Viticultural effects on arthropod diversity in the Cape Winelands Biosphere Reserve

by

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Declaration

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General summary

Agricultural land-use intensification negatively impacts biodiversity, ecosystem function, and ecosystem services at local and global scales. Biosphere reserves consist of interrelated and complementary zones of different land-use intensity, are important platforms for integrating human-environment interactions, and support effective conservation through bridging the gap between conservation science, practitioners, and other stakeholders.

This study assesses the success status of arthropod conservation within the Cape Winelands Biosphere Reserve (CWBR), a biosphere reserve situated in a global biodiversity hotspot where viticulture is the dominant agricultural land use. The focus is on viticultural management practices and their interactions with the surrounding landscape at multiple spatial scales. Assessment of a wide range of viticultural management practices and environmental variables at the local scale, showed that arthropod species richness can be enhanced through maintaining herbaceous vegetation in vineyard inter-rows, and by leaving plant litter on the vineyard floor. The results were consistent across different management regimes and landscape contexts, emphasising the broad applicability of this agro-ecological approach at the local scale, which also aligns with global trends in plant diversification in perennial crops. At the larger, farm scale, there was limited spillover of stenotopic species associated with remnant fynbos vegetation into vineyards, and no variables were identified that could enhance their spillover. This suggests that proximity of remnant patches, stepping-stone habitats, and conservation corridors may be important for improving functional landscape connectivity for these stenotopic arthropods across this vineyard mosaic. Nonetheless, ubiquitous arthropods in vineyards benefited from increased herbaceous vegetation in the inter-rows. Conversely, there was some spillover of cultural species from vineyards into fynbos, and the ecosystem consequences of this requires further investigation. Furthermore, contrary to main trends in the literature, I found no mediating effects of landscape complexity on local-scale practices (increased vegetation cover and organic farming) with regard to arthropod species richness. However, there were strong interacting effects of organic farming and landscape complexity on arthropod assemblages within vineyards, with greater assemblage dissimilarity among organic farms along a landscape complexity gradient, than among integrated farms. Lastly, at a regional scale, vineyards were nearly equal to natural vegetation in terms of alpha and beta diversity, but vineyards had significantly lower functional diversity. There were significant differences in fynbos and vineyard assemblages. Additionally, there were strong trait associations of predatory beetles with vineyards, as well as smaller sized beetles and plant-dwelling spiders to natural vegetation, indicating a shift in assemblage trait composition between natural and cultivated areas.

Deviations from main trends in the literature here highlight the natural variation among different regions, and the importance of site-specific studies for the assessment of arthropod responses to local conditions. Vineyards in the CWBR show great potential for supporting diverse and abundant arthropod assemblages that are functionally dissimilar from the surrounding natural species pool, in-turn contributing to heterogeneity across the landscape. Furthermore, there are opportunities for enhancing arthropod diversity within vineyards, benefitting wine production. The results also emphasise the value of biodiversity conservation in the buffer and transition zones of the CWBR, and in biosphere reserves in general.

Algemene opsomming

Die intensifisering van landbougrondgebruik het ‘n negatiewe impak op biodiversiteit, ekosisteemfunksie, en ekosisteemdienste vanaf ‘n plaaslike tot op ‘n wêreldwye skaal. Biosfeerreservate is saamgestel uit onderling verwante en komplementêre sones van verskillende grondgebruikintensiteite, en is belangrike platforms vir die integrasie van interaksies tussen mens en die omgewing. Dit ondersteun effektiewe bewaring deur die gaping tussen wetenskap, praktisyns, en ander belanghebbendes te oorbrug.

Hierdie studie assesseer die bewaringsukses van geleedpotiges wat voorkom in die Kaapse Wynland Biosfeerreservaat (KWBR). Die biosfeerreservaat is geleë binne ‘n wêreld-wye brandpunt vir biodiversiteit, waar wingerdbou die dominante landbougrondgebruik is. Fokus word gelê op wingerdboukundige praktyke en die interaksies daarvan met die omliggende landskap op verskillende ruimtelike skale. Die assessering van ‘n wye reeks van wingerdboukundige praktyke en omgewingsveranderlikes, op ‘n plaaslike skaal, het gewys dat die aantal geleedpotige spesies verryk kan word deur kruidagtige dekgewasse in die tussenrye van wingerde te handhaaf en deur plantvullis op die wingerd vloer te los. Hierdie resultate was bestendig oor verskillende bestuursregimes en landskapkontekste, wat die wye toepasbaarheid van hierdie agri-ekologiese benadering op ‘n plaaslike skaal beklemtoon, en is in lyn met wêreldwye tendense in plantdiversifikasie in meerjarige gewasse. Op die groter plaasskaal was daar beperkte verspreiding van fynbos geassosieerde spesies in die wingerd rigting en geen veranderlikes was geïdentifiseer wat verspreiding in hierdie rigting kon bevorder nie. Dit stel voor dat die nabyheid van oorblywende kolle van natuurlike fynbos, trapsteen habitatte, en bewaringskorridors belangrik mag wees om die funksionele konnektiwiteit van fynbos geassosieerde spesies in hierdie wingerdmosaïek te bevorder. Nietemin, alomteenwoordige geleedpotiges wat in wingerde voorgekom het, was bevoordeel deur verhoogde aantal kruidagtige plante in die tussenrye. Omgekeerd egter, het verspreiding van kulturele spesies in die fynbos rigting plaasgevind, maar die uitwerking hiervan op die ekosisteem benodig verdere ondersoek.

