce the influence of spillover from cultural species on sensitive habitats within farms, farmers can maintain local buffer strips that are ideally 80 m wide. Within this strip, indirect management interventions that manipulate vegetation structure to maintain heterogeneous conditions over short distances (e.g. maintaining fire breaks or clearing alien trees) can promote diversity of arthropods which occur in both orchards and non-crop habitats.

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Chapter 5 Managing spillover of epigaeic arthropods in perennial crops: the influence of landscape and local scale land-use intensity and permeability on species richness and beta diversity in orchards in a biosphere reserve

Abstract

Diversity and abundance of arthropods are influenced by factors at both local and landscape scales. In agricultural systems, non-crop habitats are important for promoting in-field arthropod diversity, although in perennial orchard systems, habitat contrast may impede spillover of arthropods from these non-crop areas. I compare different trophic groups of ground dwelling arthropods in pome fruit orchards and adjacent non-crop habitats, in the Kogelberg Biosphere Reserve (KBR), in terms of species richness, abundance, and beta diversity, and assess the influence of local (management) and landscape (proportion of crops in the landscape) scale land-use intensity (LUI), habitat contrast, and distance to orchard edge. Local and landscape scale LUI had contrasting effects on species richness, and on the dissimilarity between crop and non-crop habitats. For some groups, species richness within orchards showed a positive relationship with increasing landscape scale LUI. However, for most groups, the dissimilarity between crop habitats was largely due to nested differences, and exhibited lower species replacement over short geographical distances compared to non-crop habitats and crop edges. Higher landscape scale LUI increased dissimilarity between crop and non-crop communities. Reduced local LUI and orchard contrast resulted in higher in-field species richness for some trophic groups, but neither of these factors increased similarity between orchard and non-crop assemblages. Effects were mostly for species which occur in both crop and non-crop habitats, suggesting that landscape scale LUI is benefiting a subset of species which are able to exploit both habitat types and contributing to assemblage divergence. Reduced contrast can be valuable for promoting local predator species richness, but did not improve permeability of the orchards. Promoting diversity within farmland in the KBR will require integration of factors across spatial scales. Management and design can be used to promote local diversity, but non-crop habitats are essential to promote orchard biodiversity over a range of different functional groups.

Keywords: orchard, land-use intensity, scale, epigaeic arthropods, biosphere reserve, fynbos

5.1 Introduction

Agricultural intensification is resulting in the loss and alteration of natural habitats, and is threatening biodiversity across the globe (Newbold et al. 2015). Despite this, there is an agreement on the potential compatibility between food security and biodiversity conservation (Tscharntke et al. 2005, 2012; Fischer et al. 2006). Local biodiversity is important for providing important ecosystem services necessary for crop production (e.g. nutrient cycling, pollination and pest control) and high diversity within a functional group can provide the adaptive capacity required to secure this function under unpredictable external pressures, e.g. droughts or management mistakes (Gunderson and Holling 2002; Fischer et al. 2006; Tscharntke et al. 2007; Oliver et al. 2015). Accordingly, understanding how farming restricts or promotes biodiversity is important for realising conservation-agriculture win-win solutions (Tscharntke et al. 2012).

Farmland diversity is affected by a mixture of agricultural intensification at local (in-field) and landscape scales (Tscharntke et al. 2005; Clough et al. 2005; Gonthier et al. 2014). At the local scale, direct disturbances such as pesticide spray can be lethal or sub-lethal, and have been associated with a decline in farmland species diversity (Thorbek and Bilde 2004; Hyvönen 2007; Geiger et al. 2010; Stapel et al. 2000). Agricultural intensification also results in the simplification of landscape structure across different spatial scales (Fahrig et al. 2011). Monocultures and weed control lead to simplified plant communities and habitat structure within fields (Landis 2017), and at landscape-scale agricultural expansion that is focused on a single or only a few crops creates homogenous landscapes with less natural and semi-natural habitats (Tscharntke et al. 2005).

According to classic metapopulation theory, populations in low-quality habitats can be maintained by inflows of organisms from source populations (Hanski 1999). Compared to crop areas, natural and semi-natural areas (hereafter non-crop habitats) are relatively stable, and can provide essential refuges e.g. in times of pesticide application or harvesting (Fahrig et al. 2011; Tscharntke et al. 2012). Agroecosystems are therefore expected to contain a low proportion of regional richness due to their high disturbance levels, and experience immigration of individuals associated with surrounding non-crop habitats (also referred to as 'spillover' or 'mass effects'), and considered important for enhancing local diversity (Loreau et al. 2003; Bengtsson et al. 2003; Tscharntke et al. 2007). For many species, non-crop habitats also provide essential alternative resources e.g. food or overwintering sites (Bianchi et al. 2006;

Tscharntke et al. 2007; 2012), and research has shown that complex landscapes (those that contain a high percentage of non-crop habitats) maintain more diverse communities compared to simpler, agriculturally dominated landscapes (Attwood et al. 2008; Loreau et al. 2003; Tscharntke et al. 2007; 2012).

In-field biodiversity, however, addresses only a small part of the overall biodiversity, which is mainly driven by the high spatial dissimilarity in species composition (or beta diversity) between assemblages in a given landscape. Dissimilarity between assemblages can be separated into turnover (or replacement) and richness difference or nestedness-resultant components (Harrison et al. 1992; Baselga 2010; 2012). Partitioning these two components can be useful for assessing patterns of variation in species composition, as each can originate from different underlying processes. Species replacement involves the simultaneous loss and gain of species due to environmental filtering, competition, or spatial or historical constraints (Leprieur et al. 2011). Richness difference refers to one community being made up of more species than another. Nestedness is a form of richness difference where the species at a site is a strict subset of species at a richer site, and reflects a non-random process of species loss or gain due to differences in habitat suitability or selective colonization and extinction (Cook and Quin 1995; Gaston and Blackburn 2008, Baselga 2012). In real world communities, each of these components can contribute to different degrees to observed diversity patterns. Beta diversity is generally higher in natural compared to managed agricultural systems, and landscape-wide species replacement (especially within non-crop habitats) can add significantly to insurance and the maintenance of ecosystem function under conditions of environmental change (Bengtsson et al. 2003; Tscharntke et al. 2007).

When beta diversity across non-crop areas is high, sets of species that spillover from non-crop habitats to crop habitats can vary from place to place, and consist of a small (nested) subset of the regional species pool (Tscharntke et al. 2007). The degree and ease of cross-habitat movement will be determined by landscape configuration and composition (Holzschuh et al. 2010). For example, the dispersal and exchange of individuals between crop and non-crop habitats can be confounded by the proximity to non-crop habitats (Loreau et al. 2003; Bengtsson et al. 2003; Tscharntke et al. 2008). High species diversity near habitat edges is used as an indication of spillover between adjacent habitats (e.g. Hogg and Daane 2010), i.e. higher local species richness near edges is the result of the mixing of species from both habitat types (Magura 2002; Ewers and Didham 2006). Apart from species richness, there can also be

substantial differences in species composition, with community similarity decreasing with increasing distance from edge (Davis et al. 2001; Dangerfield et al. 2003).

The influence of local- and landscape-scale effects on arthropod diversity in agricultural systems have largely been studied in annual crops, which are dynamic and ephemeral habitats. Fewer studies have focused on the more stable perennial crops. Deciduous fruit orchards consist of multi-strata designs that may provide rich resources and habitats to living communities (Simon et al. 2010). However, these systems are intensively managed to produce standardized 'zero damage' fruits (Parisi et al. 2014), and the disruption caused by pesticide applications can make refuges outside of orchards essential (Landis et al. 2000). Apart from the direct effect of intensive farming practices on in-field diversity, indirect effects related to crop structure can also play a role in the permeability and recolonization of orchard habitats. In landscapes that consist of low open vegetation, crop growth can greatly alter microclimate conditions, and result in higher habitat contrast, especially among crops such as fruit orchards grown over several decades. For example, in South African fynbos (sclerophyllous shrubland) vegetation, Adu-Acheampong et al. (2016) found more grasshopper species in relatively open vineyards compared to cooler, closed-canopy orchards. In addition to crop age, crop edge orientation in relation to the sun is another important feature that can weaken or strengthen edge associated abiotic gradients (Ries et al. 2017) and which can influence arthropod distribution patterns across agricultural landscapes (Meyer and Sisk 2001; Sarthou et al. 2005).

Understanding how agricultural intensification across different scales effect diversity is important to harmonize production and conservation, especially in biosphere reserves, which aim to reconcile biodiversity conservation with their sustainable use (UNESCO MAB 1996; UNESCO 2017). Here, I assess the changes in epigaeic arthropod diversity and the diversity of different trophic groups (i.e. 'redundancy') in fruit orchards due to agricultural practices at different spatial scales in the Kogelberg Biosphere Reserve (KBR), South Africa. In orchard systems, landscape-scale land-use intensity (LUI) related to agricultural expansion, local scale LUI related to management, and indirect effects related to orchard habitat contrast, can simultaneously influence diversity. Here, I integrate these different aspects. In addition, special interest lay in species which spillover from non-crop habitats and I focus on a subset of species which occur in both crop and non-crop habitats. I compare crop interior, crop edges, and non-crop habitats in terms of species richness and beta diversity (total dissimilarity, dissimilarity due to nestedness, and dissimilarity due to turnover). I also investigate the responses of in-field species richness and cross-edge beta diversity (species replacement between crop and non-crop

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habitats) to measures of LUI at landscape and local scales, distance from orchard edge, and orchard contrast. I focus on the following predictions:

1) Non-crop habitats will be more species rich, and exhibit higher turnover rates, than crop habitats, while nestedness difference will contribute more to dissimilarity within crop habitats.

2) Orchard edges will have higher species richness and replacement compared to orchard interiors.

3) Both local- and landscape-scale factors will influence arthropod diversity within orchards.

4) Higher LUI (both local- and landscape-scale), and orchard contrast, will have a negative effect on arthropod species richness in orchards, and increase cross-edge dissimilarity.

5.2 Methods

5.2.1 Study area

The KBR is situated at the southwestern tip of South Africa. Most of the land that comprises the terrestrial parts of core and buffer zones of the KBR are in a natural or near-natural state. The dominant vegetation type in the region is fynbos, a schlerophyllous shrubland adapted to low soil nutrients, winter rainfall, and to fires. The KBR encompasses part of the Elgin district, South Africa's main pome fruit producing region.

5.2.2 Study design

Twenty sites were selected across the KBR (Figure 5.1). Orchard blocks were selected to represent the interface between orchards and natural fynbos, and to characterize the different management types present in the study area. Farmers and managers were interviewed, noting the application of pesticides, fertilizers and cover crop management about the time of sampling. All orchards received a mixture of organic and conventional (i.e. integrated) management. All orchards were irrigated with drip irrigation. Orchard ages ranged between four and 37 years (Figure 5.2), and distances between sites ranged from 300 m to 21 km.

Each site consisted of two plots (each consisting of 4 pitfall traps arranged as a 10 x 10 m square, with traps located in orchard inter-rows, i.e. between the trees) positioned in orchard blocks adjacent to fynbos at 15 m ('edge' plot) and approximately 45 m ('interior' plot) from the orchard-fynbos interface. The size of most blocks limited greater distances. An additional plot was placed in adjacent fynbos habitat at 85 m from the edge. At this distance, spillover from species that thrive in orchards is a small component of the assemblage (see Chapter 4), and I consider this plot type as reference for natural to near-natural conditions.
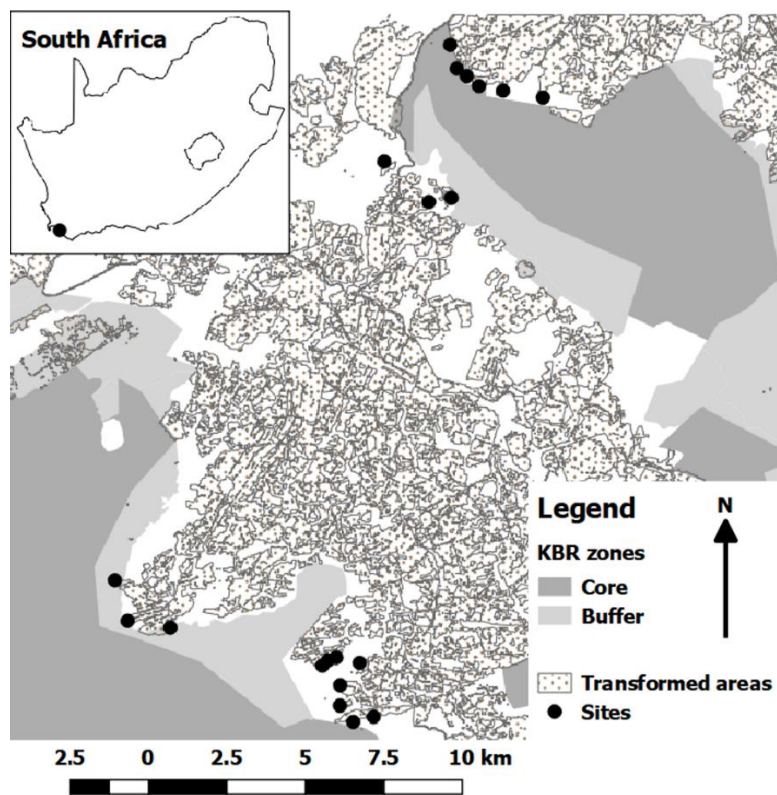
Figure 5.1 Map of study sites across the Kogelberg Biosphere Reserve (KBR)
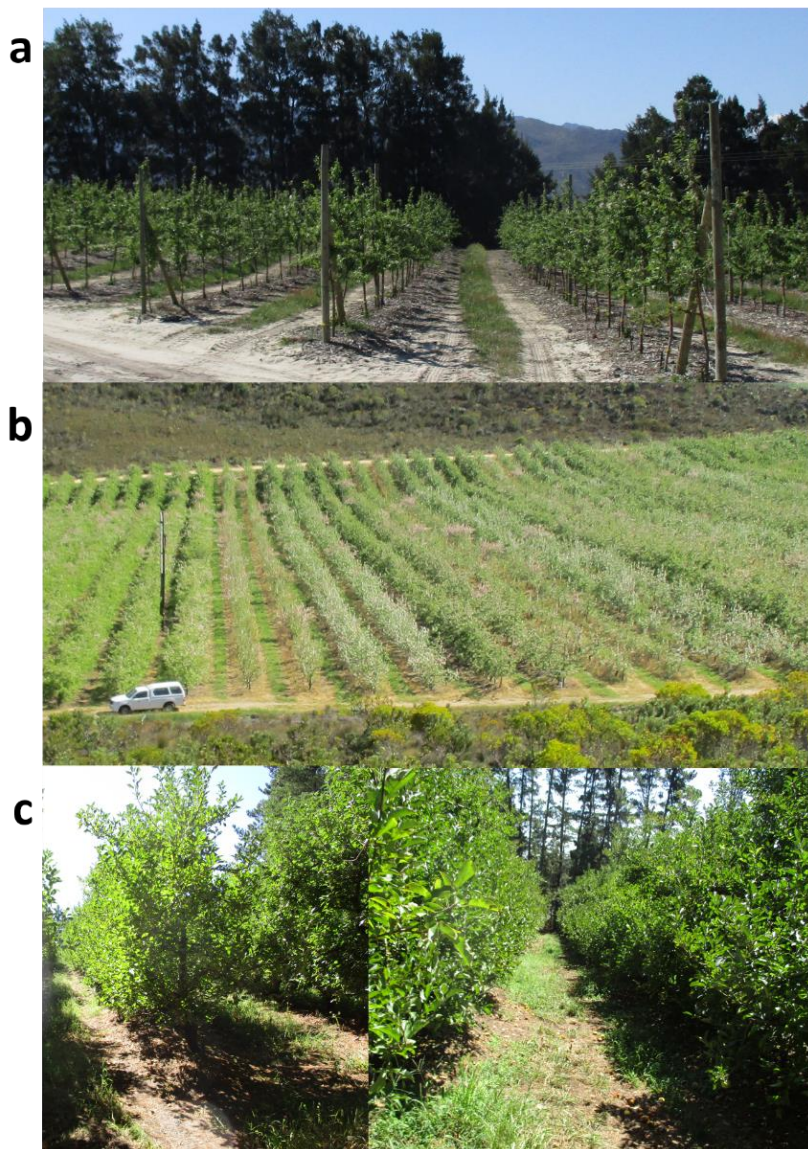
Figure 5.2 Orchards of different ages: a) 4 years, b) 16 years, c) 31 years

5.2.3 Sampling of arthropods and plants

Epigaeic arthropods were sampled over two seasons: spring (October) 2015 and autumn (March) 2016. These periods coincide with flowering and fruiting stages of the fruit orchards.

Each pitfall trap was 7 mm in diameter, filled with a 50% ethylene glycol solution, and left out for five days per season (10 days in total). Arthropods were taken back to the laboratory and sorted to genus, family or superfamily (except mites, the majority of which could only be sorted to order due to lack of taxonomic resolution), and then to morpho-species where possible. Insects were sorted using the reference guide by Scholtz and Holm (2008), except Formicideae,

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which were based on Bolton (1994). Acari were sorted with guided input from a specialist. Araneae were sent to specialists (voucher specimens are being held at the South African National Collection of Arachnida). Voucher specimens for the remaining arthropods are being held at the University of Stellenbosch. Morpho-species are referred to as species in the rest of the chapter. Functional groups were based on the predominant feeding habit at the family level (or order level for mites), namely predaceous/parasitic, herbivorous (which also included pollen feeders and wood borers), omnivorous, and detritivorous (which also included saprophages and fungivores). Within orchards, understory plants (grasses and weeds) were surveyed in the orchard alley within a 1 m^2 quadrat centred on each pitfall trap. Plants were identified to family level only.

5.2.4 Environmental variables

All environmental variables are summarized in Table 5.1.

5.2.4.1 Descriptions of land-use intensity (LUI)

5.2.4.1.1 Local scale LUI

I describe local scale LUI using a quantitative, continuous index (similar to Blüthgen et al. 2012) based on information gained from farmers. The compound index summarizes standardized intensity of pesticide application (insecticide and fungicide), cover crop management, and fertilization. For insecticide application, I summed the number of seasons that broad spectrum insecticides were applied (0: none, 1: only early in the growing season, 2: early and late in the growing season). I used a similar approach to sum fungicide applications. For cover crop management (i.e. actively sown), I used the absence of cover crop management (1: no cover crop management, 0: cover crop management present). I included the inverse of the number of weed families recorded as a measure of habitat homogenization. Fertilization used by farmers was quantified as kg nitrogen per hectare per year. To obtain a measure of local scale LUI, each component was standardized relative to its mean and then summed for each site (Blüthgen et al. 2012).

5.2.4.1.2 Landscape scale LUI

I used high-resolution orthorectified aerial photographs (obtained from the Chief Directorate: National Geo-spatial Information) to digitize and classify landscape elements as either crops (mostly fruit orchards), built up areas, water bodies or farm reservoirs, non-orchard woody vegetation (wind breaks and plantations), and non-crop areas (natural and semi-natural fynbos areas). I used circular buffers centred between the central and edge orchard plots, and calculated the proportion of each landscape element at 100, 200, 300, 400 and 500 m radii buffers. To select the most relevant scale at which landscape elements explained arthropod diversity within orchards, I used a model selection procedure based on the Akaike information criterion (AIC; Burnham and Anderson 2004) and selected the species richness model with the lowest AIC. The lowest AIC model was that which defined landscape elements at 200 m, and I used principal component analysis (PCA) on the landscape elements measured at this scale to create a new synthetic indicator. The first PCA component (PC1, 47.78% of variance explained) summarized a gradient from landscapes dominated by non-crop (natural and semi-natural) habitats (>70% of landscape consist of non-crop) to landscapes dominated by orchards (<20% of landscape consist of non-crop). The amount of crop within the landscape has previously been suggested as in indicator of land-use intensity (Persson et al. 2010) and I use PC1 to describe landscape scale LUI.

5.2.4.2 Orchard contrast

I used a composite measure to describe the amount of contrast between orchards and adjacent fynbos habitats that incorporate orchard age, as well as orchard edge (crop to non-crop interface) and tree row orientation in relation to the sun. For each site, the orientation of the nearest crop to non-crop interface was classified as either northern (orchard edge facing from northwest to northeast: 0) or southern (orchard edge facing from south west to south east: 1). For tree row orientation, I classified sites as either north-to-south orientation (0) or east-to-west orientation (1). I used simple averaging to create a composite variable describing the decrease in incoming solar energy within orchard and its nearest edge by summing the z scores of the original variables.

Table 5.1 Environmental variables used in analyses and short description of each. LUI = Land-use intensity

Parameter	Description
Local scale LUI	Compound index summarizing standardized intensity of pesticide application (insecticide and fungicide), cover crop management, and fertilization
Landscape scale LUI	First PCA component describing variation in landscape elements at 200 m. Correlated with an increase in crop cover and decrease in non-crop habitat.
Distance from orchard edge	Distance from nearest orchard edge
Contrast	Composite variable indicating contrast between crop and non-crop habitats, composed of orchard age, orientation of the nearest edge (northern or southern) and orientation of tree rows (north-south or east-west).

5.2.5 Data analyses

All analyses were conducted in R, version 3.5.0 (R Core Team 2018). The cumulative counts of arthropods pooled across both sampling sessions were used as a measure of abundance and species richness, as well as to calculate beta diversity. I analysed species richness, abundance and beta diversity separately for each functional group (predators, herbivores, omnivores and detritvores), as well as for taxa overall (additive over all groups).

As special interest lay in species which spillover from non-crop habitats, analyses on the effect of local and landscape features were repeated on a subset of the data with those species which thrive in the orchard, or 'cultural' species (Duelli and Obrist 2003), removed, and I refer to these species as 'non-cultural' species. It is possible that all species depend to some degree on non-crop habitats, and I consider cultural species to be an extreme along a continuum. To help discriminate between species habitat associations, I included additional data from 40 non-crop plots (see Chapter 4 for details). I classified cultural species using Pearson's phi coefficient of association (corrected for unequal sample sizes) using the package 'indicspecies' (De Cáceres and Legendre 2009; Tichý and Chytrý 2006). Species were assigned as cultural species when the probability of association with orchard habitats was <0.05.

5.2.5.1 Species richness and abundance

To measure the effectiveness of sampling effort, and to test for differences in species richness between non-crop habitats and the different field positions in crop habitats, species accumulation curves were plotted for non-crop and orchard plots (centre and edge) using the package 'vegan' (Oksanen et al. 2018).

I used generalized linear mixed-effects models (GLMMs) (using a Poisson distribution) with site identity as a random effect (i.e. grouping variable) to examine the influence of local scale LUI, landscape scale LUI, distance from edge and orchard contrast on arthropod species richness and abundance. I calculated the variance inflation factor (VIF) to check for multicollinearity between explanatory variables with the 'car' package (Fox and Weisberg 2011). Species richness models did not exhibit overdispersion but abundance data did. For species richness models I compared multiple models (all possible combinations of explanatory variables) based on Akaike's information criterion corrected for small sample sizes (AICc). For abundance models, I used Quasi-AIC corrected for small sample sizes (QAIc). AICc and QAICc differences were used to estimate the Akaike weight of each model (w_i). If the difference between a model's AICc and the model with the lowest AICc was less than 4, it was included in the best subset of models. To calculate the relative importance of explanatory variables, the sum of Akaike weights over all models in the best subset that included an explanatory variable was calculated. I used full model-averaging (Lukacs et al. 2009) and unconditional estimates and standard errors are reported. Input variables were standardized to a mean of 0 and SD of 0.5 before analyses. GLMMs were performed with the package 'lme4' (Bates et al. 2015), and model selection was done using the 'MuMIn' package (Barton 2018).

5.2.5.2 Beta diversity

I used the 'betapart' package (Baselga and Orme 2012; Baselga et al. 2018) to calculate distance matrices accounting for the replacement, nestedness-resultant component, and total dissimilarity (the sum of the replacement and nestedness components) between assemblages.

I used linear mixed-effects models (LMMs) to assess whether communities within orchards were more similar than within non-crop areas (i.e. crop interior vs. crop edge vs. adjacent non-crop habitats) and to test whether the slope of the distance decay is stronger within non-crop assemblages as compared to crop assemblages. I used as dependent variables the calculated

measures of beta diversity: either total dissimilarity (β_{sor}), replacement (β_{sim}) or nestedness (β_{sne}), calculated between pairs of either non-crop plots, orchard edge plots, or orchard interior plots. As explanatory variables, I included 'position' (three factors: non-crop, orchard edge, or orchard interior), geographical distance between sites, and an interaction term between position and geographical distance. To account for multiple comparisons between sites I used an approach similar to that of Knop (2016): I included two random factors representing the two sites between which dissimilarity was calculated, e.g. if dissimilarity was calculated between site 'a' and 'b' the two random factors used were 'a' and 'b'. To assess the significance of the explanatory variables, I used likelihood-ratio tests (LRT) with which I compared models with and without the variable. Where interactions were significant, I used the 'effects' package (Fox 2003) to calculate and plot interactions. Where interaction terms were not significant, I removed the interaction term and report results of models composed of main effects only. LMMs were performed with the package 'lme4' (Bates et al. 2015).

To assess how LUI and habitat contrast contributed to differences between crop and non-crop habitats, I focused on the replacement component of dissimilarity. I examined cross edge dissimilarity by comparing each plot in the orchard to every reference plot (non-crop fynbos plot) across the study area using a multiple-site dissimilarity index of species replacement (β_{SIM}). I investigated the relationship between β_{SIM} and environmental predictors (landscape scale LUI, local scale LUI, distance from edge and permeability) using LMMs (with site identity included as a random variable). Analyses was based on the same information-theoretic approach using AICc as described in section 2.5.1 above.

5.3 Results

5.3.1 Species richness and abundance

I collected a total of 11 019 individuals from 320 species. The most species rich functional groups were predators (138 species), herbivores (70 species), and omnivores (64 species). Within orchards, 47 species were cultural species, and 153 were non-cultural species.

Accumulation plots showed higher species richness within non-crop habitats compared to crop interior and crop edge habitats for all species, detritivores and omnivores. For predators

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and herbivores, crop habitats increased in species richness faster with fewer plots, but with increasing number of plots the accumulation curves for both these groups were less steep compared to non-crop habitats (Appendix 6).

Within orchards, landscape scale LUI was the most important predictor for species richness for most groups (Table 5.2). Only for herbivores was local LUI the most important predictor of species richness. The only parameter estimates for which the confidence intervals did not include zero were for the effect of landscape scale LUI on all, all non-cultural, predator, non-cultural predator, and omnivore species richness (positive effect), for the effect of local LUI on all non-cultural, non-cultural predator and non-cultural herbivore species richness (negative effect), and for the effect of orchard contrast on non-cultural predator species richness (negative effect) (Figures 5.3 and 5.4).

The most important predictors for abundance within orchards were different between the different functional groups, and for some groups, none of the measured variables were exceptionally important (Table 5.3). The only parameter estimates for which the confidence intervals did not include zero were for the effect of landscape scale LUI on non-cultural predator species abundance (positive effect) and for the effect of distance from edge on detritvore abundance (positive effect).

Table 5.2 Model-average estimates for landscape scale LUI, local scale LUI, distance from orchard edge, and orchard contrast, predicting species richness of all arthropods, predators, herbivores, omnivores and detritivores, as well as all groups excluding cultural species ('non-cultural'). Parameter estimates are standardized effect sizes and are therefore on a comparable scale. Coefficients are highlighted in bold that do not include 0. LUI = land-use intensity

Parameter	Estimate	Unconditional SE	Confidence Interval (95%)	Relative importance
All species				
Landscape LUI	0.344	0.096	**(0.149, 0.540)**	1.00
Local LUI	-0.147	0.113	(-0.374, 0.078)	0.76
Edge distance	-0.005	0.026	(-0.059, 0.049)	0.17
Contrast	-0.112	0.114	(-0.339, 0.115)	0.62
All species non-cultural				
Landscape LUI	0.544	0.130	**(0.281, 0.808)**	1.00
Local LUI	-0.350	0.121	**(-0.597, -0.104)**	1.00
Edge distance	-0.027	0.063	(-0.155, 0.100)	0.30
Contrast	-0.175	0.158	(-0.491, 0.139)	0.67
Predators				
Landscape LUI	0.323	0.092	**(0.136, 0.511)**	1.00
Local LUI	-0.121	0.108	(-0.337, 0.095)	0.68
Edge distance	-0.011	0.043	(-0.098, 0.076)	0.20
Contrast	-0.168	0.114	(-0.396, 0.059)	0.81
Predators non-cultural				
Landscape LUI	0.509	0.154	**(0.194, 0.823)**	1.00
Local LUI	-0.443	0.138	**(-0.725, -0.161)**	1.00
Edge distance	-0.013	0.068	(-0.151, 0.125)	1.00
Contrast	-0.437	0.146	**(-0.73, -0.139)**	0.22
Herbivores				
Landscape LUI	0.131	0.153	(-0.173, 0.436)	0.56
Local LUI	-0.272	0.151	(-0.576, 0.031)	0.89
Edge distance	0.023	0.073	(-0.122, 0.169)	0.23
Contrast	-0.218	0.166	(-0.550, 0.113)	0.77

Herbivores non-cultural

Landscape LUI	0.165	0.284	(-0.401, 0.732)	0.40
Local LUI	-0.705	0.279	**(-1.271, -0.139)**	1.00
Edge distance	0.002	0.118	(-0.236, 0.242)	0.17
Contrast	-0.035	0.151	(-0.341, 0.269)	0.21

Omnivores

Landscape LUI	0.573	0.257	**(0.054, 1.092)**	0.96
Local LUI	-0.012	0.094	(-0.202, 0.178)	0.16
Edge distance	-0.092	0.153	(-0.398, 0.213)	0.40
Contrast	-0.063	0.156	(-0.375, 0.248)	0.26

Omnivores non-cultural

Landscape LUI	0.543	0.281	(-0.021, 1.109)	0.92
Local LUI	-0.016	0.105	(-0.231, 0.197)	0.18
Edge distance	-0.119	0.174	(-0.466, 0.226)	0.46
Contrast	-0.074	0.170	(-0.414, 0.265)	0.29

Detritivores

Landscape LUI	0.150	0.182	(-0.212, 0.512)	0.54
Local LUI	-0.067	0.130	(-0.328, 0.193)	0.36
Edge distance	0.010	0.069	(-0.129, 0.151)	0.19
Contrast	-0.002	0.072	(-0.149, 0.143)	0.18

Detritivores non-cultural

Landscape LUI	0.497	0.277	(-0.058, 1.053)	0.89
Local LUI	-0.183	0.231	(-0.643, 0.276)	0.52
Edge distance	0.007	0.077	(-0.149, 0.164)	0.16
Contrast	-0.020	0.103	(-0.228, 0.187)	0.18
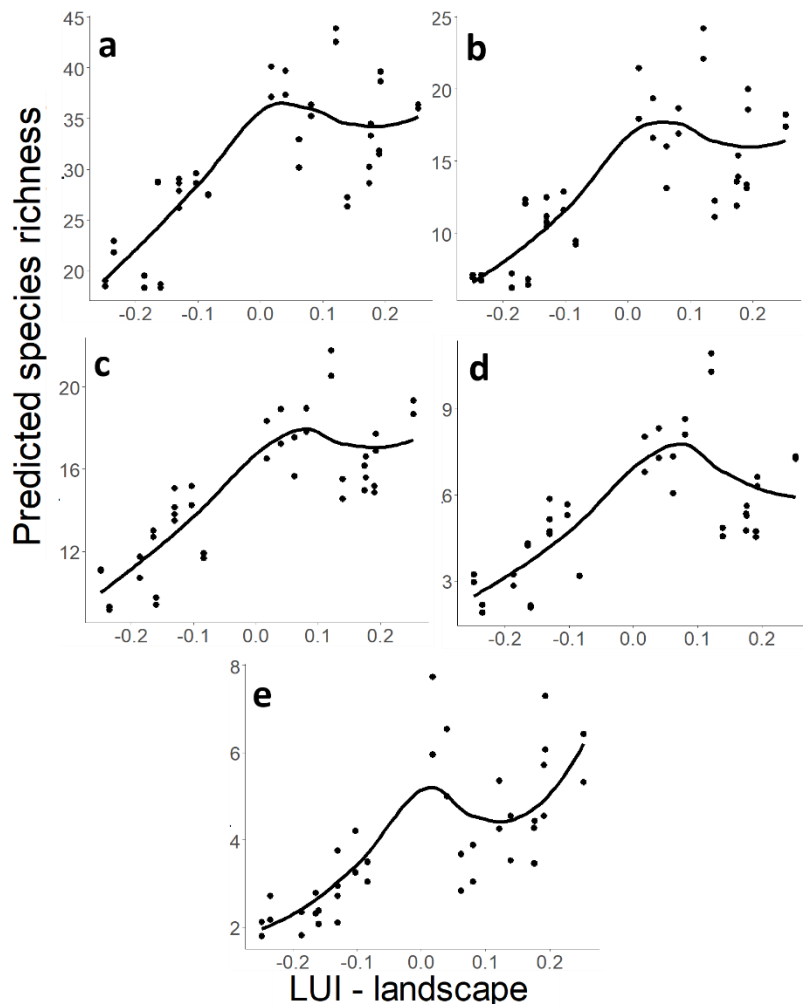
Figure 5.3 Relationship between landscape scale land-use intensity (LUI) and predicted species richness of a) all, b) all non-cultural, c) all predator, d) non-cultural predator, and e) all omnivore species
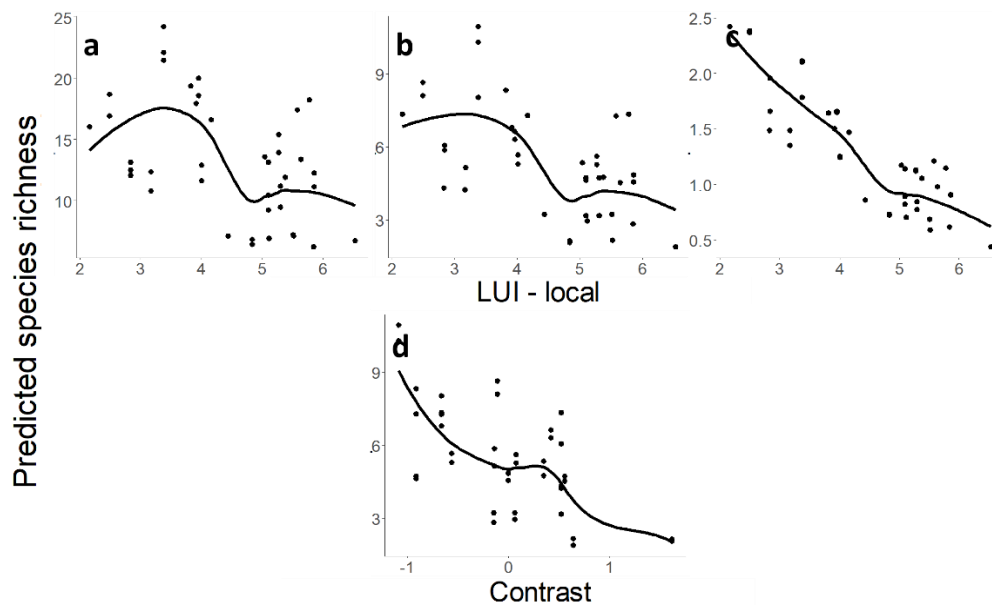
Figure 5.4 Relationship between local scale land-use intensity (LUI) and predicted species richness of a) all non-cultural, b) non-cultural predator and c) non-cultural herbivore species, and between orchard contrast, and d) non-cultural predator species

Table 5.3 Model-average estimates for landscape scale LUI, local scale LUI, distance from orchard edge, and orchard contrast, predicting abundance of all arthropods, predators, herbivores, omnivores, and detritivores, as well as all groups excluding cultural species ('non-cultural'). Parameter estimates are standardized effect sizes, and are therefore on a comparable scale. Coefficients are highlighted in bold that do not include 0. LUI = land-use intensity

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative importance
All species				
Landscape LUI	0.219	0.311	(-0.393, 0.832)	0.37
Local LUI	-0.154	0.213	(-0.575, 0.265)	0.39
Edge distance	-0.009	0.022	(-0.053, 0.034)	0.21
Contrast	-0.043	0.132	(-0.306, 0.220)	0.17
All species non-cultural				
Landscape LUI	0.532	0.599	(-0.647, 1.712)	0.47
Local LUI	-0.194	0.296	(-0.779, 0.390)	0.35
Edge distance	0.028	0.051	(-0.073, 0.129)	0.28
Contrast	-0.079	0.226	(-0.529, 0.371)	0.20
Predators				
Landscape LUI	0.082	0.163	(-0.241, 0.406)	0.27
Local LUI	-0.108	0.178	(-0.462, 0.244)	0.34
Edge distance	-0.012	0.031	(-0.075, 0.050)	0.22
Contrast	-0.081	0.161	(-0.400, 0.238)	0.27
Predators non-cultural				
Landscape LUI	0.903	0.344	**(0.216, 1.591)**	0.94
Local LUI	-0.662	0.361	(-1.380, 0.056)	0.84
Edge distance	0.131	0.134	(-0.134, 0.396)	0.57
Contrast	-0.348	0.367	(-1.074, 0.377)	0.55
Herbivores				
Landscape LUI	0.277	0.428	(-0.568, 1.123)	0.35
Local LUI	-0.138	0.259	(-0.651, 0.374)	0.29
Edge distance	-0.130	0.099	(-0.327, 0.066)	0.68
Contrast	-0.099	0.256	(-0.608, 0.410)	0.20

Herbivores non-cultural

Landscape LUI	0.475	0.517	(-0.548, 1.498)	0.53
Local LUI	-0.544	0.498	(-1.529, 0.441)	0.61
Edge distance	0.125	0.228	(-0.328, 0.580)	0.31
Contrast	-0.172	0.319	(-0.805, 0.460)	0.32

Omnivores

Landscape LUI	0.557	0.789	(-0.997, 2.112)	0.37
Local LUI	-0.043	0.176	(-0.398, 0.311)	0.15
Edge distance	-0.018	0.050	(-0.118, 0.081)	0.17
Contrast	-0.114	0.339	(-0.788, 0.560)	0.17

Omnivores non-cultural

Landscape LUI	0.569	0.801	(-1.009, 2.148)	0.37
Local LUI	-0.046	0.182	(-0.411, 0.318)	0.15
Edge distance	-0.022	0.057	(-0.135, 0.090)	0.18
Contrast	-0.108	0.332	(-0.770, 0.553)	0.16

Detritvores

Landscape LUI	0.061	0.194	(-0.325, 0.448)	0.16
Local LUI	-0.054	0.162	(-0.377, 0.268)	0.17
Edge distance	0.247	0.096	**(0.055, 0.439)**	0.93
Contrast	0.008	0.124	(-0.243, 0.260)	0.13

Detritvores non-cultural

Landscape LUI	0.254	0.506	(-0.752, 1.260)	0.29
Local LUI	-0.131	0.301	(-0.730, 0.467)	0.23
Edge distance	0.198	0.119	(-0.038, 0.434)	0.82
Contrast	0.002	0.189	(-0.381, 0.385)	0.09

5.3.2. Distance decay of beta diversity within habitats

Linear mixed-effects models of dissimilarity within different field positions (non-crop vs. crop edge vs. crop interior) detected a significant interaction between position and geographical

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distance for all species, predators, and herbivores (Table 5.4). For these analyses, the involvement of interactions can make the interpretation of main effects misleading, and so I focus on graphical plots of the interactions for interpretation (Figure 5.5). For all species, there were differences between plot positions in terms of the relationship between dissimilarity and geographical distance, but only in terms of the replacement component of dissimilarity (Figure 5.5a). Replacement of all species within each position showed a positive relationship with geographical distance, but this relationship was slightly shallower within non-crop habitat and crop edges compared to within crop interior habitats (which showed the lowest species replacement at short geographical distances, but increased more steeply with increasing geographical distance). For predators, total dissimilarity within non-crop habitats was relatively similar with increasing geographical distance (Figure 5.5b). Likewise, total predator species dissimilarity within crop edges was relatively stable with increasing geographical distance. Crop interiors showed the lowest total predator species dissimilarity at short geographical distances, but increased more steeply with increasing geographical distance compared to non-crop and crop edges. Predator dissimilarity due to species replacement showed a similar interaction between position and geographical distance, as just described for total dissimilarity (Figure 5.5c). For predators, the relationship between dissimilarity due to nestedness and geographical distance also differed between positions (Figure 5.5d). Predator nestedness was lowest within non-crop habitats, and showed a steady relationship with increasing geographical distance between sites. Predator nestedness was highest for crop interiors at short geographical distances, but this decreased with increasing geographical distance, while nestedness increased with geographical distance in crop edges. Herbivore total dissimilarity was highest within non-crop habitats at short geographical distances, and remained similar with increasing geographical distance between sites (Figure 5.5e). Herbivore total dissimilarity was similar within crop edges and crop interiors at short geographical distances, but crop edges showed a steeper increase within increasing geographical distance compared to crop interiors. Herbivore species replacement was highest within non-crop habitats at short geographical distances, but decreased with increasing geographical distance, while herbivore species replacement within both edge and interior crop habitats increased with increasing geographical distance (Figure 5.5f). The contribution of nestedness to herbivore dissimilarity did not show marked differences between positions at short distances, but increased with increasing geographical distance within non-crop habitats, and decreased with increasing geographical distance both within crop edge and crop interiors (Figure 5.5g).

Most of the results from analyses without a significant interaction between geographical distance and position reflected that reported above. For all species and detritivores, total dissimilarity and species replacement within non-crop habitats was higher than within crop interiors. Omnivore total dissimilarity was similar between crop interior and non-crop habitats, but higher within crop edges, while omnivore species replacement within non-crop and crop edges was higher than within crop interiors. For all species and detritivores, the nestedness component contributed more to dissimilarity within crop interior habitats compared to non-crop habitats. Omnivore nestedness was similar within crop interior and non-crop habitats, but higher in crop edges.