Kontrasterend met die hooftendense in die literatuur, was daar geen bemiddelende effekte van landskapkompleksiteit op plaaslike praktyke (hoër persentasie plantbedekking en 'n organiese benadering) met betrekking tot geleedpotige spesiesrykheid nie. Daar was egter sterk interaksies tussen organiese plase en landskapkompleksiteit wat betref geleedpotige samestellings binne wingerde, met groter andersheid van samestellings tussen organiese plase as tussen geïntegreerde plase. Laastens, op 'n streeksskaal het wingerde byna gelyk gevaar met die natuurlike plantegroei in terme van alfa- en beta-diversiteit, alhoewel wingerde aansienlik minder funksionele diversiteit getoon het. Geleedpotige saamestellings tussen fynbos en wingerde het ook aansienlik verskil van mekaar. Addisioneel tot hierdie was daar sterk eienskapassosiasies van predatoriese kewers met wingerde, sowel as kleiner kewers en plantbewonende spinnekoppe met natuurlike plantegroei wat 'n verandering in die samestelling van spesies-eienskappe tussen natuurlike en gekultiveerde areas aandui.

Afwykings vanaf die hooftendense in die literatuur beklemtoon die natuurlike variasie tussen verskillende streke, en die belangrikheid van lokaliteitspesifieke studies om die uitwerking van plaaslike kondisies op geleedpotiges te assesseer. Wingerde in die KWBR toon groot potensiaal om diverse en oorvloedige geleedpotige samestellings te ondersteun, wat funksioneel verskil van die omliggende natuurlike spesiespoel en om die beurt bydrae tot die heterogeniteit van die landskap. Daar is dus geleenthede om die diversiteit van geleedpotiges wat in wingerde voorkom te bevorder wat verdere voordele inhou vir wynproduskie. Hierdie resultate beklemtoon die waarde van die bewaring van biodiversiteit in die buffer- en oorgangsones van die KWBR en biosfeerreservate oor die algemeen.

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Chapter 1: General introduction

1.1 Global impacts of agriculture on biodiversity

The world's population continues to grow and is estimated to reach 9.7 billion people by 2050 (UN DESAPD, 2019). A growing population means a growing demand for agricultural products, with humans removing ecological boundaries and approaching the Earth's carrying capacity raising concerns about the sustainability of human-environmental systems (Henderson & Loreau, 2019) and concurrent ability of modern agricultural systems to meet global food demands.

Traditional forms of agriculture supported high levels of biodiversity (Batáry et al., 2015), but with the increase and intensification of agricultural practices in the 20th century, there has been a significant loss of natural and semi-natural areas and their associated biodiversity (Duelli & Obrist, 2003). Increasing mechanisation of agricultural practices and scaling up of production causes rapid and large structural changes in agricultural landscapes (Chamberlain et al., 2000), which in turn, become increasingly poor in natural elements (Stoate et al., 2009), causing once common farmland species to become rare or even disappear (Krebs et al., 1999). Many natural ecosystems have now been transformed to human-dominated landscape mosaics, where different land-use patterns are interspersed with heterogeneous natural patches (Tscharntke et al., 2012a). In addition, increased synthetic inputs, such as pesticides and inorganic fertilisers, result in ongoing degradation of farmland habitat quality (Cardoso et al., 2020; Desneux et al., 2007; Geiger et al., 2010; Tilman et al., 2001).

Intensified agricultural land use affects large terrestrial areas, and is the main driver of global biodiversity loss (Habel et al., 2019; Sánchez-Bayo & Wyckhuys, 2019). The unprecedented acceleration of farmland biodiversity loss (Sodhi & Ehrlich, 2010) alters species interactions across different spatial and temporal scales, which leads to a decline in ecosystem function and ecosystem services (MEA, 2005). Notwithstanding, agricultural land-use change will continue to pose significant threats to biodiversity and ecosystem services in the future (Veerkamp et al., 2020).

Historically, these trends have been most prevalent in temperate European and North American systems, most likely due to a strong geographical bias in previous studies (Archer et al., 2014; Batáry et al., 2011; De Palma et al., 2016; Tuck et al., 2014). However, current farmland expansion and intensification also severely threaten tropical, subtropical, and Mediterranean regions, often biodiversity-rich areas, which makes these systems particularly vulnerable to these impacts (Tscharntke et al., 2012b; Tuck et al., 2014). Globally, the importance of regenerating our agricultural systems is widely recognised, due to the important role that farmland can play in supporting native biodiversity (Driscoll et al., 2013), as well as an understanding of the reliance of farming on biodiversity (Altieri, 1999).

Traditional nature conservation focuses on preserving large continuous areas of original habitat where human activities are prohibited (Bengtsson et al., 2003). Due to the growing human population and subsequent expansion of agricultural areas, fragmented landscapes have become vitally important to the conservation of biodiversity (Fahrig, 2017; Fletcher et al., 2018; Resasco et al., 2017; Robinson et al., 1992; Saunders et al., 1991; Wintle et al., 2019). Low-intensity land use can contribute to the conservation of high-diversity systems, critical for successful large-scale conservation (Tscharntke et al., 2005).

1.2 Farmland conservation practices at different spatial scales

Many farmland conservation programmes are being developed that vary in spatial scale of implementation from the local field- or farm-scale to regional-scale initiatives (Batáry et al., 2015). A common local-scale practice is to move away from conventional farming towards an integrated, organic, or biological approach to farm management. Conventional farming practices typically use mineral fertilisers and synthetic pesticides to control potential pests and diseases in order to produce higher yields. However, these chemicals may negatively affect beneficial nontarget species (Vogelweith & Thiéry, 2018). In contrast, integrated farming promotes sustainable farming through using different management techniques to reduce chemical inputs (Döring et al., 2019). Organic farming uses a holistic management approach that prohibits the use of synthetic pesticides and mineral fertilisers, and puts emphasis on the use of nature-based management practices i.e. agronomic, biological, and mechanical practices, to enhance the health of agroecosystems which includes biodiversity, biological cycles, and soil biological activities (FAO, 1999).

Although assessing the conventional vs. organic farming dichotomy may reveal some general patterns of arthropod species in agroecosystems, there is a need to identify more detailed arthropod responses to individual management practices to further our understanding on how to effectively promote biodiversity (Puech et al., 2014). Another local-scale practice that is emerging as a key ecological intensification technique is farmland plant diversification (Isbell et al., 2017). Non-crop habitats within farmlands can positively influence arthropod activity (Jonsson et al., 2010; Kratschmer et al., 2019; Winter et al., 2018) through mechanisms that affect dispersal ability, availability of shelter, and alternative food sources (Anderson, 2012). Several recent reviews have emphasised the major role of non-crop vegetation for promoting above- and below-ground biodiversity and ecosystem service provisioning, as well as crop quality (Döring et al., 2019; Isbell et al., 2017; Winter et al., 2018). However, for ecological intensification to become a more feasible approach to farmers than a conventional approach, scientific studies need to address costs and benefits that are relevant to farmers. Evidence of benefits from ecological intensification on a farm scale is lacking, and farmers may be reluctant to adopt practices that are generic and that have not been tested on their specific farms (Kleijn et al., 2019).

At the farm or landscape scale, undisturbed natural and semi-natural habitat play a critical role in supporting farmland biodiversity (Bianchi et al., 2006). Although agricultural practices can be adapted to benefit in-field populations, their persistence in agroecosystems may be limited when there is insufficient potential for spillover from adjacent non-crop habitats following disturbances such as the application of agrochemicals, harvesting, and mowing (Kruess & Tscharntke, 1994). The spillover of pathogens, herbivorous, and predatory arthropods from natural to managed systems are important, and may benefit the managed system in terms of pest control, pollination, and seed dispersal (Blitzer et al., 2012). Additionally, dispersal opportunities through agricultural fields are important to ensure functional connectivity throughout the agricultural landscape (Donald & Evans, 2006).

The spillover of species from natural habitats to agricultural habitats have received much research attention (Landis et al., 2000; Macfadyen et al., 2015; Schneider et al., 2016), with far less attention to spillover patterns in the opposite direction (Blitzer et al., 2012; Rand et al., 2006). Possible negative effects of spillover in the opposite direction should be considered in order to conserve biodiversity in adjacent natural habitats along with the ecosystem services they provide (Balmford et al., 2012), and may be particularly important where remnant vegetation has high biodiversity value. Furthermore, most evidence on spillover effects are from regions where agriculture transformation occurred centuries earlier. In contrast, limited information is available on spillover patterns in biodiversity-rich landscapes where agricultural transformation is recent, and where agriculturally naïve species may be disproportionately vulnerable to transformation (Phalan et al., 2011). A broad understanding of edges between farmland and natural habitats, and practices or environmental variables that drive spillover of species across edges, may guide farm managers to manipulate on- and around-farm conditions to encourage or facilitate the movement of species among different farmland biotopes.

Many studies suggest that the composition of the surrounding habitat at larger spatial scales may influence habitat management strategies (Anderson, 2012). According to the intermediate landscape complexity hypothesis, the effectiveness of biodiversity conservation management varies depending on the landscape complexity (Tscharntke et al., 2012a), and states that species richness response to local-scale practices should increase along a sigmoid curve as landscape complexity increases. Batáry et al. (2011) found that landscape complexity moderated effects of agri-environmental management depending on the farming system, taxonomic, and functional group. Winqvist et al. (2011) found increased biodiversity of plants and birds on organic farms in all landscape contexts, but that increased biological control was only mediated on organic farms in heterogenous landscapes. This has major implications for optimising local-scale practices, especially where resources for implementation are limited. However, this hypothesis was designed for Central Europe, and this relationship may vary greatly depending on where in the world it is tested (Cormont et al., 2016). Future studies should focus on the combined effects of local management and landscape composition, especially in Asia and the southern hemisphere due to a lack of research from these regions (Winter et al. 2018).

An understanding of the effects of agriculture on biodiversity at a regional scale and over longer time periods is critical to ensure long-term resilience which, in turn, is associated with ecosystem function and services (Arnan et al., 2019; Brock et al., 2018; Caro et al., 2020; Tscharntke et al., 2012). Resilience in a system is important, as it pertains to the ability of species to recover after disturbances (Brock et al., 2018). When a species disappears from a system along with the function it contributed, the system could, as a whole, become less resilient to future disturbances (Sundstrom et al., 2012). Biotic communities inherently undergo compositional changes, but owing to anthropogenic activities, the rates of extinction and colonisation in communities are increasingly being altered, and in turn, so are patterns of biodiversity (Baeten et al., 2012).