Table 5.4 Analyses of dissimilarities (Sørensen pair-wise dissimilarity (β_{sor}), Simpson pair-wise dissimilarity accounting for replacement (β_{sim}) and dissimilarity accounting for nestedness fraction of Sørensen Pair-wise dissimilarity (β_{sne})) between plots located either in non-crop, crop edge or crop interior habitats. Values represent F values. Where non-significant, interactions were dropped, and results from models, including only main effects, are reported. Position = non-crop vs. crop-edge vs. crop-interior, geogr = geographical distance

		Position	Geogr	Position:Geogr
All species	β_{sor}	**68.10*****	**15.29*****	-
	β_{sim}	**49.72*****	**11.74*****	**3.77***
	β_{sne}	**33.01*****	0.40	-
Predators	β_{sor}	**149.75*****	2.99	**3.74***
	β_{sim}	**117.11*****	1.66	**5.09****
	β_{sne}	**16.78*****	0.09	**3.09***
Herbivores	β_{sor}	**27.83*****	**4.19***	**3.53***
	β_{sim}	**13.44*****	2.98	**5.88****
	β_{sne}	1.45	0.02	**3.26***
Omnivores	β_{sor}	**12.02*****	3.40	-
	β_{sim}	**43.55*****	3.42	-
	β_{sne}	**67.80*****	0.49	-
Detritivores	β_{sor}	**71.12*****	**5.18***	-
	β_{sim}	**129.25*****	0.02	-
	β_{sne}	**43.69*****	**6.61***	-
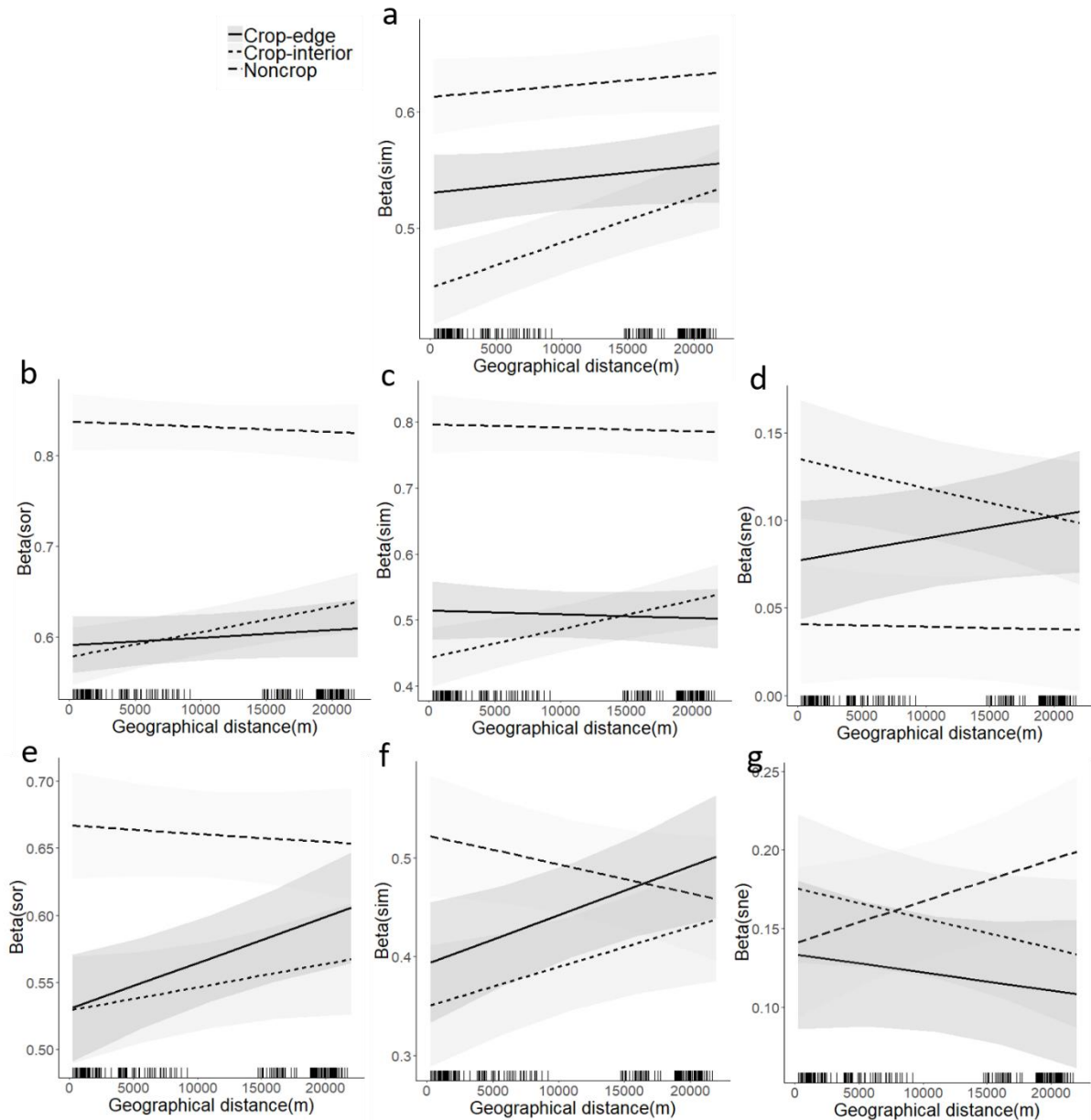
Figure 5.5 Model estimated dissimilarity of a) all species, b-d) predator species, and e-g) herbivore species for total dissimilarity (sor, left), replacement component (sim, centre), nestendess component (sne, right) with increasing geographical distance in non-crop habitats, crop interiors and crop edges [linear mixed-effects model (LMM; position x geographical distance)]

5.3.3 Cross-edge dissimilarity

For dissimilarity due to replacement (β_{SIM}) between crop-noncrop habitats, the most important predictor was landscape scale LUI, local scale LUI, and habitat contrast for all non-cultural species (Table 5.5). Landscape scale LUI was also the most important predictor for non-cultural

predators and non-cultural detritivores. For each of these groups, increasing landscape scale LUI was associated with an increase in species replacement. For all non-cultural species, an increase in local LUI and habitat contrast resulted in a reduction in species replacement. Local LUI was also an important predictor for herbivore species replacement, but parameter estimates included 0 for this group.

Table 5.5 Model-average estimates for landscape scale LUI, local scale LUI, distance from orchard edge and contrast predicting the multiple-site replacement component (β_{SIM}) of cross-edge dissimilarity of all arthropods, predators, herbivores, omnivores and detritivores, as well as all groups excluding cultural species ('non-cultural'). Parameter estimates are standardized effect sizes and are therefore on a comparable scale. Coefficients are highlighted in bold that do not include 0. LUI = land-use intensity. All values 1. X 10^{-5}

Parameter	Estimate	Uncond itional SE	Confidence Interval	Relative importance
All species				
Landscape LUI	49.04	68.39	(-87.05, 185.24)	0.48
Local LUI	-2.48	24.93	(-52.96, 47.98)	0.14
Edge distance	2.68	17.64	(-32.98, 38.36)	0.18
Contrast	15.71	43.42	(-102.57, 71.15)	0.24
All species non-cultural				
Landscape LUI	156.30	48.25	**(58.27, 254.42)**	1.00
Local LUI	-130.60	47.81	**(-227.83, -33.45)**	1.00
Edge distance	-8.61	28.10	(-65.16, 47.92)	0.24
Contrast	-129.40	48.72	**(-228.44, -30.34)**	1.00
Predators				
Landscape LUI	-24.62	49.93	(-124.28, 75.04)	0.34
Local LUI	41.27	60.36	(-78.96, 161.51)	0.46
Edge distance	3.07	24.60	(-46.74, 52.89)	0.20
Contrast	43.61	62.92	(-81.63, 168.84)	0.46
Predators non-cultural				

Landscape LUI	183.51	64.97	**(51.64, 315.36)**	1.00
Local LUI	-10.92	35.60	(-82.37, 60.53)	0.21
Edge distance	-27.18	38.15	(-103.09, 48.74)	0.47
Contrast	-12.15	38.56	(-89.48, 65.18)	0.22
Herbivores				
Landscape LUI	-125.12	140.71	(-405.20, 154.97)	0.58
Local LUI	186.08	151.03	(-115.08, 487.25)	0.75
Edge distance	26.43	74.60	(-122.83, 175.70)	0.23
Contrast	14.57	62.57	(-111.15, 140.29)	0.17
Herbivores non-cultural				
Landscape LUI	29.49	91.06	(-152.57, 211.55)	0.19
Local LUI	-307.50	184.40	(-677.10, 62.08)	0.88
Edge distance	5.11	56.16	(-108.65, 118.88)	0.12
Contrast	-17.10	73.43	(-164.61, 130.42)	0.15
Omnivores				
Landscape LUI	38.82	76.28	(-113.52, 191.16)	0.36
Local LUI	15.12	51.64	(-88.52, 118.76)	0.21
Edge distance	-10.86	36.50	(-84.12, 62.41)	0.22
Contrast	-57.95	89.50	(-236.29, 120.39)	0.44
Omnivores non-cultural				
Landscape LUI	18.63	54.24	(-90.02, 127.27)	0.24
Local LUI	10.12	41.98	(-74.26, 94.50)	0.17
Edge distance	-19.57	44.9	(-109.35, 70.22)	0.31
Contrast	-78.35	94.48	(-266.45, 109.76)	0.55
Detritvores				
Landscape LUI	27.72	76.33	(-125.07, 180.51)	0.25

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Local LUI	4.96	43.71	(-83.45, 93.37)	0.13
Edge distance	-19.69	46.54	(-112.80, 73.43)	0.30
Contrast	23.38	71.55	(-120.04, 166.81)	0.23
Detritvores non-cultural				
Landscape LUI	276.79	85.96	**(102.34, 451.22)**	1.00
Local LUI	-15.97	49.93	(-116.07, 84.14)	0.22
Edge distance	-40.79	66.36	(-173.06, 91.47)	0.41
Contrast	-17.14	52.22	(-121.79, 87.52)	0.22

5.4 Discussion

This study investigated how local and landscape characteristics of a pome fruit production landscape influenced in-field epigaeic arthropod responses in terms of species richness and beta diversity. As predicted, and in agreement with other studies (Tylianakis et al. 2005; Attwood et al. 2008), species turnover contributed more to dissimilarity in natural non-crop habitats, and nestedness contributed more to dissimilarity in crop habitats. Non-crop habitats were more species rich than crop habitats in terms of all arthropods, omnivores and detritivores. This supports other work in this region that has found lower species richness in perennial crops compared to adjacent fynbos habitats (Gaigher et al. 2015; Adu-Acheampong et al. 2016). Although I did not find an observable influence of distance from non-crop habitat on species richness, species replacement contributed more to dissimilarity in orchard edges than crop interiors for most of the arthropod functional groups. This emphasizes that the evaluation and interpretation of the effects of local and landscape factors should be based on different components of landscape species diversity (Hendrickx et al. 2007). The majority of species sampled in orchards consisted of species which did not show a strong association with crop habitats, which partly supports the idea that the majority of arthropod species occurring in agricultural landscapes depend on the presence of semi-natural habitats (Duelli and Obrist 2003), and the importance of including non-crop resources for improving arthropod conservation in agro-ecosystems (Balzan et al. 2016).

Unlike other studies which found a positive association between reduced landscape scale LUI (i.e. the amount of non-crop habitat) and local arthropod species richness (e.g. Schmidt et

al. 2005; Chaplin-Kramer et al. 2011), I found higher in-field species richness to be associated with higher percentage of crop habitat in the landscape (as defined within a 200 m radius). The higher productivity often associated with agricultural systems as compared to natural systems can provide greater resources (Tscharntke et al. 2005). For example, Westphal et al. (2003) found that bumblebee populations increased in landscapes with high amounts of oilseed rape. Considering the well-known relationship between the discovery of species and the number of individuals sampled (Gotelli and Colwell 2001), higher productivity could have been a reasonable explanation if higher land-use intensity was generally also associated with higher abundances.

The higher stability of perennial orchards as compared to more ephemeral annual crops could also contribute to the weak relationship between the amount of non-crop habitat and in-field species richness. For example, work on Australian vineyards has found only a weak relationship between local spider abundance and the amount of non-crop habitat in the landscape (D'Alberto et al. 2012). These results suggest that non-crop habitats may be less important in the context of perennial crops because these systems are more stable and provide greater structural and compositional complexity (Lefebvre et al. 2016). Here, the positive association between in-field species richness and landscape scale LUI was driven by cultural species for some groups (e.g. omnivore species richness), but for other groups this was not the case (e.g. non-cultural predator species richness and abundance). Dissimilarity between orchards was mostly due to nestedness differences, and higher landscape scale LUI resulted in higher cross-edge species replacement. The benefits of landscape scale LUI to infield species richness is therefore restricted to a subset of the overall assemblage that is able to thrive in both non-crop and crop habitats. These results suggest that agricultural LUI at the landscape scale is contributing to local community divergence (Solar et al. 2015) and potentially the homogenization of in-field communities (Jeliazkov et al. 2016).

I found reduced local LUI to increase species richness of all non-cultural species, non-cultural predators, and non-cultural herbivores. The benefits of reduced local LUI for farmland diversity is supported by other work (Picchi et al. 2016; Prieto-Benítez and Méndex 2011; Tuck et al. 2013). Interestingly, reduced local LUI was also associated with higher cross-edge species replacement. This suggests that the higher species richness associated with lower local LUI is not necessarily due to species which are relatively abundant throughout non-crop or crop habitats, but are relatively rare in both habitat types. One explanation for this could be that low input managed farms may be more capable of sustaining populations based on local resources,

and depend less on immigration from the surrounding landscape, as has been found in other orchard systems (e.g. Lefebvre et al. 2016).

When habitats are structurally more similar, organisms may perceive edges as less contrasting (Duelli et al. 1990), and this should permit at least a subset of species to move between habitats and reduce dissimilarity between habitat types. Previous studies that have compared dissimilarity (or similarity) between habitats of different contrast have found lower species replacement and higher species spillover between low contrast habitats compared to high contrast habitats (Yekwayo et al. 2016; Inclán et al. 2016). Contrary to these findings, I found lower cross-edge species replacement in high contrast orchards compared to low contrast ones, giving limited support for the potential increase in permeability with reduction in orchard contrast. The measure of contrast used in this study was related to differences in microclimate conditions, and included not only orchard age, but specific design variable regarding the orientation of edges and tree rows in relation to the sun. I found higher non-cultural predator species richness in low contrast orchards, which supports other studies which have found warmer microclimates within orchards to be beneficial for different arthropod groups, e.g. honey bees and native bees in the USA (Tepedino et al. 2007).

I did not find higher similarity between crop edge and non-crop habitats than between crop interior and non-crop habitats, which could potentially represent the influence of edge specialist species (Pryke and Samways 2012), or the fact that the centre plot (at 45 m) is not isolated from spillover. There are a number of additional potentially confounding factors which the present study did not take into account. One is the effects of management in orchards surrounding the focal orchards. For example, Rundlöf et al. (2008) found higher butterfly species richness in both organic and conventional farms as the proportion of organic farming in the landscape increased. There is also the potential for strong interaction effects between distance from crop edge and local, as well as landscape-scale, factors (Tsitsilas et al. 2006; Caballero-López et al. 2012; Jones et al. 2016). Furthermore, the results are restricted to epigaeic arthropods and different patterns may have been detected if arthropods were sampled using different methods.

The results indicate that the loss of species across the entire landscape was not only due to lower species richness in local assemblages, but also reduced species replacement between orchard assemblages. For farmers who aim to preserve or promote diversity across agricultural landscapes in the KBR, the results emphasize focusing on species enhancement of entire agricultural areas, rather than just local areas. Since the position within a field (edge vs. interior)

affected species replacement, large orchard blocks will be mostly characterized by species composition that does not diverge between patches. Farmers who wish to improve species replacement within orchards should increase the amount of edge between crop and non-crop habitats. At the same time, it is essential to conserve diversity within remaining natural non-crop habitats. Agroecosystems can function as a source or sink for arthropods, with spillover from crop to non-crop habitats, or vice versa. It is therefore important to note that species which benefit from orchard habitats, and become overly abundant, can negatively affect other species (e.g. through aggressive behaviour, competition or predation) (Tscharntke et al. 2005b; Rand et al 2006; see also Chapter 4). Buffer strips, both regional (e.g. UNESCO MAB 1996; UNESCO 2017) and local (around sensitive key habitats within a farm such as riparian areas (Hickey and Doran 2004; Vought and Lacoursièr 2010)), are therefore essential to protect native communities and ecosystem function.

Another approach to improve diversity across farmlands, which is linked to the concept of representativeness in formal conservation areas (Margules and Pressey 2000; Kukkala and Moilanen 2013), is that of reinstating heterogeneity (Fischer et al. 2006). Within the KBR, pome fruit production is concentrated on more fertile lowlands. Heterogeneity of land-uses and land-use intensities should therefore occur across environmental gradients (i.e. at least some highly productive land should be protected or kept for low intensity usage). The results also showed limited evidence that reducing orchard contrast improved permeability of orchard habitats to native communities. This suggests that corridors and stepping stones may be essential, especially for less mobile groups such as epigaeic arthropods (as compared to birds or bees) (Fischer et al. 2006; Samways 2007; Concepción et al. 2008).

Studies which evaluate the impact of local and landscape factors on farmland diversity usually break down farming systems into two opposing types: organic and conventional (e.g. Clough et al. 2005; Roschewitz et al. 2005; Holzschuh et al. 2010; Tuck et al. 2013). Although this classic opposition can be useful to detect general patterns, it may not be the most relevant approach. The index of local LUI used was based on nitrogen input, pesticide and fungicide application, absence of cover crop management, and the homogenization of local weed communities. These circumstances can all be altered to a certain degree, so that the orchard does not favour only a subset of the community. The results indicated that strategies that reduce the intensity of local management will promote herbivore and predator species richness. High species numbers of predators and alternative prey may ensure the presence of a predator when pest densities are about to rise (Bianchi and van der Werf 2004). The effects were mostly for

species which are not restricted to crop habitats (non-cultural), which can be especially valuable considering that these species will stay in the landscape when the target pest is absent or in low abundance. Since the amount of non-crop habitat can be important in determining the importance of management intensity, the benefits of reduced local LUI for promoting species richness is likely to become even more important in orchards that are further away from the core and buffer areas of the KBR (Roschewitz et al. 2005; Schmidt et al. 2005; Holzschuh et al. 2010; Batáry et al. 2011).

The development of sustainable agriculture will depend largely on developing multifunctional landscapes that are capable of both maintaining biodiversity and agricultural production (Balmford et al. 2012). Arthropods are one of the most important groups for providing ecosystem services to agriculture (Losey and Vaughan 2006; Lavelle et al. 2006). The results suggest that when planning agricultural landscapes that are aimed at promoting epigaeic arthropod diversity and resilience within orchards, both the landscape-scale and local-scale should be considered, which is in accord with other studies on invertebrates (Gonthier et al. 2014). Overall, the results suggest that landscape scale LUI is an important driver of diversity patterns, and that increasing landscape-scale LUI is benefiting a subset of the species pool that are capable of exploiting both orchard and non-crop habitats. Compared to adjacent non-crop habitats, beta diversity in crop habitats was mostly driven by nestedness differences, indicating a non-random loss (or gain) of species. Additionally, reduced local LUI and orchard contrast can promote farmland arthropod diversity. Apart from orchard edge and row orientation, another approach which can be explored is to manipulate the orchard microclimate (and potentially edge contrast), including altering orchard architecture through tree training or genetics so as to increase the amount of incoming solar radiation (Simon et al. 2010). Overall, non-crop habitats are important for preserving biodiversity and limiting biotic homogenization at the farm level. These findings are not only important in terms of biodiversity conservation, but also carry important weight in terms of ecosystem service provision and resilience.

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Chapter 6 Conclusion

The aim of this thesis was to assess the success of biodiversity conservation of the different zones of the Kogelberg Biosphere Reserve (KBR) in response to increasing land-use intensity away from the core. I approached this by investigating sub-questions related to the ecological function of each zone using arthropods as study organisms and principles based on systematic conservation planning and landscape ecology. In this chapter I summarize the findings of the individual chapters, and link them to the original research objective.

6.1 Summary of results

Ecological environments important for epigaeic arthropod turnover were relatively well represented in core areas (Chapter 3). This is because those variables associated with high epigaeic arthropod turnover, namely low soil clay content, shale band intrusions and climatic variability, are well represented across the topographically rugged terrain of the core zones. The core zones also contained a subset of the variables important for congruence in plant and overall arthropod turnover (Chapter 2). However, edaphic interfaces, which were also important for congruence between plants and arthropods, are restricted to lower elevations and not well represented in core areas. The lower elevation of buffer sites was also an important feature determining their complementary value, as this allowed these areas to contribute to the climatic variability across the landscape. The results indicate that epigaeic arthropod diversity is relatively well represented within core areas, but that the buffer areas have important complementary value by adding ecological environments not present in core areas, and also improve the comprehensiveness of the reserve by establishing strong environmental gradients.

The absence of a continuous buffer was reflected by the influence of anthropogenic activities (i.e. proximity to deciduous fruit farming) on diversity in core zones (Chapter 3). This influence reached up to 1 km, decreasing the effective conservation area of core zones where the buffer zone is absent or not wide enough. Arthropod turnover was higher near orchard edges, but these results should be interpreted with caution and require further investigation. Closer investigation showed that the observed edge responses were the result of differential responses of arthropod groups to edge related variables that could be predicted by intrinsic characteristics related to species habitat specialization, i.e. species which prefer fynbos, species

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which prefer orchards, and species which occur in either (Chapter 4). The results highlighted the variegated nature of transformed landscapes (McIntyre and Barrett 1992; Ingham and Samways 1996) that are not captured by patch-orientated views of fragmentation (e.g. Stouffer et al. 1995; Homan et al. 2004), the importance of management actions within orchards on diversity in adjacent habitats and the associated hidden heterogeneity (Chloé et al. 2013).

Arthropod diversity in orchards showed contrasting responses to increasing land-use intensity (LUI) at different scales (Chapter 5). The results showed that while local LUI (management intensity) had a negative influence on some groups, landscape scale LUI (in the form of more orchards in the landscape) increased species richness of a subset of species and contributed to the homogenization of orchard arthropod diversity across the landscape. The results showed that the influence of LUI on diversity should be considered at different scales. Although reducing contrast and local LUI was important for promoting local diversity, neither of these approaches increased similarity between orchard and non-crop habitats, and non-crop habitats were important for improving arthropod species replacement for a range of different trophic groups.

6.2 Limitations and future research

Every study has limitations, which can identify future research priorities. This assessment focused strongly on the complementary value of buffer areas for increasing local representativeness of epigaeic arthropods. Future assessments can also include other biodiversity features. For example structure (e.g. habitat types), genetic diversity, function (e.g. dispersal and recruitment), and ecosystem services. Effective biodiversity conservation also entails promoting long-term persistence (Cabeza and Moilanen 2001). This requires considering factors related to changes in threat intensity (e.g. habitat alteration or climate change), population viability analysis (and associated source-sink dynamics), as well as ecological and evolutionary processes (e.g. Araújo et al. 2002; Harwood et al. 2016).

Another important limitation of the present study is its short duration and the results can offer only a snap shot of biodiversity patterns. Due to the large number of individuals that needed to be processed, it would not be feasible to increase the temporal scale of this study. Species accumulation plots also did not reach asymptotes, indicating that there are many more species than which were sampled. However, it would be difficult to increase sampling intensity

for species rich groups such as arthropods, considering the time it takes to process and identify the material. This makes continued monitoring of species rich groups such as invertebrates very challenging (Żmihorksi et al. 2013). Future research should investigate the possible value of specific arthropod biodiversity indicators (McGeoch 2007) as well as rapid surveys (e.g. Oliver and Beattie 1996; Biaggini et al. 2007; Sueur et al. 2008; Yu et al. 2012). Again, both these methods should be effective surrogates for landscape scale arthropod diversity, but the overall aim should also include long term monitoring.