Beta diversity is a key factor in determining broad-scale patterns of diversity and for conservation planning (Kraft et al., 2011; Socolar et al., 2016). Beta diversity may capture patterns of diversity better than measures of alpha diversity alone, as it indicates compositional changes due to local and regional filtering (Soininen et al., 2018), and can be measured along individual environmental gradients (Fitzpatrick et al., 2013). In some regions, beta diversity may be more important than alpha diversity in contributing to the total regional diversity, and the relative contribution of beta diversity to total diversity can be taxon specific (Flohre et al., 2011).

The species turnover and nestedness components of beta diversity may also be used to track patterns of biotic homogenisation across space and time (Olden & Rooney, 2006).

Trait-based functional diversity can be defined as the relative abundance, range, and dispersion of functionally meaningful traits of organisms (Gallé et al., 2019), and has a direct influence on ecosystem properties and function (Petchey & Gaston, 2006). Due to beta diversity being a useful measure of landscape- or regional-scale diversity, and functional diversity being a useful measure of ecosystem function and services (Díaz & Cabido, 2001), within a specific system assessing beta diversity alongside functional diversity at a regional scale may reveal whether agriculture has a homogenising effect on biodiversity, ecosystem function, and ecosystem services.

A major challenge for biodiversity studies in agricultural landscapes is that management practices, environmental variables, landscape context, and temporal variation create site-specific conditions (Fahrig et al., 2011; Krebs et al., 1999; Vasseur et al., 2013). Adding to this complexity is the wide range of different responses of different taxa to changes in the environment (Bruggisser et al., 2010; Pryke & Samways, 2012). These regional differences mean that trends in biodiversity response to agricultural land-use change cannot be easily extrapolated among regions (De Palma et al., 2016).

1.3 The Cape Floristic Region agricultural mosaic

Most information on agroecosystems originate from European countries, with little known of biodiversity patterns in perennial cropping systems in regions with a Mediterranean climate. For centuries, viticulture has been a dominant practice in European countries, in contrast with the more recent developments in viticultural management practices in countries such as South Africa (Li et al., 2018; Pelegrín-Borondo et al., 2019). The Cape Floristic Region (CFR) of South Africa is a region of exceptional floral diversity, in terms of local and beta diversity (Rebelo et al., 2006). It is a global biodiversity hotspot which covers an area of 90 000 km^2, and is home to about 9 383 plant species, of which about 68% are endemic (Allsopp et al., 2014; Rebelo et al., 2006). A considerable area of the CFR has been transformed to an urban-agricultural matrix of formal urban settlements (1.6%) and agriculture (25.9%), and fynbos has been impacted by invasive alien vegetation (2.6%) (Rouget et al., 2003).

In 2007, the International Coordinating Council of the UNESCO Man and the Biosphere Programme designated an area of 322 032 ha within the CFR as the Cape Winelands Biosphere Reserve (CWBR) (Figure 1.1). A biosphere reserve is representative of the natural and cultural landscape, demarcated into three inter-related zones: a natural core zone, a buffer zone, and a transition zone. The core zone is characterised by the exclusion of human pressures external to the system, while the buffer zone surrounds the core zone and permits limited recreational and agricultural activities. Around these two zones is the transition zone, which includes settlements, croplands, forestry, intensive recreation, and other economic activities. Essentially, the transition zone is where humans and nature meet and requires conservation, knowledge, and management skills in order to coexist (Biswal et al., 2013). Considering the importance of biosphere reserves as platforms for integrating conservation and economic activities, it is surprising how little research on enhancing the effectiveness of biosphere reserves is available. The major crop in the urban-agricultural matrix of the CFR is the common wine grape (*Vitis vinifera*). Around 88 366 ha of the CFR is under vine cultivation, which accounts for around 96% of South Africa's total wine grape industry (SAWIS, 2019). Within the CWBR, viticulture dominates the buffer and transition zones, highlighting the importance of managing these vineyards in a manner that will enhance their conservation potential as refuges, reservoirs, and sites of alternate resources (Landis et al., 2000; Sáenz-Romo et al., 2019; Vogelweith & Thiéry, 2017), which in turn hold biodiversity beneficial to wine production (Viers et al., 2013).

South Africa is a top wine producing country. A better understanding of how viticultural management practices enhance or threaten biodiversity and functioning in and around CFR vineyards is paramount for the support and validation of the CWBR, and for the sustainable production of wines (Viers et al., 2013). Harmonising conservation and wine production within the region should be a priority to producers, as the biodiversity here is largely irreplaceable, and the revenue generated by the wine industry is vital for the economic development of the region.

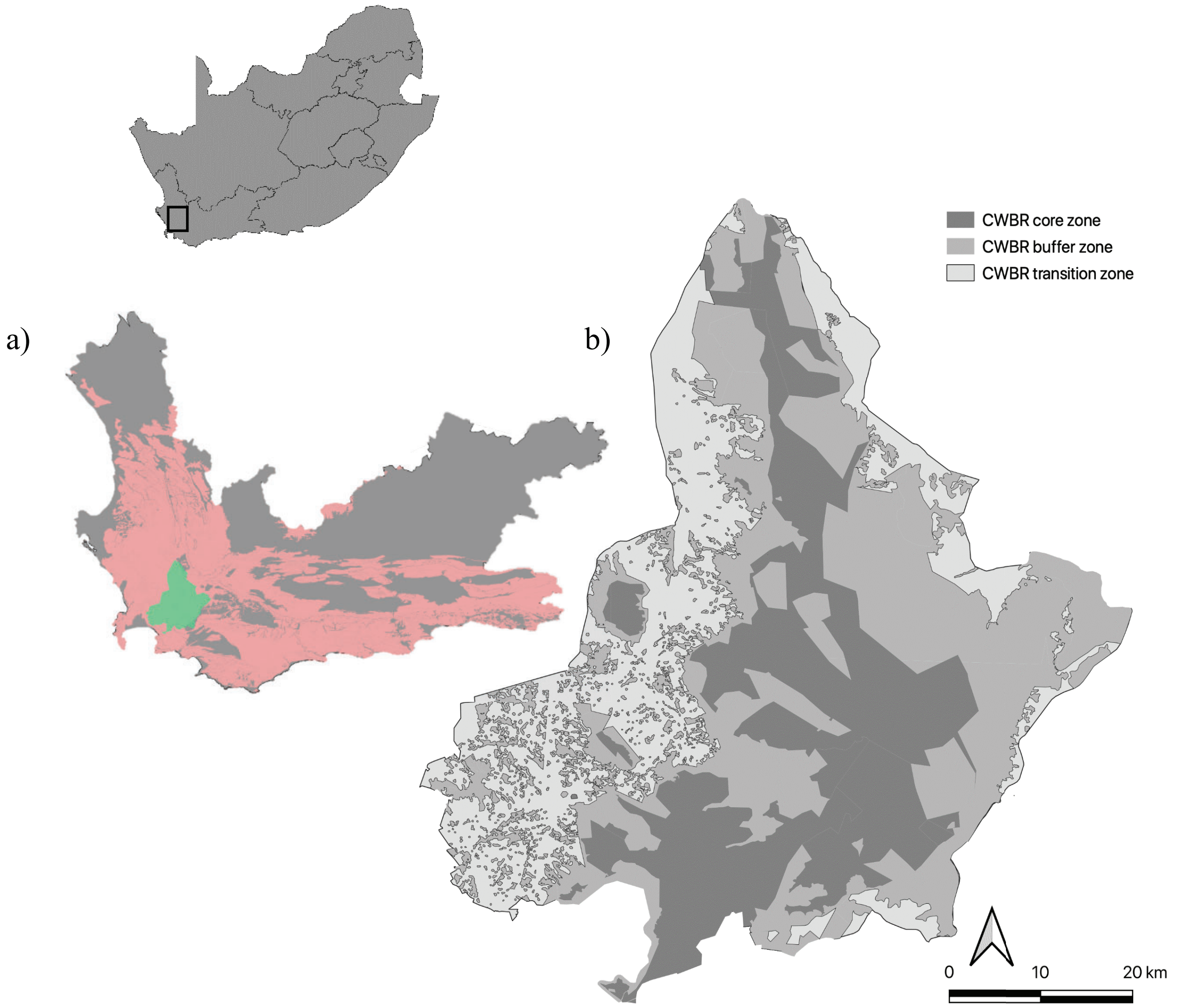

Figure 1.1: a) The Cape Winelands Biosphere Reserve's location (green) within the Cape Floristic Region (pink) of South Africa, and b) the demarcation of the three zones of the CWBR.

There are several initiatives in the South African wine industry that aim to improve sustainability and farmland conservation. Wine farms that are neither organically nor biodynamically certified within the CFR, all take part in a voluntary environmental sustainability scheme, the Integrated Production of Wine Scheme of South Africa (IPW). These farms have moved away from conventional vineyard management, and have all adopted a more integrated approach. Wine production that is compliant with the guidelines of the scheme receive certification under the jurisdiction of the Wine and Spirit Board (WSB) of South Africa. In turn, IPW certification assures consumers that the wine was produced sustainably and with integrity from the growing of the wine grapes to the final bottled product (IPW, 2020). Furthermore, stewardship initiatives that align conservation with wine production (i.e. the WWF-SA Biodiversity Champion Programme) have had major success in conserving natural habitat adjacent to vineyards, and since 2006 have protected an area of more than 112 000 ha of fynbos habitat through land sparing (Cox & Underwood, 2011). Several conservancies also exist in the CFR, and are especially common in the CWBR, where neighbouring farms in a catchment co-operate to manage natural habitat shared across farm boundaries and to streamline conservation activities. A better understanding of biodiversity response to farmland structure and management would contribute substantially to conservation management at different spatial scales.

1.4 Study organisms

Previous conservation efforts have focussed largely on birds and mammal species, with the inclusion of some charismatic insects i.e. butterflies, but more recently the general public has become aware of the importance of insects to our survival, and the massive global decline in insect diversity and abundance (Cardoso et al., 2020). Arthropods are a dominant terrestrial group in terms of their abundance and diversity (Zhang, 2011), and play an important role in the maintenance of diverse agroecosystems (Paoletti et al., 1999). They occupy a wide range of ecological niches, and show great variation in distributional, population, and dispersal traits (Kremen et al., 1993). They maintain ecosystem processes and provide important ecosystem services in agroecosystems, many of which are of major economic importance i.e. biological pest control, nutrient cycling, pollination, regulating microclimate and hydrological processes, detoxifying agrochemicals, and reducing soil erosion (Altieri, 1999; Altieri & Rogé, 2010; Anderson, 2012; Daane et al., 2018; Košulič et al., 2014; Sunderland & Samu, 2000; Wilson et al., 2017). They are an effective group to use for monitoring the effects of agricultural practices on biodiversity due to their sensitivity to disturbances (McGeoch et al., 2011; Thomson et al., 2004), their significant contribution to global biodiversity, biomass, and ecological function, and their extensive life history and behavioural diversity (Balvanera et al., 2005; Davis et al., 2001; Lu & Samways, 2002). It is due to their availability, sensitivity in responding to disturbances, and ecological importance that I use here three arthropod taxa (Araneae, Coleoptera, and Hemiptera) as focal species for my work. These three taxa were selected as they were the most abundant and speciose in samples, and represent different feeding guilds among the various species. Spiders were classified as predators. Beetles were classified as either predators, detritivores, or herbivores, based on their primary feeding mode according to Scholtz & Holm (2012). In turn, bugs belonging to one of five easily identifiable predatory Hemipteran families/subfamilies (Reduviidae, Anthocoridae, Phamatidae, Asopinae, and Nabidae) were classified as predators, with the rest being classified as herbivores. A taxonomic list for each chapter is given in Appendices A, B, C, and D. These three taxa are good bioindicators of habitat types, environmental quality, and are useful for biodiversity studies (Gerlach et al., 2013; Goulet et al., 2004; Pearce & Venier, 2006; Rainio & Niemelä, 2003). All three taxa include natural enemies of economically important agricultural pest species (Costello & Daane, 1999; Östman et al., 2001; Weibull et al., 2003).