Here I did not find plants to be a good surrogate for arthropod diversity and environmental variables performed better, but there is still room for improvement. Models used to predict dissimilarity across core and buffer areas explained only 22% of the turnover in epigaeic arthropds, which can reflect important limitations related to the modelling procedure or missing environmental variables. There are also important questions regarding the generality of the results. Do these results apply to other fynbos vegetation types and for arthropod groups which were not well represented in the samples (e.g. the more mobile groups such as Lepidoptera or Diptera)? The sampling methods used were biased towards epigaeic arthropods in chapters where I only used pitfall trapping (Chapters 3-5), and different diversity patterns may have been observed if I used different sampling methods. Future work can also explore the possibility of incorporating secondary biological data (e.g. herbaria, museum records, literature, or online databases) to assess congruence patterns across other vegetation types and arthropod groups. Congruence in assemblage variation was only present between plants and those arthropods associated with the foliar component of the habitat. It could therefore also be interesting to compare arthropod diversity associated with the foliar component between crop and non-crop habitats.

6.3 Conservation implications and recommendations

Despite the limitations highlighted above, the results have important conservation implications.

A comprehensive reserve system is one that includes a portion of every biodiversity feature (e.g. species, habitat types, ecosystem services etc.) (Wilson et al. 2009). For any region, data on all aspects of biodiversity are not available, a problem that is especially severe in megadiverse regions in developing countries. It is therefore strictly not possible to design a fully comprehensive reserve system; comprehensiveness can only be realised for a set number

of biodiversity features, in a specific landscape, and at a restricted spatial resolution (Wilson et al. 2009; Kukkala and Moilanen 2013).

Well-known biodiversity features are often used with the hope that these features will act as effective surrogates for other, lesser-known features. Vascular plants are relatively easy to sample, are taxonomically well known, and often represent more complete datasets compared to other taxa (Santi et al. 2010, Stork and Habel 2013). For these reasons, vascular plants are often used for defining biodiversity hotspots and in the selection of nature reserves (Myers et al. 2000; Ryti 1992), and have also featured strongly in conservation planning in the Cape Floristic Region (CFR) (e.g. Cowling et al. 2003).

As shown in Chapter 2, plant diversity cannot be considered a good surrogate for arthropod diversity at the scale assessed here (i.e. within a single reserve). These results imply that a different surrogate(s) should be used and that many conservation plans based on plant data alone may require revision. This was emphasized by Cowling et al. (2003) when the authors advocated that their conservation plan be constantly updated as new data became available. The problem is that the new data is strongly biased towards vascular plants (also partly driven by the economic uses of some fynbos species (e.g. Proteaceae)), and therefore important developments and assessments will also tend to be biased (e.g. Williams et al. 2004; Lombard et al. 2010; Wise et al. 2012; Schurr et al. 2012). These assessments and plans generally span larger spatial scales, and solace can be found in the fact that plant diversity may well be a good surrogate for arthropod diversity at these coarse scales (Procheş et al. 2009; Colville 2009).

Such coarse scales have value for the initial stages of conservation planning, but offer little practical value for real world planning scenarios (e.g. identifying critical habitats within established reserves, informing land-use planning, or efficient expansion through private partnerships) (Reyers et al. 2002; Ricketts et al. 2002; Stork and Habel 2014). Here I found environmental predictors to be better surrogates for arthropod diversity than plant diversity (Chapter 2), which supports other work in the CFR at local scales (Colville 2009). Continuous environmental surrogates that are not based on targets can be valuable for finer scale planning and management. Extrapolative methods such as generalized dissimilarity modelling can be used to assess patterns of beta diversity and can contribute to the prioritization of conservations efforts. This is especially useful for less well known and exceptionally species rich groups such as invertebrates. GIS can play an important role for promoting cooperation among

stakeholders (Kwaku Kyem 2004) and the maps produced by this assessment can be used to guide restoration and planning (e.g. Cowling et al. 2003), and also to engage with stakeholders.

Representativeness of arthropod diversity will be improved if conservation areas include a range of abiotic variables, especially gradients related to climate and geology. Conservation efforts should not be restricted to core areas only, as the buffer can add significantly to the representativeness of the KBR (Chapter 3), especially the lower laying buffer areas. Conservation management should also target areas of relatively high congruence in beta diversity for arthropods and plants (i.e. areas of strong environmental gradients). This would ensure the reserve system is more representative of both plants and arthropods, improving comprehensiveness of biodiversity measured as species composition for these two taxa (Wilson et al. 2009).

The expansion and intensification of land-use surrounding protected areas can alter ecological processes and biodiversity within protected areas (Hansen and DeFries 2007). One ecological mechanism by which surrounding land-use can alter ecological processes within reserves involves altering the flow of materials, energy and organisms (Hansen and DeFries 2007). Orchard edges showed higher species turnover than orchard interiors (Chapter 5). This suggests orchard blocks with a relatively low edge-to-interior ratio will have lower diversity than orchard blocks with a higher edge-to-interior ratio (e.g. small or elongate orchard blocks). For this approach to be effective, diversity in adjacent non-crop habitats should also be conserved or promoted. This can entail restoration of adjacent non-crop habitats, local buffer strips to protect key farm habitats (such as riparian areas (Hickey and Doran 2004; Vought and Lacoursièr 2010)), as well as the establishment and maintenance of corridors and stepping stones. Corridors and stepping stones are an important intervention that will need to be included in future land-use planning, as the present work showed limited evidence that reducing orchard contrast improved permeability of orchard habitats to native arthropod communities (Chapter 5).

Transformed habitats can also affect the spread of invasive species and the susceptibility of communities to invasions (With 2002) and species which benefit from transformed habitats can negatively affect other species (e.g. through aggressive behaviour, competition or predation) (Tscharntke et al. 2005; Rand et al. 2006). To minimize spillover from species which thrive in the matrix on adjacent natural habitats, local buffer strips around orchards should be at least 80 m wide. These buffer strips can be actively managed to promote diversity. For

example, management that enhance structural heterogeneity of the vegetation (e.g. the maintenance of fire breaks and the removal of alien plants), will increase species richness (Chapter 4).

Strategies that reduce the intensity of local management will promote species richness of predators and their prey within orchards (Chapter 5). This would entail a reduction in chemical input as well as the maintenance of diverse cover crops. Predator species richness in orchards can be promoted by reducing orchard contrast (i.e. increasing the amount of incoming solar radiation throughout the year). This can be achieved through orchard design and, possibly, manipulating tree architecture (Simon et al. 2010). Another approach to improve diversity across farmlands, which is linked to the concept of representativeness in formal conservation areas (Margules and Pressey 2000; Kukkala and Moilanen 2013), is that of reinstating heterogeneity (Fischer et al. 2006). Within the KBR, pome fruit production is concentrated on more fertile lowlands. Heterogeneity of land-uses and land-use intensities should therefore occur across environmental gradients (i.e. at least some highly productive land should be protected or kept for low intensity usage).

The biosphere reserve concept is considered one of the better approaches to integrate conservation with the surrounding landscape. The reason for this is not only that it acknowledges the landscape surrounding intact habitats, but also because it avoids impact on these remaining intact habitats (Palomo et al. 2014). Edge effects associated with land-use change can have important conservation implications, as they can lead to significant changes in ecosystems function (Blitzer et al. 2012; Rand et al. 2006; Ries and Sisk 2004). BRs address this by implementing regional buffers (e.g. UNESCO MAB 1996; UNESCO 2017). The absence of a continuous buffer around the core areas of the KBR means that the influence of activities in the transition is impacting the diversity in the core.

Despite this, the buffer zone has significant conservation value by adding ecological environments not present in the core (Grant and Samways 2011). Maximizing environmental diversity within conservation networks not only guarantees representativeness (Faith and Walker 1996), but may also ensure long term persistence by allowing adaptive responses to occur (Smith et al. 2001; Cowling et al. 2003; Rouget et al. 2003). Prioritizing sites with enduring features (e.g. geophysical features, such as elevation and soil properties) are also considered a mitigation strategy against climate change (Hunter et al. 1988; Rouget et al. 2003;

Lawler et al. 2015; Beier et al. 2015). The value of the KBR buffer zones therefore go far beyond only buffering the core.

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Table S1 Environmental variables (66 in total) selected as candidate for modelling. Of these, 18 are site measured and 48 are derived from spatial layers. The number of variables in each explanatory groups are: geology - 5, disturbance - 8, local site characteristics - 18, refuge - 8, mesoclimate - 18, terrain – 9. Appendix 2 described each explanatory group and site measure variables in more detail. DEM – digital elevation model, NDVI – Normalized difference vegetation index

Description	Grouping	code	Data type	Data set/source
Distance (Euclidean) to edaphic interfaceareas	Geology	soilTypeTr	Spatial	BSS 2003a
Distance (Euclidean) to upland-lowland interfaces	Geology	UplLowL	spatial	BSS 2003b
Distance (Euclidean) to shale bands	Geology	distShale	spatial	Mucina et al. 2006
Average soil depth	Geology	ave_SoilDepth	Spatial	ARC-ISCW (2006)
Average percentage clay	Geology	Ave_Clay	Spatial	ARC-ISCW (2006)
Distance (Euclidean) to nearest orchards.	Disturbance	OrchDist	Spatial	CapeNature (2016b)
Distance (Euclidean) to nearest timber plantation.	Disturbance	plantDist	Spatial	CapeNature (2016b)
Distance (Euclidean) to nearest transformed area (all agricultural and other built up areas).	Disturbance	transDist	Spatial	CapeNature (2016b)
Fire frequency in last 5 years	Disturbance	fireFreq_5	Spatial	CapeNature (2016a)
Fire frequency in last 10 years	Disturbance	fireFreq_10	Spatial	CapeNature (2016a)
Fire frequency in last 20 years	Disturbance	fireFreq_20	Spatial	CapeNature (2016a)
Number of years since last fire	Disturbance	age	Spatial	CapeNature (2016a)
Standard deviation of vegetation at 30 m resolution	Disturbance	ageStdev	Spatial	CapeNature (2016a)
Normalized difference vegetation index (August 2015)	Site characteristic	NDVI_0810	Spatial	Landsat 8
Normalized difference vegetation index (September 2015)	Site characteristic	NDVI_0919	Spatial	Sentinel 2

Normalized difference vegetation index (December 2015)	Site characteristic	NDVI_1218	Spatial	Sentinel 2
Maximum litter cover per site (maximum measure within a plot)	Site characteristic	littCovMax	Site measured	Site measured
Minimum litter cover per site (minimum measure within a plot)	Site characteristic	LittCovMin	Site measured	Site measured
Maximum vegetation cover per site (maximum measure within a plot)	Site characteristic	vegCovMax	Site measured	Site measured
Minimum vegetation cover per site (minimum measure within a plot)	Site characteristic	vegCovMin	Site measured	Site measured
Maximum rock cover per site (maximum measure within a plot)	Site characteristic	rockCovMax	Site measured	Site measured
Minimum rock cover per site (minimum measure within a plot)	Site characteristic	rockCovMin	Site measured	Site measured
Minimum bare ground per site (minimum measure within a plot)	Site characteristic	grCovMin	Site measured	Site measured
Average moisture (moisture readings per plot average over number of readings)	Site characteristic	moistAve	Site measured	Site measured
Maximum moisture (maximum moisture reading per site)	Site characteristic	moistMax	Site measured	Site measured

Minimum moisture (minimum moisture reading per site)	Site characteristic	MoistMin	Site measured	Site measured
Maximum vegetation density calculated highest number of touches per plot	Site characteristic	vegDenMax	Site measured	Site measured
Minimum vegetation density calculated as lowest number of touches per plot	Site characteristic	vegDensMin	Site measured	Site measured
Maximum vegetation height calculated as maximum touch height	Site characteristic	vegHeightMax	Site measured	Site measured
Minimum vegetation height calculated as minimum touch height	Site characteristic	vegHeightMin	Site measured	Site measured
Vertical complexity calculated as standard deviation for average vegetation height	Site characteristic	vertComplex	Site measured	Site measured
Distance (Euclidean) to riparian vegetation	Refuge	dsitRpiVeg	spatial	CAPE (2009)
Distance (Euclidean) to rocky mountain fynbos	Refuge	distRckMnt	Spatial	CapeNature (2016b)
Distance (Euclidean) to bare rock	Refuge	distBareRO	Spatial	CapeNature (2016b)
Distance (Euclidean) to wetland	Refuge	distWetlan	Spatial	CAPE (2009)
Distance (Euclidean) to permanent and seasonal wetlands and dams	Refuge	distPSwetldam	Spatial	CapeNature (2016b)
Distance (Euclidean) to permanent wetlands and dams	Refuge	distPwetldam	Spatial	CapeNature (2016b)

Distance (Euclidean) to seasonal wetlands and dams	Refuge	distSwetlda m	Spatial	CapeNature (2016b)
Standard deviation of NDVI calculated from three satellite images for spring to summer 2015	Refuge	NDVISTD	Spatial	Calculated from NDVI_0810, NDVI_0919 and NDVI_1218 using QGIS
Mean yearly maximum temperature (◦C)	Mesoclimat e	mean_maxT e	Spatial	van Niekerk & Joubert 2011
Mean yearly minimum temperature (◦C)	Mesoclimat e	Mean_minT emp	Spatial	van Niekerk & Joubert 2011
Standard deviation of mean monthly maximum temperature across the year (◦C)	Mesoclimat e	stdevMaxTe mp	Spatial	van Niekerk & Joubert 2011
Standard deviation of mean monthly minimum temperature across the year (◦C)	Mesoclimat e	stdevMinTe mp	Spatial	van Niekerk & Joubert 2011
Mean yearly precipitation (mm)	Mesoclimat e	meanRain	Spatial	van Niekerk & Joubert 2011
Minimum monthly mean precipitation across the year (mm)	Mesoclimat e	minRain	Spatial	van Niekerk & Joubert 2011
Maximum monthly mean precipitation across the year (mm)	Mesoclimat e	maxRain	Spatial	van Niekerk & Joubert 2011
Standard deviation in mean monthly precipitation across the year (mm)	Mesoclimat e	stdevRain	Spatial	van Niekerk & Joubert 2011
Distance to ocean (meters).	Mesoclimat e	distOcean	Spatial	CGA 2016
Output insolation time	Mesoclimat e	insol360d	Spatial	Calculated using DEM and GRASS GIS 7 in QGIS
Ground reflected irradiation.	Mesoclimat e	grdrefl360	Spatial	Calculated using DEM and GRASS GIS 7 in QGIS
Wind exposition index: Indicates exposed versus shadowed areas according to DEM.	Mesoclimat e	wind_expo	Spatial	Calculated using DEM and SAGA (2.3.2) in QGIS

Output global (total) irradiance/irradiation	Mesoclimate	globalIrr3	Spatial	Calculated using DEM and GRASS GIS 7 in QGIS
Irradiation raster map	Mesoclimate	irradi360	Spatial	Calculated using DEM and GRASS GIS 7 in QGIS
Mean site measure temperature	Mesoclimate	meanTemp.S	Site measured	Site measured
Maximum site measured temperature	Mesoclimate	maxTemp.S	Site measured	Site measured
Minimum site measured temperature	Mesoclimate	minTemp.S	Site measured	Site measured
Standard deviation of site measure temperature	Mesoclimate	StdTemp.S	Spatial	Site measured
Elevation	Terrain	sudem_lo19	Spatial	Five meter resolution DEM (van Niekerk 2001)
Catchment/flow accumulation. Accumulated flow is calculated as the accumulated weight of all upslope cells connected to it through a flow path.	Terrain	catchm	Spatial	Calculated using DEM and SAGA (2.3.2) in QGIS
Topographic wetness index as function of slope and specific catchment area.	Terrain	topo_wetness	Spatial	Calculated using DEM and SAGA (2.3.2) in QGIS
Hillshade as the amount of sun or shade for a 3D surface.	Terrain	hillshade	Spatial	Calculated using DEM and GDAL in QGIS
Relief	Terrain	relief	Spatial	Calculated using DEM and SAGA (2.3.2) in QGIS
Aspect as the compass bearing of the slope.	Terrain	aspect	Spatial	Calculated using DEM and GDAL in QGIS
Terrain ruggedness index	Terrain	ruggedness	Spatial	Calculated using DEM and GDAL in QGIS
Slope	Terrain	Slope	Spatial	Calculated using DEM and GDAL in QGIS

Topographic position index	Terrain	topogrPosI	Spatial	Calculated using DEM and GDAL in QGIS

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Table S2 Genera with either exceptional species richness within Kogelberg Sandstone Fynbos or for which most of extant species occur within this vegetation type (Rebelo et al. 2006). Shaded genera were sampled

Genus	Number of species sampled
Anaxeton	1
Aulax	1
Bolusafra	0
Brunia	2
Capelio	0
Calopsis	0
Chrysitrix	0
Cliffortia	4
Diastella	1
Dilatris	2
Disa	0
Elegia	6
Erica	21
Euryops	1
Grubbia	1
Helichrysum	2
Hermas	0
Hypocalyptus	0
Klattia	0
Liparia	0
Metalasia	3
Mimetes	1
Muraltia	1
Oldenburgia	0
Osmitopsis	2
Prismatocarpus	0
Protea	10
Raspalia	0
Restio	18
Siphocodon	0
Spatalla	1
Staavia	0
Syncarpha	4
Thaminophyllum	0
Thesium	5
Ursinia	1
Wachendorfia	1

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Table S3 Result of generalized linear models showing effect of either species richness of all plants or Kogelberg Sandstone Fynbos endemics on arthropod species richness (modelled as rates instead of counts to account for differences in sampling intensity). Significance tests were based on Wald tests. KSF: Kogelberg Sandstong Fynbos; KSFend: plant genera with high richness or endemism in KSF; non-ant: data set excluding ants; foliar: sampled from vegetation; epigaeic: sampled using pitfalls

	All plants		KSF-end	
Response group:	Estimate	p-value	Estimate	p-value
All Arthropods	-0.01	0.09	-0.01	0.15
Arthropod(non-ant)	-0.01	0.17	-0.01	0.14
Foliar	-0.01	0.37	-0.01	0.30
Foliar(non-ant)	-0.01	0.85	-0.01	0.69
Epigaeic	-0.01	0.35	-0.01	0.26
Epigaeic(non-ant)	-0.01	0.17	-0.01	0.18
Herbivore	-0.01	0.61	-0.01	0.52
Predator	-0.01	0.14	-0.02	0.12
Omnivore	0.01	0.68	-0.01	0.92
Detritivore	-0.01	0.15	-0.01	0.33

Table S4 Results of linear models and linear mixed-effect models (where spatial autocorrelation was significant) of relationship between plant and arthropod assemblage variation. Models were run separately with either all plants or KSF endemics as predictors on each of the arthropod groups: all arthropods, all arthropods non-ant, epigaeic, epigaeic non-ant, foliar, foliar non-ant, and each of the arthropod functional groups (herbivores, predators, omnivore, detritivores). This was repeated across three scales: cluster, location and landscape. Where spatial autocorrelation was detected, location was included as a random variable in linear mixed-effects models. Values in parentheses are weighted by sampling frequency. LM: linear model; LMM: linear mixed-effects model; R^2 (marginal): variance explained by fixed effects; KSF: Kogelberg Sandstong Fynbos; KSFend: plant genera with high richness or endemism in KSF; non-ant: data set excluding ants; foliar: sampled from vegetation; epigaeic: sampled using pitfalls

Response group	model	Fixed effect	Linear models			Linear mixed-effects models		
			R^2	F-statistic	P-value	R^2(marginal)	F-statistic	P-value
Cluster scale								
All arthropods	LM	All plants	0.01 (0.01)	0.01 (0.18)	0.92 (0.68)	-	-	-
	LM	KSFend	0.01 (0.01)	0.04 (0.01)	0.84 (0.96)	-	-	-
All arthropods non-ant	LM	All plants	0.05 (0.08)	1.69 (2.52)	0.20 (0.12)	-	-	-
	LM	KSFend	0.01 (0.03)	0.36 (0.81)	0.55 (0.38)	-	-	-
Epigaeic	LM	All plants	0.11 (0.06)	3.46 (1.91)	0.07 (0.18)	-	-	-
	LM	KSFend	0.04 (0.04)	1.06 (1.06)	0.31 (0.31)	-	-	-
Epigaeic non-ant	LM	All plants	0.04 (0.02)	1.23 (0.67)	0.28 (0.42)	-	-	-
	LM	KSFend	0.01 (0.01)	0.31 (0.18)	0.58 (0.67)	-	-	-
Foliar	LM	All plants	0.13 (0.12)	3.99 (3.89)	0.06 (0.06)	-	-	-
	LM	KSFend	0.07 (0.16)	2.19 (1.65)	0.15 (0.21)	-	-	-
Foliar non-ant	LM	All plants	0.23 (0.24)	8.24 (8.69)	0.01 (0.01)	-	-	-
	LM	KSFend	0.12 (0.12)	3.95 (3.70)	0.06 (0.06)	-	-	-
Herbivore	LM	All plants	0.01 (0.04)	0.33 (1.24)	0.57 (0.27)	-	-	-
	LM	KSFend	0.01 (0.01)	0.15 (0.01)	0.70 (0.99)	-	-	-
Predator	LM	All plants	0.01 (0.03)	0.26 (0.77)	0.61 (0.38)	-	-	-
	LM	KSFend	0.01	0.29	0.60	-	-	-

			(0.01)	(0.40)	(0.53)			
omnivore	LM	All plants	0.11 (0.07)	3.46 (2.12)	0.07 (0.16)	-	-	-
	LM	KSFend	0.09 (0.08)	2.77 (2.33)	0.12 (0.14)	-	-	-
Detritivore	LM	All plants	0.02 (0.01)	0.56 (0.23)	0.46 (0.63)	-	-	-
	LM	KSFend	0.05 (0.03)	1.55 (0.82)	0.22 (0.37)	-	-	-
All arthropods	LM	All plants	0.01 (0.01)	0.02 (0.01)	0.89 (0.95)	-	-	-
	LM	KSFend	0.01 (0.01)	0.02 (0.01)	0.88 (0.93)	-	-	-