1.5 Overall study aims

My aim here is to gain an in-depth understanding of the effect of viticultural management practices, environmental variables, and landscape composition on arthropod biodiversity from a local to a regional scale within the buffer and transition zones of the CWBR. Identifying key factors that enhance biodiversity in these vineyard-dominated landscapes and understanding how the production areas interact with the surrounding landscape to the benefit of both wine production and biodiversity conservation in the CFR. It will be a step in the right direction for the sustainable future of viticulture within the CWBR and validate the conservation potential of vineyards within the buffer and transition zones of a biosphere reserve. Furthermore, I assess whether agroecological principles in a biodiversity-rich Southern Hemisphere system, are consistent with those in better-studied regions.

1.6 Chapter aims

Chapter 2 – This chapter assesses whether a holistic farming approach or targeted individual practices are better to promote in-field arthropod diversity, which is a major gap in our knowledge about the relative biodiversity benefits of organic farming (Hole et al. 2005). In this region, organic wine farming has been identified as an important approach for promoting arthropod conservation (Gaigher & Samways, 2010, 2014; Kehinde & Samways, 2012; Reinecke et al., 2008), but no in-depth assessments have been done on the individual drivers. Here, a wide range of local vineyard management practices, environmental variables, and the overall farming approach, i.e. organic vs. integrated, were assessed to determine which factors have the strongest influence on a range of arthropods in different taxonomic groups, feeding guilds, and microhabitats in vineyards across the CWBR. This work may contribute to the implementation of more extensive viticultural management practices that can benefit on-farm biodiversity. Identifying less-intensive practices that can essentially replace intensive practices and still achieve the same production goals would be highly beneficial for the preservation of biodiversity in the context of a biosphere reserve.

I expect to find reduced arthropod diversity on farms with a more intensive management approach with regard to spray intensity, tillage frequency, and clearing of non-crop vegetation in the vineyard inter-rows. I also expect to find increased arthropod diversity on organic farms, and in vineyards that are managed more extensively i.e. integrated farms where ecological intensification is being promoted.

Chapter 3 – The aim is to identify direct drivers of bidirectional arthropod spillover among vineyards and fynbos. I assess how management practices, environmental variables, and overall farming approach affect arthropod distribution patterns across the edges between vineyards and adjacent fynbos, using species habitat fidelity as a way to interpret spillover direction. Previous work in this region has shown that certain sensitive arthropods may experience the fynbos-vineyard boundary as a hard edge (Gaigher et al., 2015), but that certain practices may enhance vineyard accessibility for arthropods (Theron et al., 2020). Environmental drivers may facilitate spillover of fynbos-associated species into vineyards, while spillover in the opposite direction are also important, especially in the context of a biosphere reserve, as crop-associated species may alter fynbos-associated arthropod population dynamics. Additionally, this work will give an indication of the degree to which vineyards might contribute to connectivity in the buffer and transition zones of a biosphere reserve.

I expect to identify management and environmental drivers that promote arthropod spillover in the fynbos-vineyard direction e.g. increased relative soil moisture and an increased presence of palatable herbaceous vegetation in vineyard inter-rows. Furthermore, I will identify drivers that promote spillover in the vineyard-fynbos direction e.g. spray and tillage intensity, and increased number of plant species in fynbos. I hypothesise that arthropod assemblage structures within the edge environment between vineyards and fynbos will be different to the assemblage structure within each of the two biotopes.

Chapter 4 – I assess the concept of the intermediate landscape complexity hypothesis within a global biodiversity hotspot, with special focus on how the proportion of natural vegetation surrounding vineyards affects the species richness and assemblage structures of three arthropod taxa within vineyards. Previous work in the CFR has indicated that bee diversity and abundance in vineyard systems is driven by the surrounding landscape complexity (Kehinde et al., 2018). I expand on this work by assessing how arthropods with different biotope associations i.e. crop-associated, fynbos-associated, or ubiquitous, respond to the landscape. Additionally, I assess interactions between landscape- and local-scale variables that may indicate possible synergistic or mediating effects of landscape complexity and on-farm complexity. This work may reveal the relevance of the intermediate landscape hypothesis in the CFR and improve management decisions based on the landscape complexity surrounding a specific vineyard, which is particularly important in the CWBR with its varying degrees of landscape transformation.

There are likely to be positive linear relationships between increased complexity in the surrounding landscape and increased arthropod diversity within vineyards, and that there will be a synergistic or mediating effect of increased landscape complexity and local management practices, i.e. increased non-crop vegetation in vineyard inter-rows, on local arthropod diversity.

Chapter 5 – Here I determine the degree to which vineyards cause biotic homogenisation in the buffer and transition zones of a biosphere reserve. I assess the alpha, beta, and functional diversity of two arthropod taxa, and compare how patterns of these diversity measures differ between vineyards and fynbos on a regional scale. Additionally, I determine which species-specific traits drive assemblage structures among vineyards and fynbos. This work contributes towards furthering our understanding of the factors associated with viticulture that may drive biotic homogenisation, and in turn the provisioning of ecosystem services and resilience within vineyard systems. Due to the hyper-diversity associated with fynbos, higher alpha, beta, and functional diversity of arthropods in fynbos is more likely when compared to vineyards. Additionally, I expect to find species-specific traits that drive different assemblage structures of arthropods within each of the two biotopes.

With the information from these chapters, I aim to make recommendations for the IPW programme for improved biodiversity conservation while still optimising wine production. Furthermore, I also intend to provide recommendations on how the CWBR, and even biosphere reserves in general, might benefit from instigating improved management options that stem from this research.

1.7 References

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Chapter 2: Diverse herbaceous cover crops promote vineyard arthropod diversity across different management regimes

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2.1 Abstract

Agricultural intensification threatens biodiversity, requiring a shift to agroecological farming. Identifying locally-specific management practices that can effectively enhance biodiversity can help guide farmland conservation efforts. We assess the effect of management practices and environmental variables on arthropod diversity under varying vineyard management regimes in a South African biosphere reserve. We also determine whether the implementation of these practices and their combined effect on arthropods differ between integrated and organic vineyards. Arthropod morphospecies richness and evenness were assessed for different taxonomic groups (spiders, beetles, and true bugs), in different positions in the crop (ground level, on cover crops, and on vine foliage) and for different feeding guilds (herbivores, detritivores, and predators). Percentage herbaceous vegetation cover had a consistent positive effect on morphospecies richness across taxa, microhabitats, and guilds. Other vegetation-related variables, such as volume of plant litter, plant species richness, and plant height positively influenced several of the biodiversity responses. We did not detect any negative effect of agrochemicals used in an integrated approach, or a strong effect of overall farming approach (organic vs. integrated) on the species richness or evenness of any of the focal taxa, sampled positions, or guilds. These results indicate that the maintenance of dense and diverse cover crops is a strategic way to enhance vineyard arthropod diversity where other management practices are already implemented sensitively. This highlights that minimal adjustment of management practices can greatly benefit farmland biodiversity conservation and is in keeping with the ethos of the concept of a biosphere reserve.

Keywords: Arthropod conservation, agrochemicals, biodiversity-friendly farming, biosphere reserve, non-crop vegetation, vineyards.

2.2 Introduction

Intensive agriculture is one of the greatest global threats to arthropod biodiversity (Cardoso et al., 2020; Habel et al., 2019; Sánchez-Bayo & Wyckhuys, 2019). Declines in arthropod diversity and abundance due to conventional agricultural intensification significantly impact the functioning of ecosystems (Biesmeijer et al., 2006). In addition, intensification threatens the sustained productivity of farming systems due to the loss of vital arthropod-mediated ecosystem services (Geiger et al., 2010; Losey & Vaughn, 2006; Potts et al., 2010). Growing concern over the consequences of intensive agriculture has motivated the adoption of a wide range of agroecological farming methods worldwide (Batáry et al., 2015; Klein et al., 2011). These approaches generally aim to reduce agronomic disturbances (Mäder et al., 2002, Zehnder et al., 2007), and to preserve natural and resource-rich farmland habitat (Batáry et al., 2015), thereby enhancing farmland habitat quality.

Although the value of a landscape-scale approach to farmland conservation has been emphasised (Gonthier et al. 2014; Tscharntke et al., 2012), an important component is to improve conditions in the cultivated areas (Alignier et al., 2020; Donald & Evans, 2006). Various field-scale management interventions can effectively promote in-field arthropod diversity. Prominent examples include the conservation and diversification of non-crop vegetation (Isbell et al., 2017; Lichtenberg et al., 2017), reduced agrochemical use (Bommarco et al., 2011; Geiger et al., 2010), reduced tillage intensity (Rowen et al., 2020), and crop type diversification (Alignier et al., 2020; Fahrig et al., 2011). However, the efficacy of these methods depends on characteristics of the local context, which means that tailored strategies are needed for agroecosystems in different settings (Cunningham et al., 2013; Tscharntke et al., 2012). Identification of locally relevant practices that promote biodiversity could provide valuable guidance to farmland conservation efforts. Measures that are feasible to farmers and that can be applied without major changes to overall farming strategy may be most easily adopted (Sattler & Nagel, 2010; Sutherland, 2010), and may be particularly important in production systems where large-scale adaptations are challenging.

The biodiversity benefits of holistic approaches such as organic farming have been widely demonstrated (Bengtsson et al., 2005; Hole et al., 2005; Letourneau & Bothwell, 2008; Tuck et al., 2014). In organic crops, a combination of biodiversity-friendly practices is applied simultaneously, including avoidance of agrochemicals and synthetic fertilisers, and a range of regenerative practices that aim to improve agroecosystem resilience. It has been proposed that the combination of complementary practices generates the greatest positive environmental effects, and that it may also have synergistic effects, i.e. positive effects over and above the additive effects of individual practices (Hole et al., 2005; Rigby & Caceres, 2001). However, the relative biodiversity benefit of a holistic strategy over carefully targeted individual practices is largely untested (Hole et al., 2005). Most comparative studies to date have taken a binary approach to classifying farms as either organic or non-organic, based on whether farms are formally certified. Yet, few studies have attempted to tease apart the effects of individual management practices (but see Gosme et al., 2012; Marliac et al., 2016; Puech et al., 2014), which could be influential in view of the diversity of farming practices that can occur within a given farming approach (Vasseur et al., 2013).