Location scale

All arthropods non-ant	LM	All plants	0.01 (0.01)	0.16 (0.19)	0.69 (0.67)	-	-	-
	LM	KSFend	0.04 (0.05)	0.88 (1.32)	0.36 (0.26)	-	-	-
Epigaeic	LM	All plants	0.01 (0.01)	(0.27) (0.29)	0.61 (0.59)	-	-	-
	LM	KSFend	0.02 (0.03)	0.65 (0.79)	0.43 (0.38)	-	-	-
Epigaeic non-ant	LM	All plants	0.01 (0.01)	0.37 (0.11)	0.55 (0.74)	-	-	-
	LM	KSFend	0.02 (0.01)	0.59 (0.32)	0.45 (0.58)	-	-	-
Foliar	LM	All plants	0.03 (0.01)	0.98 (0.33)	0.33 (0.57)	-	-	-
	LM	KSFend	0.06 (0.04)	1.66 (1.05)	0.21 (0.31)	-	-	-
Foliar non-ant	LM	All plants	0.09 (0.06)	2.73 (1.68)	0.11 (0.21)	-	-	-
	LM	KSFend	0.13 (0.11)	4.16 (3.54)	0.05 (0.07)	-	-	-
Herbivore	LM	All plants	0.05 (0.02)	1.43 (0.50)	0.24 (0.49)	-	-	-
	LM	KSFend	0.10 (0.06)	3.21 (1.81)	0.08 (0.19)	-	-	-
Predator	LMM	All plants	-	-	-	0.05 (0.02)	1.92 (1.04)	0.18 (0.32)
	LMM	KSFend	-	-	-	0.03 (0.01)	1.16 (0.32)	0.29 (0.57)
omnivore	LMM	All plants	-	-	-	0.01 (0.01)	0.01 (0.14)	0.91 (0.71)
	LMM	KSFend	-	-	-	0.01 (0.01)	0.04 (0.21)	0.84 (0.65)
Detritivore	LM	All plants	0.01 (0.02)	0.24 (0.50)	0.63 (0.49)	-	-	-

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	LM	KSFend	0.01 (0.02)	0.31 (0.54)	0.58 (0.47)	-	-	-
Landscape scale								
All arthropods	LMM	All plants	-	-	-	0.03 (0.03)	1.59 (1.82)	0.22 (1.88)
	LMM	KSFend	-	-	-	0.04 (0.01)	2.29 (2.23)	0.14 (0.15)
All arthropods non-ant	LMM	All plants	-	-	-	0.01 (0.01)	0.34 (0.25))	0.56 (0.62)
	LM	KSFend	0.13 (0.12)	4.05 (3.69)	0.05 (0.06)	-	-	-
Epigaeic	LM	All plants	0.01 (0.01)	0.43 (0.10)	0.52 (0.75)	-	-	-
	LM	KSFend	0.02 (0.01)	0.44 (0.08)	0.51 (0.78)	-	-	-
Epigaeic non-ant	LM	All plants	0.08 (0.06)	2.37 (1.73)	0.14 (0.20)	-	-	-
	LM	KSFend	0.10 (0.08)	2.98 (2.32)	0.10 (0.14)	-	-	-
Foliar	LM	All plants	0.04 (0.03)	1.07 (0.81)	0.31 (0.38)	-	-	-
	LM	KSFend	0.07 (0.05)	1.96 (1.47)	0.17 (0.24)	-	-	-
Foliar non-ant	LM	All plants	0.06 (0.06)	1.87 (1.92)	0.18 (0.18)	-	-	-
	LMM	KSFend	0.12 (0.14)	3.94 (4.38)	0.06 (0.05)	-	-	-
Herbivore	LM	All plants	0.08 (0.04)	2.44 (1.29)	0.13 (0.27)	-	-	-
	LM	KSFend	0.09 (0.06)	2.79 (1.63)	0.11 (0.21)	-	-	-
Predator	LMM	All plants	-	-	-	0.03 (0.01)	1.18 (0.25)	0.29 (0.62)
	LMM	KSFend	-	-	-	0.07 (0.07)	0.01 (0.71)	0.94 (0.41)
omnivore	LMM	All plants	-	-	-	0.01 (0.03)	0.27 (1.12)	0.61 (0.30)
	LMM	KSFend	-	-	-	0.02 (0.01)	1.27 (2.97)	0.27 (0.09)
Detritivore	LM	All plants	0.01 (0.01)	0.34 (0.24)	0.56 (0.63)	-	-	-
	LM	KSFend	0.01 (0.01)	0.30 (0.15)	0.59 (0.70)	-	-	-

Table S5 List of significant variables selected for model 1 (spatial and site measured variables) with variable importance. Relative variable importance was determined by summing the I-spline coefficients

Grouping	Variables	Percent deviance explained	Permutations
	Full model 2	25.19%	500
Site measured or spatial	Environmental variable	Relative importance	
Spatial	Standard deviation in average monthly minimum temperature	0.383	500
Spatial	Standard deviation of vegetation age (30 m resolution)	0.233	500
Site	Average vegetation height	0.221	500
Site	Minimum soil moisture	0.173	500
Spatial	Ave soil clay content	0.163	500
Spatial	Distance to nearest orchard	0.125	500
Spatial	Distance to shale band intrusion	0.091	500
Spatial	Fire frequency in past 5 years	0.057	500
Spatial	Geographical distance	0.054	500
Spatial	Fire frequency in past 10 years	0.028	500

Table S6 List of significant variables selected for model 2 (spatial variables) with variable importance and significance. Relative variable importance was determined by summing the I-spline coefficients

Variables	Percent deviance explained	Permutations
Full model 2	22.12%	500
	Variable importance	
Standard deviation in average monthly minimum temperature	0.371	500
Standard deviation of vegetation age (30 m resolution)	0.269	500
Ave soil clay content	0.174	500
Distance to shale band intrusion	0.114	500
Distance to nearest orchard	0.101	500
Fire frequency in past 5 years	0.076	500
Geographical distance	0.065	500
Fire frequency in past 10 years	0.028	500

Table S7 Hybrid multidimensional scaling (HMDS) stress values for randomly selected sites for (A) environmental variables excluding all disturbance variables, (B) environmental variables excluding fire related disturbance variables, and (C) all variables

Run	Number of sites	HMDS stress A	B	C
1	4000	0.087	0.127	0.198
2	4000	0.088	0.127	0.198
3	4000	0.088	0.130	0.198
4	4000	0.089	0.127	0.197
5	4000	0.089	0.128	0.201
6	4000	0.089	0.129	0.199
7	4000	0.088	0.127	0.197
8	4000	0.088	0.128	0.198
9	4000	0.089	0.128	0.198
10	4000	0.089	0.132	0.198

A: standard deviation of monthly minimum temperature across the year, average soil clay content, distance to nearest shale band intrusion
B: A + distance to nearest orchard
C: B + standard deviation of vegetation age (at 30 m resolution), fire frequency in past five years, fire frequency in past 10 years

Table S8 List of all insecticides sprayed in orchard blocks which A) only spray broad-spectrum insecticides early in the growing season, B) spray broad-spectrum insecticides early and late in the growing season as well as the major target pests (according to interviews). MB – mealybug species, SI - scale insect species, BFW – banded fruit weevil (*Phlyctinus callosus*), CM - Codling moth (*Cydia pomonella*), BW – bollworm (*Helicoverpa armigera*), TSM – twospotted mite (*Tetranychus urticae*), WAA – wooly apple aphid (*Eriosoma lanigerum*), Various – various pests (none specified)

Active ingredient	Trade name	Target pests	Sprayed early	Sprayed late
A				
Chlorpyrifos	Chlorpyrifos	MB, SI	x	
Prothiophos	Tokuthion	MB	x	
Novaluron	Rimon	CM, BW	x	
Spinetoram	Delegate	CM, BW, BFW		x
Thiacloprid	Topstar	CM		x
Chlorantraniliprole	Altacor	CM, BW	x	x
Indoxacarb	Steward	CM, BW, BFW	x	x
B				
Chlorfenapyr	Hunter	BFW	x	
Carbaryl	Sevin XLR	BFW	x	
Chlorpyrifos	Chlorpyrifos	MB, TSM	x	
Prothiophos	Tokuthion	MB	x	
Lambda-cyhalothrin	Karate	BW, TSM	x	x
Azinphos-methyl	Azinphos	Various	x	x
Acetamiprid	Mospilan	CM	x	x
Imidacloprid	Confidor	WAA	x	x
Chlorantraniliprole	Altacor	CM, BW	x	x
Indoxacarb	Steward	TSM, Various	x	x
Thiacloprid	Calypso	CM	x	x
Novaluron	Rimon	CM, BW	x	
Methoxyfenozid	Runner	CM	x	x

Table S9 Environmental variables selected to represent background environmental heterogeneity

Description	Grouping	code	Data type	Data set/source
Fire frequency in last 10 years	Disturbance	fireFreq_10	Spatial	CapeNature (2016)
Standard deviation of vegetation at 30 m resolution	Disturbance	ageStdev	Spatial	CapeNature (2016)
Standard deviation of mean monthly minimum temperature across the year (◦C)	Mesoclimate	stdevMinTemp	Spatial	van Niekerk & Joubert 2011
Average percentage clay	Geology	Ave_Clay	Spatial	ARC-ISCW (2006)
Distance (Euclidean) to shale bands	Geology	distShale	spatial	Mucina et al. 2006
Average vegetation height calculated as average touch height	Site characteristic	vegHeightAve	Site measured	Site measured
Average moisture (moisture readings per plot average over number of readings)	Site characteristic	moistAve	Site measured	Site measured

References/data sources

CapeNature (2016) CapeNature Fires – All 2016/17 [Vector] 2016. Available from the Biodiversity GIS website, bgis.sanbi.org

Van Niekerk A, Joubert SJ (2011) Input variable selection for interpolating high-resolution climate surfaces for the Western Cape. Water SA 37: 271-280

ARC-ISCW (Agricultural Research Council – Institute for Soil, Climate and Water) (2006) Land types of South Africa: Digital map (1:250 000 scale) and soil inventory datasets [vector]

Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland [vector]. Strelitzia 19. South African National Biodiversity Institute, Pretoria

Table S10 Background environmental variables selected by forward selection procedure for all, all excluding cultural, stenotopic, cultural and ubiquitous species

	All species	All min cultural	Stenotopic	Cultural	Ubiquitous
Including singletons	fireFreq_10	fireFreq_10	fireFreq_10	-	fireFreq_10
	distShale	distShale	distShale		
	moistAve	vegHeightAve	moistAve		
Excluding singeltons	fireFreq_10	fireFreq_10	fireFreq_10	-	fireFreq_10
	distShale	distShale	distShale		
	vegHeightAve	vegHeightAve	moistAve		

Appendix 1

Species accumulation curves for arthropod (a and b, weighted by sampling frequency) and plant (c) groups. KSF: Kogelberg Sandstong Fynbos; KSF-endemics: plant genera with high richness or endemism in KSF; non-ant: data set excluding ants; foliar: sampled from vegetation; epigaeic: sampled using pitfalls.
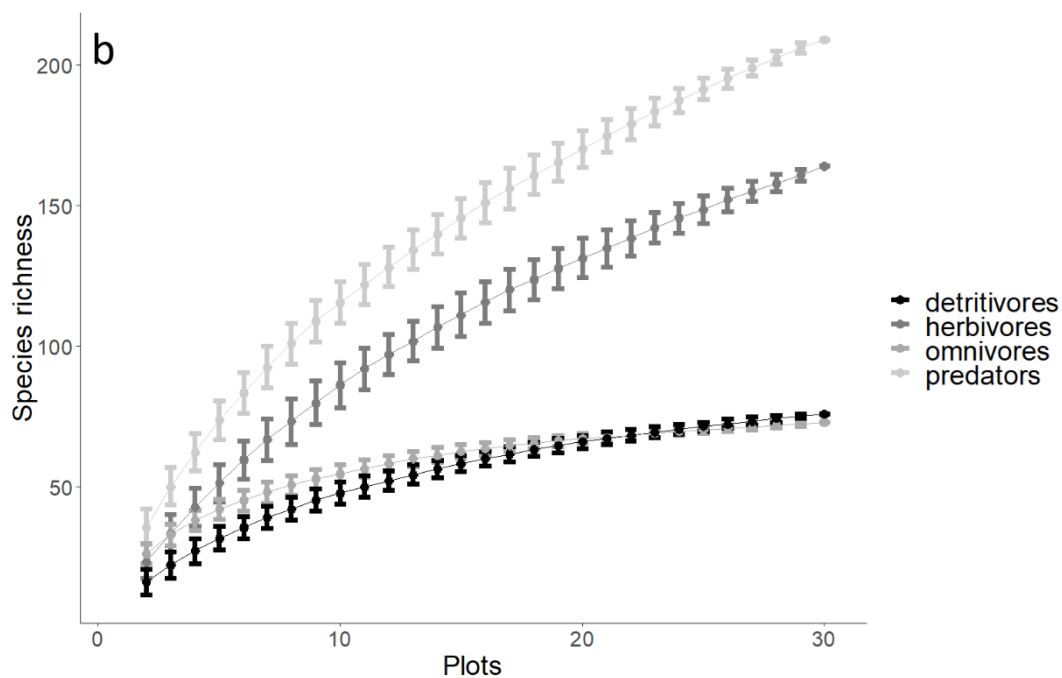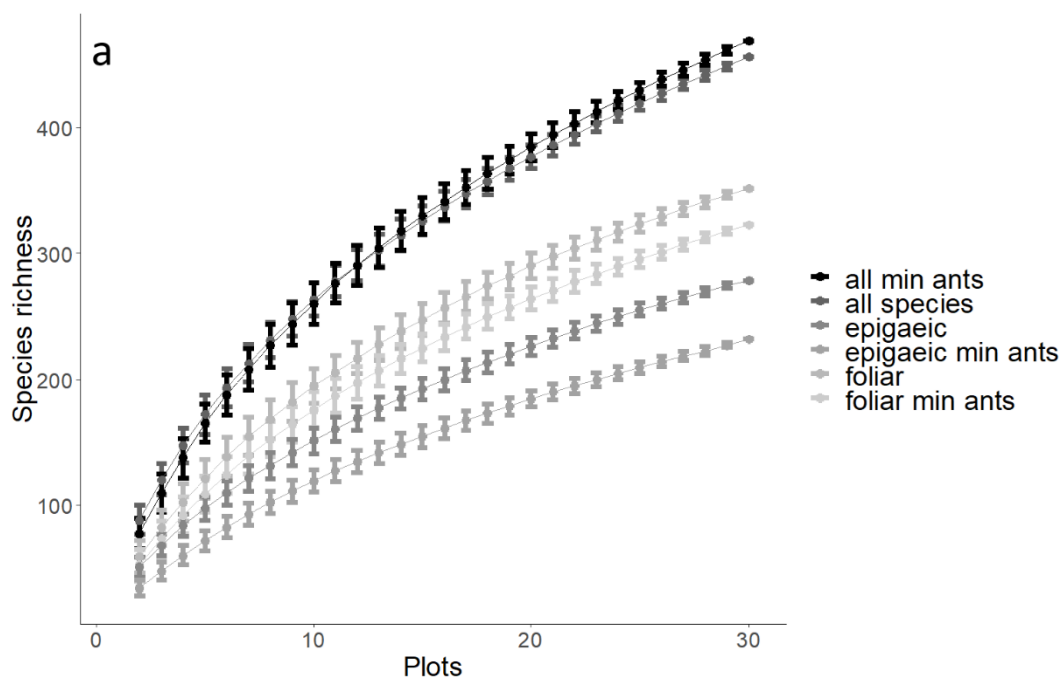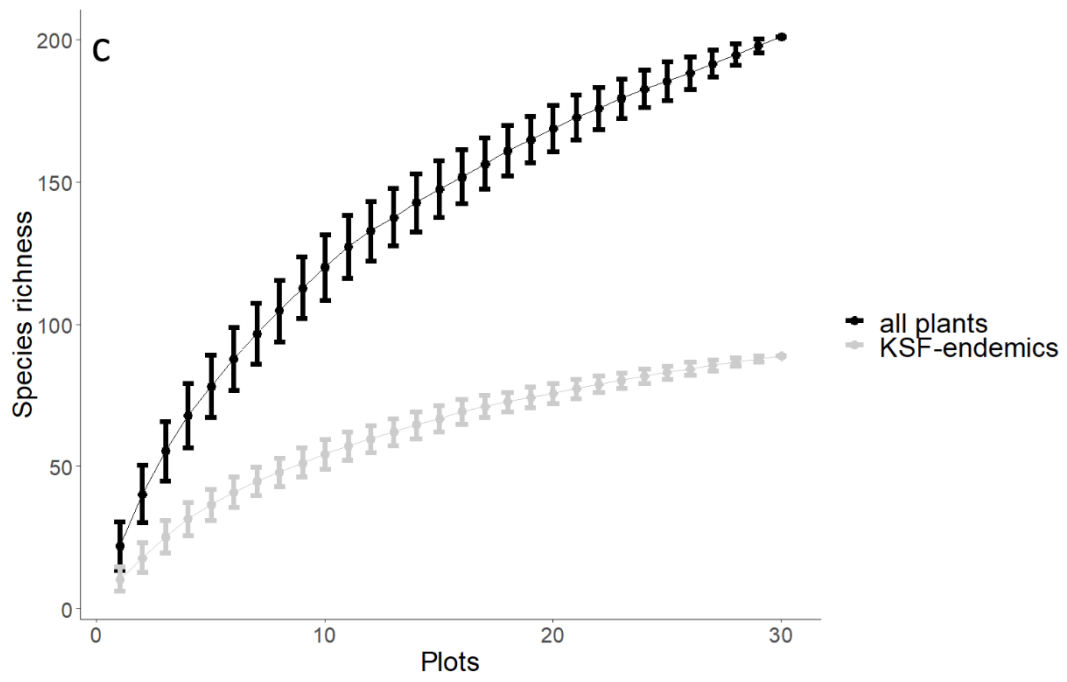
Appendix 2
Description of explanatory groups and environmental variables included in modelling

1. Background

Ecological processes are important for maintaining and generating biodiversity across temporal and spatial scales (Gilmore et al. 2007; Pressey et al. 2007). An environmental variable can function as a resource as well as a condition that fulfils the necessities for efficient functioning of physiological processes (Williams et al. 2012). Spatially explicit surrogates of ecological processes can be associated with ecological and evolutionary processes (e.g. edaphic interfaces or riverine corridors) (Rouget et al. 2003; Williams et al. 2012), while several measures of geographic and topographic positions (e.g. elevation, slope, aspect) represent indirect/secondary environmental gradients that influence biodiversity via connected proximal variables (Austin 2002). In cases where data are missing for particular factors, issues with spatial resolution or where biophysical processes are not completely specified, the use of such secondary variables in ecological models can be justified (Williams et al. 2012).

The general model for terrestrial diversity assumes responses to both physical and biological environmental components (McKenzie et al. 2000b, 2004; George et al. 2011, McKenzie and Bullen 2012). Climate, regolith, and terrain are facets that can describe the physical components, while vegetation patterns or indirect physical environmental correlates can describe biological components.

2. Description of explanatory groups and related variables

Biodiversity patterns are driven by a variety of factors that operate over different spatial and temporal scales (Willis and Whittaker 2002). The importance of these factors are in part determined by the scale of the study area, e.g. within a single climatic region geophysical factors can be more important for diversity than climatic factors (Anderson and Ferree 2010). Environmental variables used in generalized dissimilarity modeling (GDM; Ferrier et al. 2007) of plant and arthropod diversity across the Kogelberg Biosphere Reserve (KBR) included both site measured variables and variables derived from spatial layers. For sites visited more than once variables were averaged across both sampling occasions.

The initial set of candidate predictor variables totaled 55. These were divided into six categories (in order of *a priori* of importance): 1) geology, 2) disturbance, 3) site characteristics, 4) refuge, 5) mesoclimate, 6) terrain. These explanatory groups are by no means independent, e.g. Local site characteristics such as vegetation structure is not only affected by burn history (van Wilgen et al. 1994), but also by terrain or mesoclimate (Armesto and Martínez 1978, Stemberg and Shoshany 2001) and geology (Dodd and Lauenorth 1997). At the same time these factors can interact, e.g. topography can affect fire frequency through its influence on ignition and fuel characteristics (Defratti 2015). Below is a description of each of these groups (See Table S2 for list of all candidate variables).

2.1 Geology

Geology can be an important factor for plant diversity as it delineates the available environments, controls the location of important habitats and stimulates diversification (Kruckeberg 2002). Across the Cape Floristic Region (CFR) geology is an important driver of floral biodiversity patterns (Cowling 1992). Edaphic interfaces (specific juxtaposed soil types) have been identified as important areas of plant diversification (Goldblatt 1982; Linder and Mann 1998) and incorporated into conservation planning (Cowling et al. 2003).

The majority of the terrestrial core and buffer areas of the Kogelberg Biosphere Reserve (KBR) consist of acidic sandstone derived soils (Table Mountain Group). Prominent shale bands (Cedarberg Formation) occur throughout and an important edaphic interface occurs between sandstone and shale derived soils (Bokkeveld Group) at lower elevations (Cowling et al. 2003).

Geological variables used in analyses included spatial information on soil characteristics (e.g. average clay content, average soil depth (ARC-ISCW 2006)), distances to edaphic interfaces (BSS 2003), as well as distance to shale bands (Mucina et al. 2006).

2.2 Disturbance

Fynbos is a fire-prone system in which prescribed burning has been considered an important management practice for over 40 years (van Wilgen 2009). Due to factors related to funding, safety, invasive alien plant management and the inaccessibility of rugged mountain areas (van

Wilgen 2009; van Wilgen 2013), fire management has only been actively implemented in about 11% of the fynbos biome (van Wilgen 2013).

The past century has seen an increase in fire frequency in fynbos that is linked to a growing human population and the associated increased risk of ignition (Forsyth and van Wilgen 2008; van Wilgen et al. 2010). In these areas prescribed burning may not be appropriate (van Wilgen et al. 2010). There is concern that repeated short term fires are becoming too common (Forsyth and van Wilgen 2008) and are detrimental to the floral biodiversity of the region (van Wilgen and Forsyth 1992; van Wilgen 2010). Relative to plants little work has been done on the effects of fire on fynbos invertebrates. Work on post-fire recovery in fynbos arthropod communities show great variation between taxa, with some groups (e.g. ants) showing remarkable resilience and rapid recovery (Janion-Scheepers et al. 2016; Pryke and Samways 2012).

Fruit farming (deciduous pome fruit) is a major economic activity within the KBR. Compared to the surrounding natural vegetation, these orchards present a sharp switch in cover types. Agricultural practices (including herbicide and pesticide input) act as repeated disturbances that result in the dominance of a few tolerant species (Lee et al. 2001, Blitzer et al. 2012). Impacts are not only restricted to the transformed area, but also include potential edge mediated effects on adjacent native communities. Apart from the effect that pesticide drift (Burn et al. 2003) and edge related gradients in abiotic variables (e.g. soil moisture) can have on species in immediate adjacent communities, edges can also alter ecological processes through-edge spillover of individuals (Fagan et al. 1999; Rand 2006; Blitzer et al. 2012). In addition, transformed habitats can facilitate the introduction of native communities to human commensal species (such as the argentine ant, *Linepithema humile*) (Bolger 2007). It is therefore not surprising that for even very small organisms such as insects edge effects can penetrate up to 1 km into adjacent habitats (Ewers and Didham 2008). These anthropogenic edge related influences on the spatial distribution of species can act synergistically with punctuated disruptive disturbances (e.g. fires) that can promote the invasion of natural communities (Hobbs and Huenneke 1992).

Vegetation age, standard deviation in vegetation age (at 30 m) and fire frequency (in 5, 10 and 20 years) were calculated using spatial data of fire history (CapeNature 2016a). A 30 m resolution land cover map (CapeNature 2016b) was used to calculate distance to nearest orchard, distance to nearest alien plantation and distance to all transformed areas (including all agricultural and built up areas).

2.3 Site characteristics

Work indicates that fire can have strong indirect effect on plant and insect communities through the associated changes in vegetation structure (Vlok and Yeaton 1999; Kim and Holt 2012). Differences in habitat structure can explain a significant amount of variation in arthropod turnover at local scales (e.g. Foord et al. 2008). This is also true for fynbos invertebrate assemblages (Pryke and Samways 2009). Vegetation structure can also have a strong influence on other habitat variables such as soil moisture (Aalto et al. 2013). Combined with exceptionally high turnover in plant species composition (Rebelo et al. 2006) this results in high heterogeneity in local site conditions across small spatial scales.

Local site variables consisted of habitat structure measurements, soil moisture content, and plant productivity (NDVI). Habitat structure was measured in terms of vertical and horizontal vegetation characteristics. Vegetation structure was measured using similar methods as Parr et al. (2004) and Munyai and Foord (2012). At each pitfall trap (i.e. each corner of the 10 x 10 m plot) vertical vegetation height profiles were measured at four points located at 90 degrees apart on a 1.5 m radius centered on each trap. At each point, a 1.5 m pole (1 cm diameter) was held vertically and the total times vegetation came into contact with the pole was noted at 25 cm intervals. Horizontal structure was measure by placing a 1 m^2 quadrat over each trap and visually estimating the percentage of vegetation cover. Visual estimations were also made of percentage bare ground, litter cover and rock around each trap. To keep visual estimates consistent across sites, photos of quadrats were taken and all estimates were done by the same person with the aid of a visual estimation guide as reference. At each trap soil moisture was measured using a soil moisture meter (ZD-05 pH and Moisture Meter).

2.4 Refuge

Refuges are defined as landscape features that facilitate the survival or persistence of organisms (or species) in the face of disturbance events that would otherwise result in their mortality, displacement or extinction (Mackey et al. 2002; Robinson et al. 2013). The concept of refugia is related to that of refuges and the terms are often treated as equivalent (Mackey et al. 2012). The distinction between these terms are based on the former reflecting much longer time-scales that are linked to species-range dynamics and global climate change (Keppel et al. 2011).

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Considering the relatively short time scales associated with human-induced rapid climate change, habitat locations that may function as refuges can also be called "potential climate-change refuges" (Mackey et al. 2012).

Droughts and changes in the timing of rainfall are characteristics of the climate of southern Africa, but these features have been increasing in variability and intensity over the past 50 years (Stringer et al. 2009; IPCC 2012). Projected climate change for the CFR include a decrease in winter rainfall and an increase in temperature (Hewitson and Crane 2006; de Wit and Stankiewicz 2006). At the present moment the already water-stressed Western Cape is experiencing a drought which can be attributed to climate variability.

There is ample evidence supporting the interconnectedness of terrestrial and stream food webs (Baxter et al. 2005; Holmquist et al. 2011; Erös and Grant 2015; Datry et al. 2016). Areas that are wetter during the dry season can function as seasonal habitat refuges where species can persist and then disperse and repopulate the surrounding landscape when conditions are more favorable (Woinarski et al. 1992; Mackey et al. 2012). In the face of climate change induced changes in moisture distribution, wetlands and riparian areas have been identified as important potential refuges (Holmquist et al. 2011, Millar et al. 2015, Davies 2010; Bogan et al. 2015, Morelli et al. 2016).

The higher incidences of ignition in close vicinity to humans and increase/changes in fire regimes due to climate change (Bradstock 2010), fire refuges can be crucial in fire prone landscapes. Fire refuges can play an important role by 1) enabling the survival of organism during and after a fire event, 2) enabling *in situ* persistence of organisms and populations within the fire boundary, and 3) supporting re-establishment of populations as the burnt area recovers (Robinson et al. 2013). Fire frequency and intensity may be less on rocky outcrops because of the physical barrier the outcrop provides (Clarke 2002; Procheş 2016) and the availability of less flammable features. For fynbos plants rocky outcrops can reduce mortality rates (e.g. Cousins et al. 2015). There is a paucity of work on the role of rocky areas for fynbos fauna (especially invertebrates, but see Pryke and Samways (2012)).

Ideal refuges should provide protection from multiple stressors (Reside et al. 2014). Rocky areas can also act as drought refuges and riverine areas as fire refuges. Afromontane forests occur in sheltered ravines and are not penetrated by fires because the fuel occurs in compacted, relatively moist litter layers that do not burn (van Wilgen et al. 1990). Ravines are also hidden from winds that can drive fires. Areas surrounding rocky outcrops can have relatively higher

soil moisture (Couper and Hoskin 2008), provide micro refuges during dry periods (e.g. Braithwaite and Muller 1997) and aid seedling establishment in dry environments (Lévesque 2001).

A 30 m resolution land cover map (CapeNature 2016b) was used to calculate distance to rocky mountain fynbos and bare rock. Distance to the nearest wetland and riparian areas were calculated from spatial information on water bodies (CAPE 2009). A spectral vegetation index was used to measure temporal variability in vegetation greenness for the time of sampling. Standard deviation of normalized-difference vegetation index (NDVI) was calculated across three satellite images captured in spring to summer 2015 for the months of August (Landsat 8), September (Sentinel 2) and December (Sentinel 2). These images were chosen as they were close to the period of sampling, had the least amount of cloud cover and preceded the fire of February 2016.

2.5 Mesoclimate

Important climatic factors that can determine species distributions include temperature and climatic water balance (Lutz et al. 2010; Bale 2002). The climate of mountainous areas experienced *in situ* is the result of both regional advective and local terrain influences (Pepkin and Lundquist 2008). This is referred to as the 'mesoclimate' (Geiger 1965) (also known as the 'topoclimate' (Thornthwaite 1953)). Local physiographical factors influence meteorological elements that result in variation in mesoclimate with topographic position (Dobrowski 2010). E. g. near-surface temperatures and water availability is in part determined by exposure to solar radiation and wind, which in turn can be influenced by slope and aspect (Barry 1992; Bolstad et al. 1998). Topographically driven mesoclimate in mountainous areas have been found to influence plant (Gallardo-Cruz et al. 2009) and insect species composition (Gollan et al. 2015).

GIS was used to extract climatic parameters (monthly mean precipitation, monthly minimum temperature, monthly maximum temperature) for each site from high resolution (90x90m) climate surfaces based on long term meteorological data (30 year) and specific topographical variables (van Niekerk and Joubert 2011). These climatic parameters characterize general patterns of temperature and rain. To also take into account temperature influences during the time of sampling, one ibutton (TC Thermocron Temperature Logger) was buried (3 cm below soil surface) at each site and set to measure temperature at 30 minute

intervals for 5 days. Care was taken to burry iButtons in areas with direct exposure to sunlight. Terrain derived meteorological elements that can influence *in situ* temperature or moisture conditions (e.g. solar radiation, wind exposure) were derived indirectly from terrain information using QGIS (see 2.6 below).

2.6 Landscape/terrain

Apart from the important role that topography or terrain plays in near surface temperature and the climatic water balance, terrain can also influence numerous other abiotic and biotic conditions important for local diversity patterns. Most of these conditions have been studied in relation to plant diversity patterns. Of these the most important is likely topographically controlled soil moisture (Normand et al. 2006; Moeslund et al. 2013). Topography not only effects soil moisture conditions by influencing incoming solar radiation (i.e. mesoclimate, see section 2.5 above), but also through topographic drainage. Topographical controlled soil moisture gradients have been found to be important for structuring fynbos plant communities (Araya et al. 2011).

Other processes and conditions that can be affected by terrain include geochemistry (Maun 1994; Courtwright and Findlay 2011), propagule and litter distribution (e.g. exposed or steep areas may accumulate less litter or seeds than flat areas), seed establishment (Biederman and Whisenant 2011), and biotic interactions (through topographically influenced spatial propagule distribution (Li et al. 2009)). The various mechanisms involved are multifaceted and challenging to tease apart (see Figure 3 in Moeslund et al. 2013). Moeslund et al. (2013) suggest transforming terrain variables into functional variables that directly represent the topographic effects being investigated (e.g. topographic wetness).

Digital elevation models (DEMs) can be used to obtain indices that capture variation in topography and landform (Wilson and Gallant 2000). Terrain information was sourced from a 5 m resolution DEM (van Niekerk 2001). Terrain parameters (aspect, slope, ruggedness etc.) and associated functional variables (flow accumulation, topographic wetness, hillshade) were calculated using QGIS.

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Appendix 3

Variance partitioning of epigaeic arthropod species turnover among the selected site-measured variables, spatial variables and geographical distance. Values represent fractions of total percent deviance explained. Shaded areas represent fractions explained selected explanatory data sets.
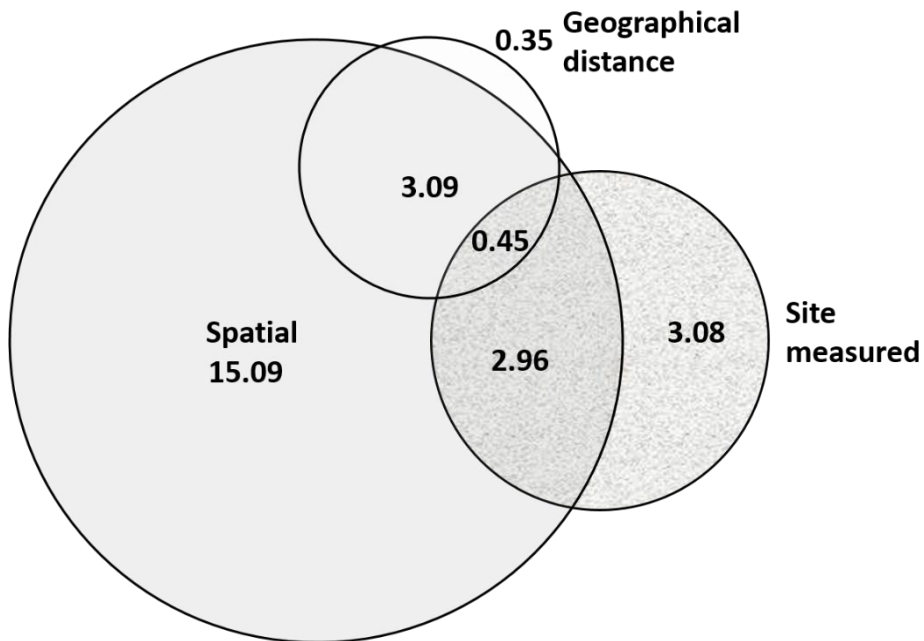
Appendix 4

Proportion of sampling of ecological environments (scaled by epigaeic arthropod data) by study sites. Values have been range standardized between 0 and 1. A) all variables excluding disturbance variables, B) all variables
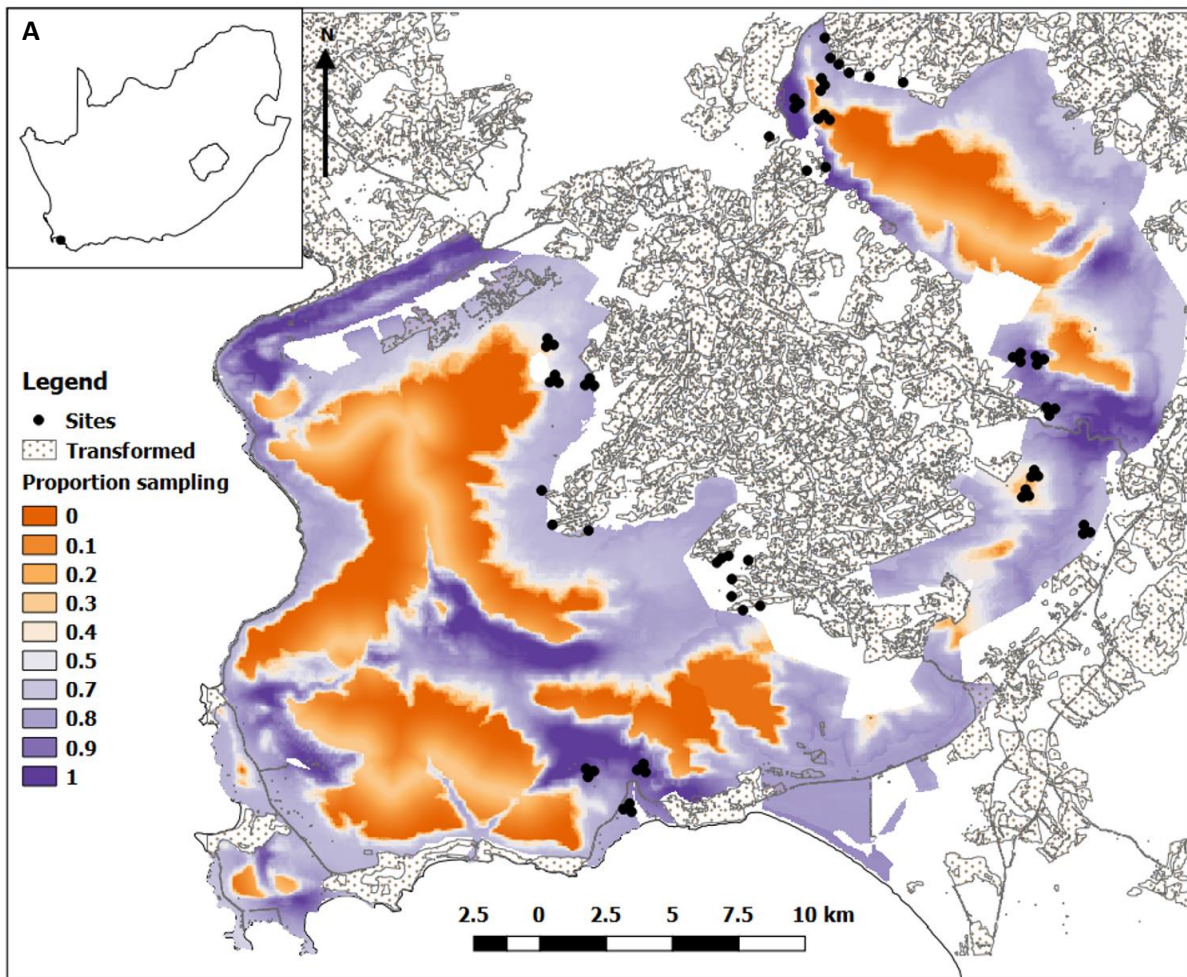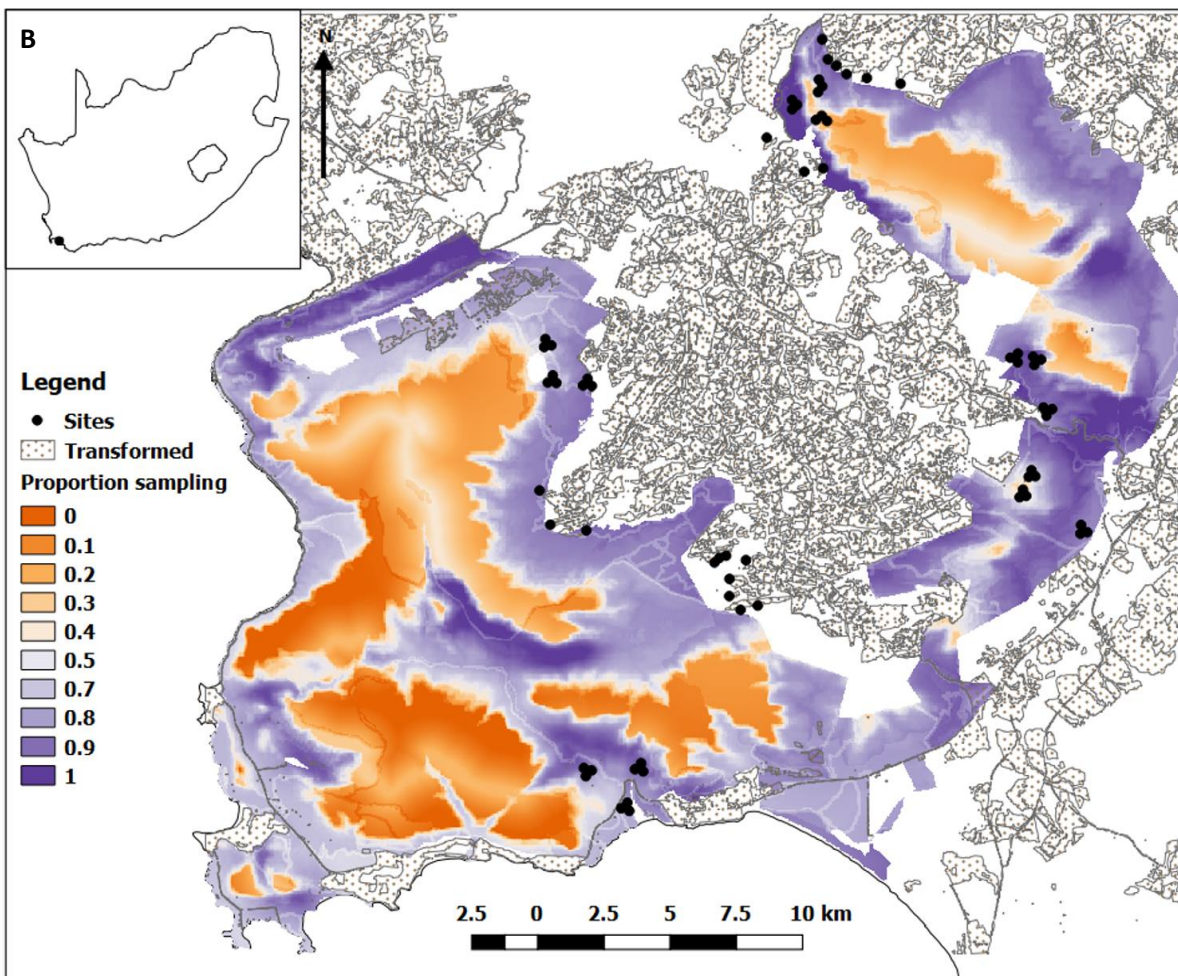
Appendix 5
Species accumulation curves for a) all species and b) all species without singletons.
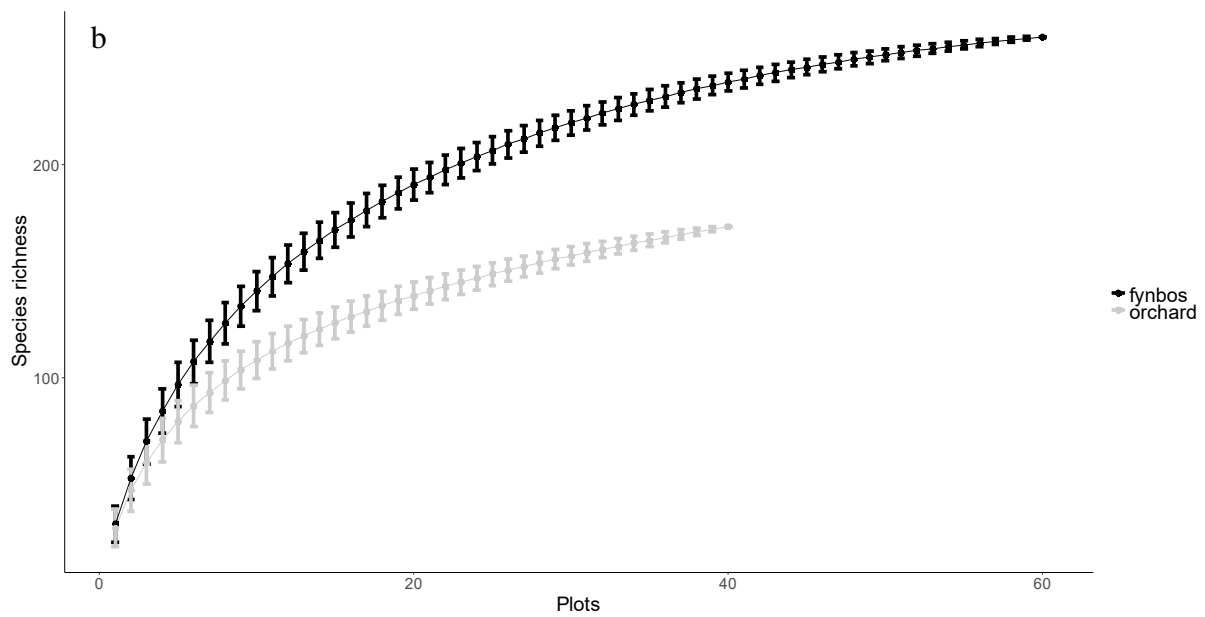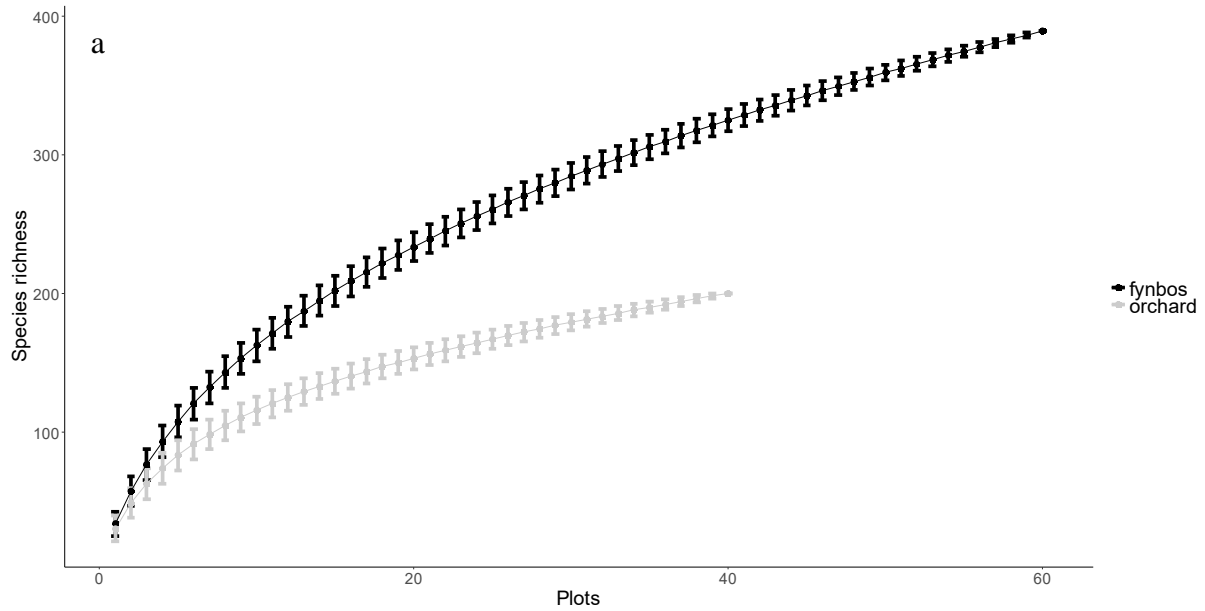
Appendix 6

Species accumulation curves between noncrop, crop-edge and crop-interior plots for a) all species, b) predators, c) herbivores, d) omnivores, and e) detritivores.
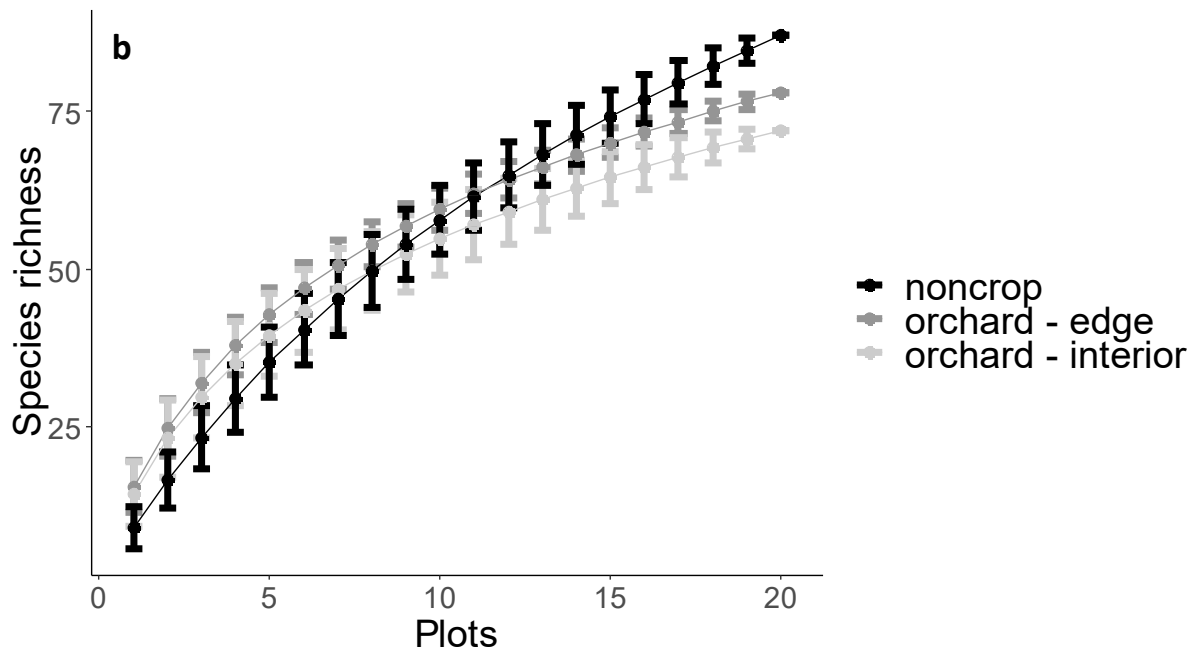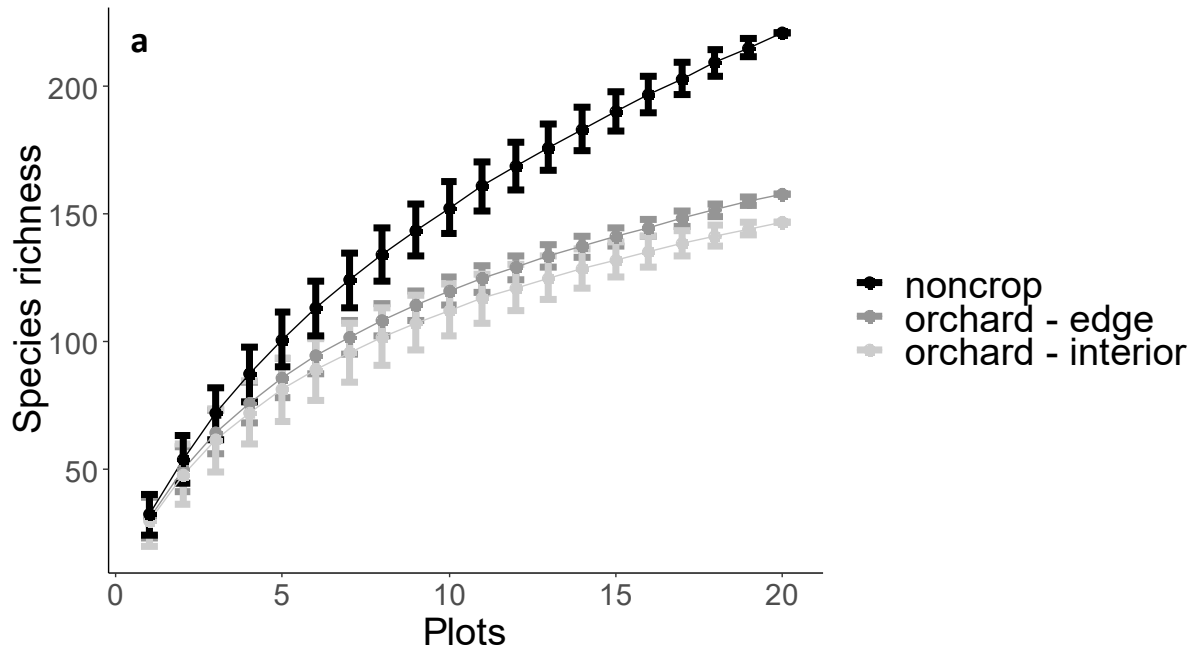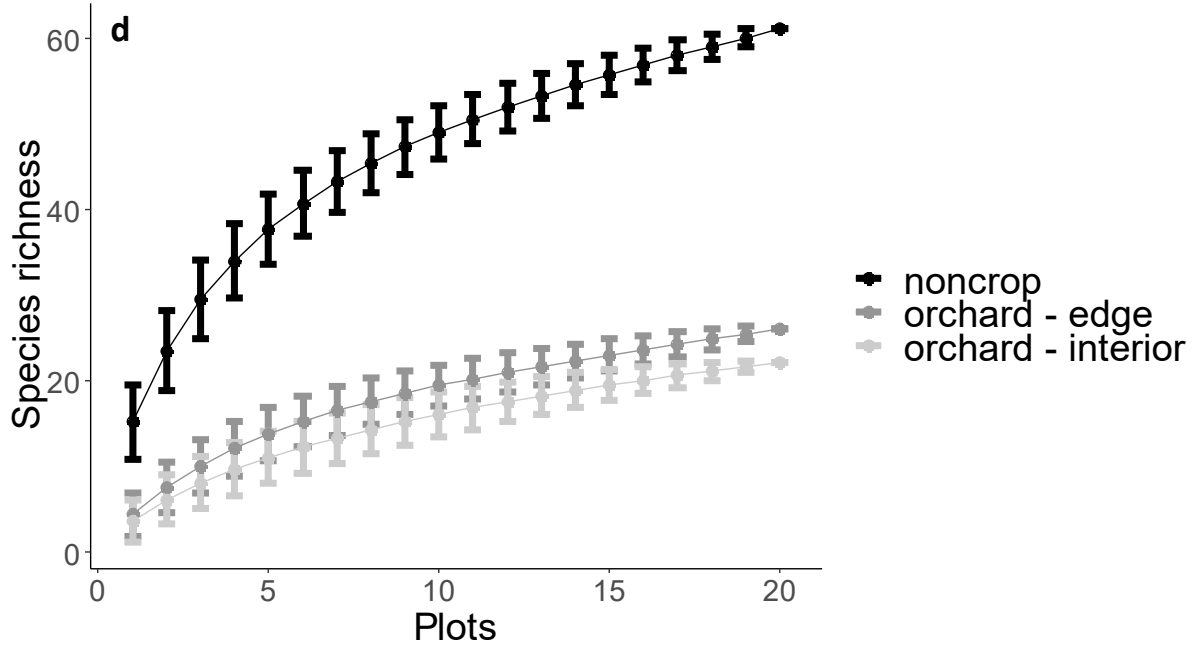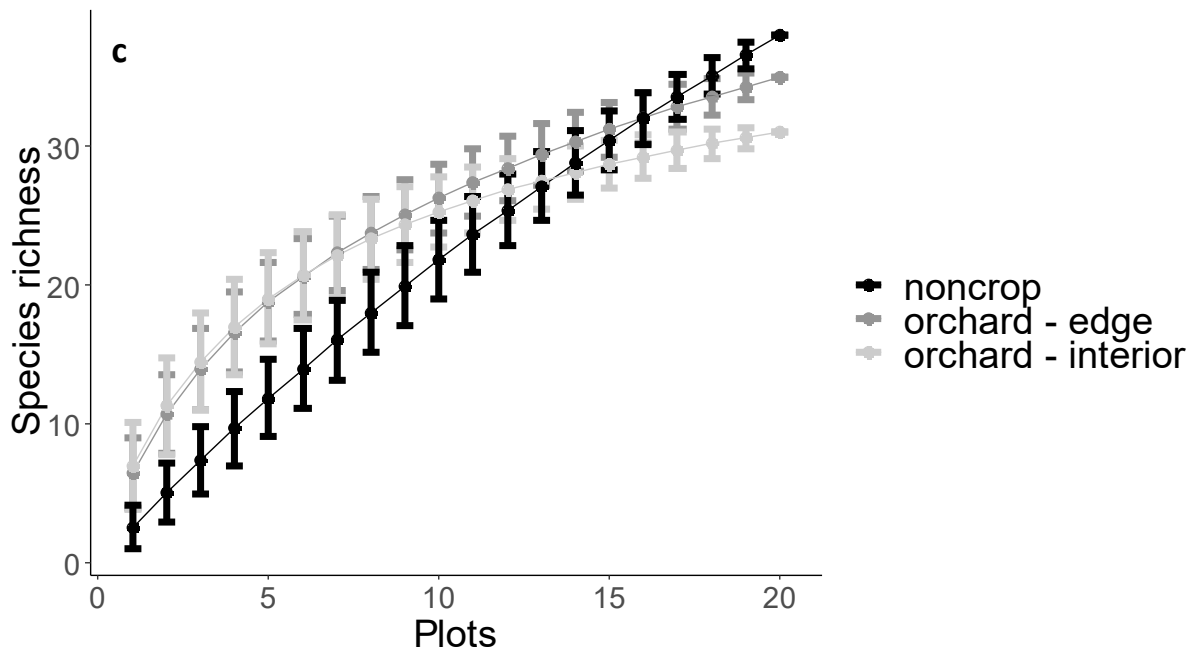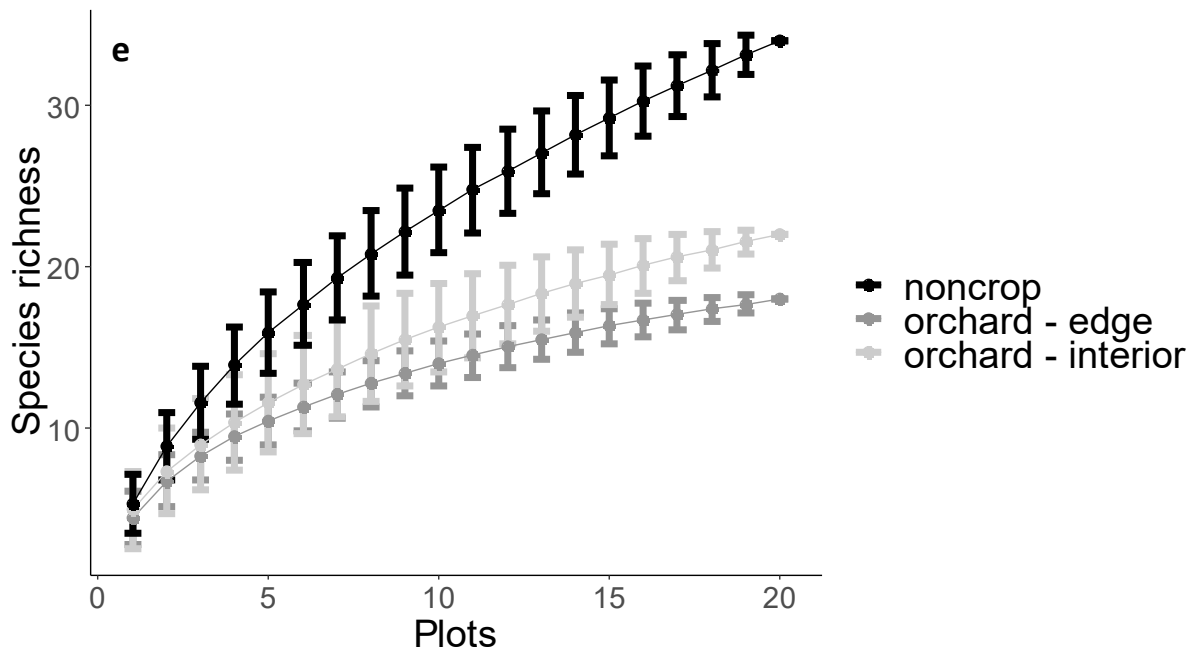
Appendix 7
Species check list of 201 plant species/morphospecies sampled in fynbos habitats, compiled
by order and family.

Order	Family	Species/morphospecies
Apiales	Apiaceae	*Licthensteinia lacera*
Asparagales	Iridaceae	*Gladiolus debilis*
		Gladiolus sp.
		Hesperantha falcata
		Iris sp. 1
		Iris sp. 2
		Moraea tripetala
		Nivenia stokoei
		Tritoniopsis ramosa
	Asphodelaceae	*Trachyandra tabularis*
Asterales	Asteraceae	*Anaxeton asperum*
		Corymbium villosum
		Disparago laxifolia
		Edmondia sesamoides
		Euryops abrotanifolius
		Gerbera linnaei
		Gerbera sp.
		Helichrysum sp. 1
		Helichrysum sp. 2
		Metalasia cephalotes
		Metalasia densa
		Metalasia lichtensteinii
		Osmitopsis afra
		Osmitopsis parviflora
		Osteospermum imbricatum
		Osteospermum moniliferum
		Osteospermum moniliferum

Order	Family	Species/morphospecies
		Othanna sp.
		Othonna parviflora
		Phaenocoma prolifera
		Senecio sp. 1
		Senecio sp. 2
		Stoebe aethiopica
		Stoebe spiralis
		Stoebe sp. 1
		Stoebe sp. 2
		Syncarpha canescens
		Syncarpha gnaphaloides
		Syncarpha speciosissima
		Syncarpha vestita
		Ursinia paleacea
		Zyrphelis taxifolia
	Campanulaceae	*Lobelia pinifolia*
		Lobelia tomentosa
	Campanulaceae	*Roella* sp.
	Menyanthaceae	*Villarsia capensis*
Bruniales	Bruniaceae	*Berzelia abrotanoides*
		Brunia laevis
		Brunia nodiflora
		Nebelia paleacea
Caryophyllales	Aizoaceae	*Erepsia anceps*
	Droseraceae	*Drosera cistiflora*
		Drosera trinervia
		Drosera sp.
Commelinales	Haemodoraceae	*Dilatris pillansii*
		Dilatris viscosa

Order	Family	Species/morphospecies
		Wachendorfia paniculata
Cornales	Grubbiaceae	*Grubbia tomentosa*
Ericales	Ericaceae	*Erica coccinea*
		Erica coriifolia
		Erica cumuliflora
		Erica eriocephala
		Erica fastigiata
		Erica globiceps
		Erica hispidula
		Erica imbricata
		Erica massonii
		Erica placentiflora
		Erica plukenetii
		Erica pulchella
		Erica sessiliflora
		Erica sphaeroidea
		Erica viscaria
		Erica sp. 1
		Erica sp. 2
		Erica sp. 3
		Erica sp. 4
		Erica sp. 5
		Erica sp. 6
Fabales	Fabaceae	*Aspalathus* sp.
		Aspalathus excelsa
		Indigofera filiformis
		Sp. 1
	Polygalaceae	*Muraltia heisteria*
		Polygala bracteolata

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Order	Family	Species/morphospecies
		Polygala sp.
Gleicheniales	Gleicheniaceae	*Gleichenia polypodioides*
Lamiales	Stilbaceae	*Campylostachys cernua*
		Retzia capensis
	Scrophulariaceae	*Microdon dubius*
		Pseudoselago serrata
Malpighiales	Violaceae	*Viola decumbens*
	Peraceae	*Clutia alaternoides*
Malvales	Thymelaeaceae	*Gnidia anomala*
		Gnidia juniperifolia
		Gnidia pinifolia
	Malvaceae	*Hermannia concinnifolia*
		Hermannia sp.
	Thymelaeaceae	*Lachneae* sp.
		Struthiola striata
Myrtales	Penaeaceae	*Penaea mucronata*
		Saltera sarcocolla
		Sonderothamnus speciosus
Oxalidales	Oxalidaceae	*Oxalis* sp. 1
		Oxalis sp. 2
Poales	Restionaceae	*Ceratocaryum* sp.
		Elegia decipiens
		Elegia filacea
		Elegia spathacea
		Elegia stipularis
		Elegia sp. 1
		Elegia sp. 2
		Hypodiscus argenteus
		Hypodiscus aristatus

Order	Family	Species/morphospecies
		Hypodiscus laevigatus
		Hypodiscus argenteus
		Mastersiella digitata
		Nevillea obtusissima
		Restio asperus
		Restio bifarius
		Restio bifidus
		Restio bifurcus
		Restio burchelli
		Restio dispar
		Restio distichus
		Restio egregius
		Restio filiformis
		Restio multiflorus
		Restio paludosus
		Restio similis
		Restio subverticellatus
		Restio tenuispicatus
		Restio tenuissimus
		Restio triticeus
		Restio villosus
		Restio sp.
		Staberoha cernua
		Thamnochortus gracilis
		Thamnochortus arenarius
		Thamnochortus dumosus
		Thamnochortus pulcher
		Thamnochortus sp.
		Willdenowia sp.

Order	Family	Species/morphospecies
	Cyperaceae	*Ficinia* sp.
		Tetraria thermalis
		Tetraria sp.
	Poaceae	*Pentaschistis curvifolia*
		Sp. 1
		Sp. 2
		Sp. 3
Proteales	Proteaceae	*Aulax umbellata*
		Diastella divaricata
		Leucadendron coniferum
		Leucadendron laureolum
		Leucadendron salignum
		Leucadendron anthoconus
		Leucadendron sp. 1
		Leucadendron sp. 2
		Leucospermum oleifolium
		Leucospermum truncatulum
		Leucospermum sp.
		Mimetes cucullatus
		Paranomus spicatus
		Protea cordata
		Protea cynaroides
		Protea grandiceps
		Protea longifolia
		Protea scabra
		Protea sp. 1
		Protea sp. 2
		Protea sp. 3
		Protea sp. 4

Order	Family	Species/morphospecies
		Protea sp. 5
		Serruria elongata
		Serruria fasciflora
		Sorocephalus clavigerus
		Spatalla curvifolia
Rosales	Rhamnaceae	*Phylica astrata*
		Phylica boxifolia
		Phylica humilis
		Phylica lasiocarpa
		Phylica parviflora
		Phylica strigulosa
	Rosaceae	*Cliffortia atrata*
		Cliffortia exilifolia
		Cliffortia ruscifolia
		Cliffortia tuberculata
Santalales	Santalaceae	*Thesium carinatum*
		Thesium euphorbioides
		Thesium spicatum
		Thesium sp. 1
		Thesium sp. 2
Sapindales	Anacardiaceae	*Rhus* sp.
Sapindales	Rutaceae	*Adenandra* sp.
		Adenandra acuta
		Adenandra brachyphylla
		Adenandra villosa orbicularis
		Diosma hirsuta
		Diosma oppositifolia
Saxifragales	Crassulaceae	*Crassula fascicularis*
Schizaeales	Schizaeaceae	*Schizaea pectinata*

Appendix 8
List of weed families sampled in orchards

Order	Family
Poales	Poaceae
Asterales	Asteraceae
Brassicales	Brassicaceae
Caryophyllales	Amaranthaceae
	Polygonaceae
Ericales	Primulaceae
Fabales	Fabaceae
Geraniales	Geraniaceae
Lamiales	Plantaginaceae
	Verbenaceae
Malpighiales	Euphorbiaceae
Oxalidales	Oxalidaceae

Appendix 9

Species checklist of all 733 arthropod species sampled from 37 701 individuals. Trophic group classification was based on the dominant feeding habitat of lowest taxonomic resolution. P – predator/parasite, H – herbivore, O – omnivore, D - detritivore

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
Arachnida	Araneae	Anapidae	*Crozetulus rhodesiensis* (Brignoli, 1981)	P
		Araneidae	*Araneus* sp. 1	P
			Araneus sp. 2	P
			Araneus sp. 3	P
			Araneus sp. 4	P
			Araneus sp. 5	P
			Araneus sp. 6	P
			Caerostris sp.	P
			Larinia sp. 1	P
			Larinia sp. 2	P
			Neoscona subfusca (Koch, 1837)	P
		Caponiidae	*Caponia capensis* (Purcell, 1904)	P
		Clubionidae	*Clubiona* sp. 1	P
			Clubiona sp. 2	P
			Clubiona sp. 3	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Clubiona sp. 4	P
		Corinnidae	*Afroceto capensis* (Lyle & Haddad, 2010)	P
			Castianeira sp.	P
			Copa flavoplumosa (Simon, 1886)	P
		Ctenidae	*Ctenus* sp.	P
		Cyatholipidae	*Cyatholipus avus* (Griswold, 1987)	P
			Cyatholipus quadrimaculatus (Simon, 1894)	P
			Ilisoa conjugalis (Griswold, 2001)	P
		Cyrtaucheniidae	*Ancylotrypa* sp.	P
		Drymusidae	*Drymusa capensis* (Simon, 1893)	P
		Eutichuridae	*Cheiramiona ansiae* (Lotz, 2003)	P
			Cheiramiona sp.	P
		Gallieniellidae	*Drassodella septemmaculata* (Strand, 1909)	P
		Gnaphosidae	*Amusia cataracta* (Tucker, 1923)	P
			Aphantaulax inornata (Tucker, 1923)	P
			Asemesthes montanus (Tucker, 1923)	P
			Asemeshes sp. 1	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Asemeshes sp. 2	P
			Asemeshes sp. 3	P
			Camillina cordifera (Tullgren, 1910)	P
			Megamyrmaekion schreineri (Tucker, 1923)	P
			Trachyzelotes jaxartensis (Kroneberg, 1875)	P
			Xerophaeus capensis (Purcell, 1907)	P
			Zelotes fuligineus (Purcell, 1907)	P
		Hahniidae	*Hahnia laticeps* (Simon, 1898)	P
		Linyphiidae	*Agyneta habra* (Locket, 1968)	P
			Meioneta prosectoides (Locket & Russel-Smith 1980)	P
			Mermessus fradeorum (Berland, 1932)	P
			Pelecopsis janus (Jocqué, 1984)	P
		Lycosidae	*Allocosa lawrencei* (Roewer, 1951)	P
			Foveosa foveolata (Purcell, 1903)	P
			Hogna unicolor (Roewer, 1959)	P
			Minicosa neptuna (Alderweireldt & Jocqué, 2007)	P
			Pardosa crassipalpis (Purcell, 1903)	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Pardosa sp.	P
			Proevippa biampliata (Purcell, 1903)	P
			Proevippa sp.	P
			Trabea purcelli (Roewer, 1951)	P
			Trabea sp.	P
		Migidae	*Moggridgea peringueyi* (Simon, 1903)	P
		Opiliones	*Opiliones* sp. 1	P
			Opiliones sp. 2	P
			Opiliones sp. 3	P
			Opiliones sp. 4	P
		Oxyopidae	*Oxyopes longispinosus* (Lawrence, 1938)	P
			Oxyopes sp.	P
		Philodromidae	*Philodromus* sp.	P
			Suemus punctata (Lawrence, 1938)	P
			Thanatus lamottei (Jézéquel, 1964)	P
		Pholcidae	*Spermophora suurbraak* (Huber, 2003)	P
		Phyxelididae	*Malaika delicatula* (Griswold, 1990)	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Malaika sp. (new species)	P
		Pisauridae	*Chiasmopes lineatus* (Pocock, 1898)	P
			Euprosthenopsis pulchella (Pocock, 1902)	P
			Rothus aethiopicus (Pavesi, 1883)	P
		Prodidomidae	*Theuma* sp.	P
		Saliticidae	*Aelurullinae* sp. 1	P
			Aelurullinae sp. 2	P
			Aelurullinae sp. 3	P
			Baryphas ahenus (Simon, 1902)	P
			Heliophanus sp. 1	P
			Heliophanus sp. 2	P
			Langona sp. 1	P
			Langona sp. 2	P
			Langona sp. 3	P
			Mashonarus guttatus (Wesołowska & Cumming, 2002)	P
			Massagris regina (Wesolowska, 1993)	P
			Myrmarachne sp.	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Pellenes tharinae (Wesołowska, 2006)	P
			Pellenes sp.	P
			Pseudicius sp.	P
			Rhene lingularis (Haddad & Wesołowska, 2011)	P
			Rumburak bellus (Wesołowska, Azarkina & Russell-Smith, 2014)	P
			Rumburak sp. 1	P
			Rumburak sp. 2	P
			Rumburak sp. 3	P
			Thyene thyenioides (Lessert, 1925)	P
			Thyene sp.	P
			Thyenula sp. 1	P
			Thyenula sp. 2	P
			Thyenula sp. 3	P
			Xuriella prima (Wesołowska & Russell-Smith, 2000)	P
		Scytodidae	*Scytodes flagellata* (Purcell, 1904)	P
		Segestriidae	*Ariadna scabripes* (Purcell, 1904)	P
			Olios sp.	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Palystes castaneus (Latreille, 1819)	P
		Theridiidae	*Episinus* sp. 1	P
			Episinus sp. 2	P
			Euryopis episinoides (Walckenaer, 1847)	P
			Euryopis funebris (Hentz, 1850)	P
			Phycosoma sp.	P
			Theridion sp. 1	P
			Theridion sp. 2	P
		Theridiosomatidae	*Theridiosomatidae* sp.	P
		Thomisidae	*Diaea puncta* (Karsch, 1884)	P
			Heriaeus muizenberg (Niekerk & Dippenaar-Schoeman, 2013)	P
			Hewittia gracilis (Lessert, 1928)	P
			Monaeses pustulosus (Pavesi, 1895)	P
			Ozyptila caenosa (Jézéquel, 1966)	P
			Pherecydes tuberculatus (O. P.-Cambridge, 1883)	P
			Phrynarachne melloleitaoi (Lessert, 1933)	P
			Simorcus capensis (Simon, 1895)	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Synema imitator (Pavesi, 1883)	P
			Synema riflense (Strand, 1909)	P
			Thomisops sulcatus (Simon, 1895)	P
			Thomisus sp.	P
			Xysticus sagittifer (Lawrence, 1927)	P
		Trachelidae	*Fuchibotulus bicornis* (Haddad & Lyle, 2008)	P
		Zodariidae	*Caesetius globicoxis* (Lawrence, 1942)	P
			Chariobas cylindraceus (Simon, 1893)	P
			Chariobas lineatus (Pocock, 1900)	P
			Cydrela sp. 1	P
			Cydrela sp. 2	P
			Cydrela sp. 3	P
			Cydrela sp. 4	P
			Diores simoni	P
			Diores sp.	P
			Heradida speculigera (Jocqué, 1987)	P
			Psammoduon arenicola (Simon, 1910)	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
	Mesostigmata		Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
			Sp. 5	P
			Sp. 6	P
			Sp. 7	P
			Sp. 8	P
			Sp. 9	P
			Sp. 10	P
			Sp. 11	P
			Sp. 12	P
			Sp. 13	P
			Sp. 14	P
			Sp. 15	P
			Sp. 16	P
			Sp. 17	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 18	P
	Opiliones		Sp. 1	P
			Sp. 2	P
	Oribatida		Sp. 1	D
			Sp. 2	D
			Sp. 3	D
			Sp. 4	D
			Sp. 5	D
			Sp. 6	D
			Sp. 7	D
			Sp. 8	D
			Sp. 9	D
			Sp. 10	D
			Sp. 11	D
			Sp. 12	D
			Sp. 13	D
			Sp. 14	D

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 15	D
			Sp. 16	D
			Sp. 17	D
			Sp. 18	D
			Sp. 19	D
			Sp. 20	D
			Sp. 21	D
			Sp. 22	D
			Sp. 23	D
			Sp. 24	D
			Sp. 25	D
			Sp. 26	D
			Sp. 27	D
			Sp. 28	D
			Sp. 29	D
			Sp. 30	D
			Sp. 31	D

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 32	D
			Sp. 33	D
			Sp. 34	D
			Sp. 35	D
			Sp. 36	D
			Sp. 37	D
			Sp. 38	D
			Sp. 39	D
			Sp. 40	D
			Sp. 41	D
			Sp. 42	D
			Sp. 43	D
			Sp. 44	D
			Sp. 45	D
			Sp. 46	D
			Sp. 47	D
			Sp. 48	D

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 49	D
			Sp. 50	D
			Sp. 51	D
			Sp. 52	D
			Sp. 53	D
			Sp. 54	D
			Sp. 55	D
	Prostigmata		Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
			Sp. 5	P
			Sp. 6	P
			Sp. 7	P
			Sp. 8	P
			Sp. 9	P
			Sp. 10	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 11	P
			Sp. 12	P
			Sp. 13	P
			Sp. 14	P
			Sp. 15	P
			Sp. 16	P
			Sp. 17	P
			Sp. 18	P
			Sp. 19	P
			Sp. 20	P
			Sp. 21	P
			Sp. 22	P
			Sp. 23	P
			Sp. 24	P
			Sp. 25	P
			Sp. 26	P
			Sp. 27	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 28	P
			Sp. 29	P
			Sp. 30	P
			Sp. 31	P
			Sp. 32	P
			Sp. 33	P
			Sp. 34	P
			Sp. 35	P
			Sp. 36	P
			Sp. 37	P
			Sp. 38	P
			Sp. 39	P
			Sp. 40	P
			Sp. 41	P
			Sp. 42	P
			Sp. 43	P
			Sp. 44	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 45	P
			Sp. 46	P
			Sp. 47	P
			Sp. 48	P
			Sp. 49	P
			Sp. 50	P
			Sp. 51	P
			Sp. 52	P
			Sp. 53	P
			Sp. 54	P
			Sp. 55	P
			Sp. 56	P
			Sp. 57	P
			Sp. 58	P
			Sp. 59	P
			Sp. 60	P
			Sp. 61	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 62	P
			Sp. 63	P
			Sp. 64	P
			Sp. 65	P
			Sp. 66	P
	Pseudoscorpiones		Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
			Sp. 5	P
			Sp. 6	P
			Sp. 7	P
			Sp. 8	P
			Sp. 9	P
	Scorpiones		Sp. 1	P
			Sp. 2	P
			Sp. 3	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 4	P
Chilopoda	Lithobiomorpha		Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
Diplopoda			Sp. 1	D
			Sp. 2	D
			Sp. 3	D
			Sp. 4	D
			Sp. 5	D
			Sp. 6	D
Insecta	Archeognatha	Meinertellidae	Sp. 1	D
			Sp. 2	D
			Sp. 3	D
	Blattodea		Sp. 1	O
			Blatella germanica (Linnaeus, 1767)	O
			Saltoblatella montistabularis (Bohn, Picker, Klass & Colville, 2009)	O

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Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Temnopteryx phalerata (Saussure, 1864)	O
			Sp. 2	O
			Sp. 3	O
			Sp. 4	O
			Sp. 5	O
			Sp. 6	O
			Sp. 7	O
			Sp. 8	O
			Sp. 9	O
			Sp. 10	O
			Sp. 11	O
			Sp. 12	O
			Sp. 13	O
			Sp. 14	O
	Coleoptera	Alticinae	Sp. 1	H
		Anobiidae	Sp. 1	H
		Anthicidae	Sp. 1	O

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
		Bostrychidae	Sp. 1	H
		Cantharidae	Sp. 1	P
			Sp. 2	P
			Sp. 3	P
		Carabidae	*Thermophilum decemguttatum* (Linnaeus, 1764)	P
			Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
			Sp. 5	P
			Sp. 6	P
			Sp. 7	P
			Sp. 8	P
			Sp. 9	P
			Sp. 10	P
			Sp. 11	P
		Cerambycidae	Sp. 1	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 2	H
		Chrysomelidae	Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H
			Sp. 8	H
			Sp. 9	H
			Sp. 10	H
			Sp. 11	H
			Sp. 12	H
			Sp. 13	H
			Sp. 14	H
		Cicindelidae	Sp. 1	P
		Ciidae	Sp. 1	D
		Cleridae	Sp. 1	P
			Sp. 2	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 3	P
			Sp. 4	P
		Coccinellidae	Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
		Corylophidae	Sp. 1	D
		Cryptophagidae	Sp. 1	D
			Sp. 2	D
			Sp. 3	D
			Sp. 4	D
		Curculionidae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 7	H
			Sp. 8	H
			Sp. 9	H
			Sp. 10	H
			Sp. 11	H
			Sp. 12	H
			Sp. 13	H
			Sp. 14	H
			Sp. 15	H
			Sp. 16	H
			Sp. 17	H
			Sp. 18	H
			Sp. 19	H
			Sp. 20	H
			Sp. 21	H
			Sp. 22	H
			Sp. 23	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 24	H
			Sp. 25	H
		Cybocephalidae	*Cybocephalus* sp.	P
		Dermestidae	Sp. 1	D
		Elateridae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H
			Sp. 8	H
		Geotrupidae	Sp. 1	H
			Sp. 2	H
		Histeridae	Sp. 1	P
			Sp. 2	P
		Lymexylidae	*Melittomma* sp.	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
		Melolonthinae	Sp. 1	H
			Sp. 2	H
		Melyridae	*Malachiinae* sp.	P
		Mordellidae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
		Mycetophagidae	Sp. 1	D
			Sp. 2	D
		Nitidulidae	*Lasiodactylus* sp. 1	D
			Lasiodactylus sp. 2	D
			Sp. 1	H
			Sp. 2	H
		Omaliinae	Sp. 1	P
		Phalacridae	Sp. 1	H
		Pimelinae	Sp. 1	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
		Pselaphidae	Sp. 1	P
			Sp. 2	P
			Sp. 3	P
			Sp. 4	P
		Rutelinae	*Hopliini* sp. 1	H
			Hopliini sp. 2	H
		Scarabaeinae	Sp. 1	D
			Sp. 2	D
			Sp. 3	D
			Sp. 4	D
			Sp. 5	D
		Scydmaenidae	Sp. 1	P
		Silphidae	Sp. 1	D
		Staphylinidae	Sp. 1	P
			Sp. 2	P
			Sp. 3	D
			Sp. 4	D

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 5	P
			Sp. 6	P
			Sp. 7	P
			Sp. 8	P
			Sp. 9	P
			Sp. 10	P
			Sp. 11	P
			Sp. 12	P
			Sp. 13	P
			Sp. 14	P
			Sp. 15	P
			Sp. 16	P
			Sp. 17	P
			Sp. 18	P
			Sp. 19	P
		Tenebrionidae	Sp. 1	H
			Sp. 2	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 2	O
			Sp. 3	O
			Sp. 4	O
			Sp. 2	D
		Tenebrioninae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H
			Sp. 8	H
		Trogidae	*Trox* sp. 1	D
			Trox sp. 2	D
		Unknown	Sp. 1	H
			Sp. 2	H
			Sp. 3	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H
	Dermaptera		Sp. 1	D
			Sp. 2	D
			Sp. 3	D
			Sp. 4	D
	Hemiptera	Aphidoidea	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H
			Sp. 8	H
			Sp. 9	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 10	H
			Sp. 11	H
			Sp. 12	H
			Sp. 13	H
			Sp. 14	H
			Sp. 15	H
			Sp. 16	H
		Asopinae	Sp. 1	P
		Blissidae	Sp. 1	H
			Sp. 2	H
		Cicadellidae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 8	H
			Sp. 9	H
			Sp. 10	H
			Sp. 11	H
			Sp. 12	H
			Sp. 13	H
			Sp. 14	H
			Sp. 15	H
			Sp. 16	H
			Sp. 17	H
		Cixiidae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
		Cydnidae	Sp. 1	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
		Dictyopharidae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
		Emesinae	Sp. 1	P
		Fulgoroidea	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 8	H
			Sp. 9	H
			Sp. 10	H
			Sp. 11	H
			Sp. 12	H
			Sp. 13	H
			Sp. 14	H
			Sp. 15	H
			Sp. 16	H
			Sp. 17	H
			Sp. 18	H
			Sp. 19	H
			Sp. 20	H
			Sp. 21	H
			Sp. 22	H
			Sp. 23	H
			Sp. 24	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 25	H
			Sp. 26	H
			Sp. 27	H
			Sp. 28	H
			Sp. 29	H
			Sp. 30	H
			Sp. 31	H
			Sp. 32	H
			Sp. 33	H
			Sp. 34	H
			Sp. 35	H
			Sp. 36	H
			Sp. 37	H
			Sp. 38	H
			Sp. 39	H
			Sp. 40	H
			Sp. 41	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 42	H
			Sp. 43	H
			Sp. 44	H
			Sp. 45	H
			Sp. 46	H
			Sp. 47	H
		Lygaeidae	Sp. 1	H
		Ochteridae	Sp. 1	P
		Pentatominae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
		Psamminae	*Psammium* sp.	H
			Sp. 1	H
		Pyrrhocoridae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
		Reduvidae	Sp. 1	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 2	P
			Sp. 3	P
		Rhyparochrominae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
		Tingidae	*Cantacaderinae* sp.	H
			Tinginae sp. 1	H
			Tinginae sp. 2	H
		Unknown	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 7	H
			Sp. 8	H
			Sp. 9	P
			Sp. 10	P
			Sp. 11	H
			Sp. 12	H
			Sp. 13	H
			Sp. 14	H
			Sp. 15	H
			Sp. 16	H
			Sp. 17	H
	Hymenoptera	Formicidae	*Linepithema* sp.	O
			Tapinoma sp. 1	O
			Tapinoma sp. 2	O
			Cerapachys sp. 1	P
			Cerapachys sp. 2	P
			Dorylus sp.	P

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Camponotus sp. 1	O
			Camponotus sp. 2	O
			Camponotus sp. 3	O
			Camponotus sp. 4	O
			Camponotus sp. 5	O
			Camponotus sp. 6	O
			Camponotus sp. 7	O
			Camponotus sp. 8	O
			Camponotus sp. 9	O
			Camponotus sp. 10	O
			Camponotus sp. 11	O
			Anoplolepis sp.	O
			Brachymyrmex sp. 1	O
			Brachymyrmex sp. 2	O
			Brachymyrmex sp. 3	O
			Lepisiota sp.	O
			Plagiolepis sp. 1	O

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Plagiolepis sp. 2	O
			Pheidole sp. 1	O
			Pheidole sp. 2	O
			Pheidole sp. 3	O
			Trichoscapa sp.	P
			Crematogaster sp. 1	O
			Crematogaster sp. 2	O
			Meranoplus sp.	O
			Ocymyrmex sp.	O
			Oligomyrmex sp.	O
			Rhoptromyrmex sp. 1	O
			Rhoptromyrmex sp. 2	O
			Tetramorium sp. 1	O
			Tetramorium sp. 2	O
			Tetramorium sp. 3	O
			Tetramorium sp. 4	O
			Tetramorium sp. 5	O

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Tetramorium sp. 6	O
			Tetramorium sp. 7	O
			Tetramorium sp. 8	O
			Tetramorium sp. 9	O
			Tetramorium sp. 10	O
			Tetramorium sp. 11	O
			Tetramorium sp. 12	O
			Monomorium sp. 1	O
			Monomorium sp. 2	O
			Monomorium sp. 3	O
			Monomorium sp. 4	O
			Monomorium sp. 5	O
			Monomorium sp. 6	O
			Monomorium sp. 7	O
			Myrmicaria sp.	P
			Solenopsis sp. 1	O
			Solenopsis sp. 2	O

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Hypoponera sp. 1	P
			Hypoponera sp. 2	P
			Leptogenys sp.	P
			Pachycondyla sp.	P
			Probolomyrmex sp.	P
			Tetraponera sp. 1	O
			Tetraponera sp. 2	O
			Tetraponera sp. 3	O
	Orthoptera	Anostostomatidae	*Henicus brevimucronatus* (Griffini, 1911)	O
			Henicus sp. 1	O
			Henicus sp. 2	O
			Henicus sp. 3	O
		Cophogryllus	Sp. 1	O
			Sp. 2	O
			Sp. 3	O
			Sp. 4	O
		Gryllacrididae	*Eremus* sp.	O

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
		Gryllidae	Sp. 1	O
			Sp. 2	O
			Cophogryllus sp.	O
		Gryllus	Sp. 1	O
		Lentulidae	Sp. 1	H
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
			Sp. 6	H
			Sp. 7	H
			Sp. 8	H
			Sp. 9	H
			Sp. 10	H
		Pamphagidae	Sp. 1	H
			Sp. 2	H
		Tetrigidae	Sp. 1	H

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 2	H
		Tettigoniidae	*Megalotheca* sp.	H
		Unknown	Sp. 1	O
			Sp. 2	H
			Sp. 3	H
			Sp. 4	H
			Sp. 5	H
	Pscocoptera	Liposcelidae	Sp. 1	D
			Sp. 2	D
			Sp. 3	D
			Sp. 4	D
	Thysanura	Ctenolepisma	Sp. 1	O
		Ctenolepisma	Sp. 2	O
Malacostraca	Amphipoda		Sp. 1	D
	Isopoda		Sp. 1	D
			Sp. 2	D
			Sp. 3	D

Class	Order/suborder	Superfamily/ family/subfamily	Species/morphospecies	Trophic group
			Sp. 4	D
			Sp. 5	D
			Sp. 6	D
			Sp. 7	D