There has been substantial research on the effectiveness of different agroecological practices, mostly in Western European and North American systems (Batáry et al., 2015; Winter et al., 2018). But knowledge on the performance of these practices is limited for less studied regions, such as tropical, subtropical, and Mediterranean regions (Kleijn et al., 2003; Tuck et al., 2018).

The Cape Floristic Region (CFR) of South Africa is a Mediterranean-type ecosystem and a global biodiversity hotspot (Mittermeier et al., 2004). The region supports an exceptional diversity of endemic plants (Goldblatt & Manning, 2000; Manning & Goldblatt, 2012), and with arthropod diversity appearing to match that of plant diversity (Janion-Scheepers et al., 2020; Kemp & Ellis, 2017; Proçhes & Cowling, 2006). However, the CFR is challenged by considerable transformation to agriculture (Cowling et al., 2003), with vineyards covering around 88 366 ha in the CFR (SAWIS, 2019). Globally, there is a trend for vineyard intensification, but vineyards also have the potential to support high levels of biodiversity (Isaia et al., 2006; Paiola et al., 2020). Understanding the factors that create favourable conditions for biodiversity in vineyards would contribute substantially to conservation in vineyard-dominated landscapes.

Most South African wine farms comply with international wine industry sustainability criteria through the Integrated Production of Wine Scheme of South Africa (IPW) certification (http://www.ipw.co.za). Although conventional agrochemical use is permitted, it is used cautiously and in combination with non-chemical plant protection measures. A limited number of CFR vineyards have received organic certification (Duminy, 2004; Kelly & Metelerkamp, 2015). However, previous studies in the region have demonstrated the significant potential of organic vineyard management for enhancing biodiversity, which has been linked to higher non-crop plant diversity and lower management intensities on organic farms than on integrated farms (Gaigher & Samways, 2010; 2014; Kehinde & Samways, 2012). As these studies focused on the contrast between organic and non-organic management approaches, farms were selected to maximise differences between management regimes. This work has not yet been expanded to include approaches along the whole management spectrum at a larger spatial scale.

Here, we assess the effect of various management practices on arthropod diversity in vineyard agroecosystems, within the boundaries of a CFR biosphere reserve, the Cape Winelands Biosphere Reserve (CWBR). We also determine how the implementation of these practices and their combined effect on arthropod diversity differ between integrated and organic vineyards, to assess whether there is added benefit of an organic approach compared to sensitive management practices applied within an integrated farming framework. In addition to species richness, we consider evenness, because species-abundance relationships in communities can greatly influence agroecosystem functioning (Crowder et al., 2010) and resilience to disturbance (Wittebolle et al., 2009). As different taxa respond differently to disturbances (Bengtsson et al., 2005; Birkhofer et al., 2014), and responses may also differ between trophic levels (Bruggisser et al., 2010) and among microhabitats within perennial crops (Shapira et al., 2018), we assess responses of different subsets of the arthropod assemblage to determine whether the patterns are consistent across different groups. In particular, we test whether responses differ between a) dominant taxonomic groups (spiders, beetles, and true bugs), b) crop positions (on the ground, on the cover crop, and on the vine foliage), and c) functional feeding guilds (predators, herbivores, and detritivores).

2.3 Materials and methods

2.3.1 Study sites and sampling design

Our study locations in the CFR were primarily in the buffer and transition zones of the UNESCO-designated CWBR, where vineyards are the dominant crop. Biosphere reserves aim to integrate conservation and sustainable development, and are implemented through a zonation system of different land-use intensities, with core protected zones, transition zones where sustainable land use is practiced and intermediate buffer zones (Pool-Stanvliet & Giliomee, 2013). Farms were selected to represent a wide range of management practices and localities throughout the CWBR (Figure 2.1). A total of 40 vineyard blocks were sampled, spread across 18 commercial wine farms. Although certain management practices were consistent among vineyard blocks occurring on the same farm (insecticide and herbicide application), other practices (tillage intensity and fungicide application) and environmental variables varied among vineyards on the same farm. Individual vineyard blocks were therefore considered independent, and the nestedness within farm was accounted for statistically. Vineyard blocks ranged in size from 1 to 14.4 ha. Eleven of the 40 vineyards were located on five organically certified farms, with mean vineyard block sizes of 2.82 ha. Organic farms were certified by Ceres (http://www.ceres-cert.com), Demeter (http://www.demeter.net), or Ecocert (http://www.southafrica.ecocert.com). The remaining 29 vineyard blocks were spread across 13 integrated farms that all operate under the IPW scheme, with mean vineyard block sizes of 4.21 ha. Where more than one vineyard block was selected on a single farm, the vineyard blocks were spaced >170 m apart to ensure statistical independence, with a maximum distance of 1360 m between vineyard blocks on a single farm. Sampling was conducted >20 m from the vineyard edge to minimise edge effects. Sampling was undertaken over two seasons, May 2016 (autumn, post-harvest), and October 2016 (spring, early in the growing season during fruit set).

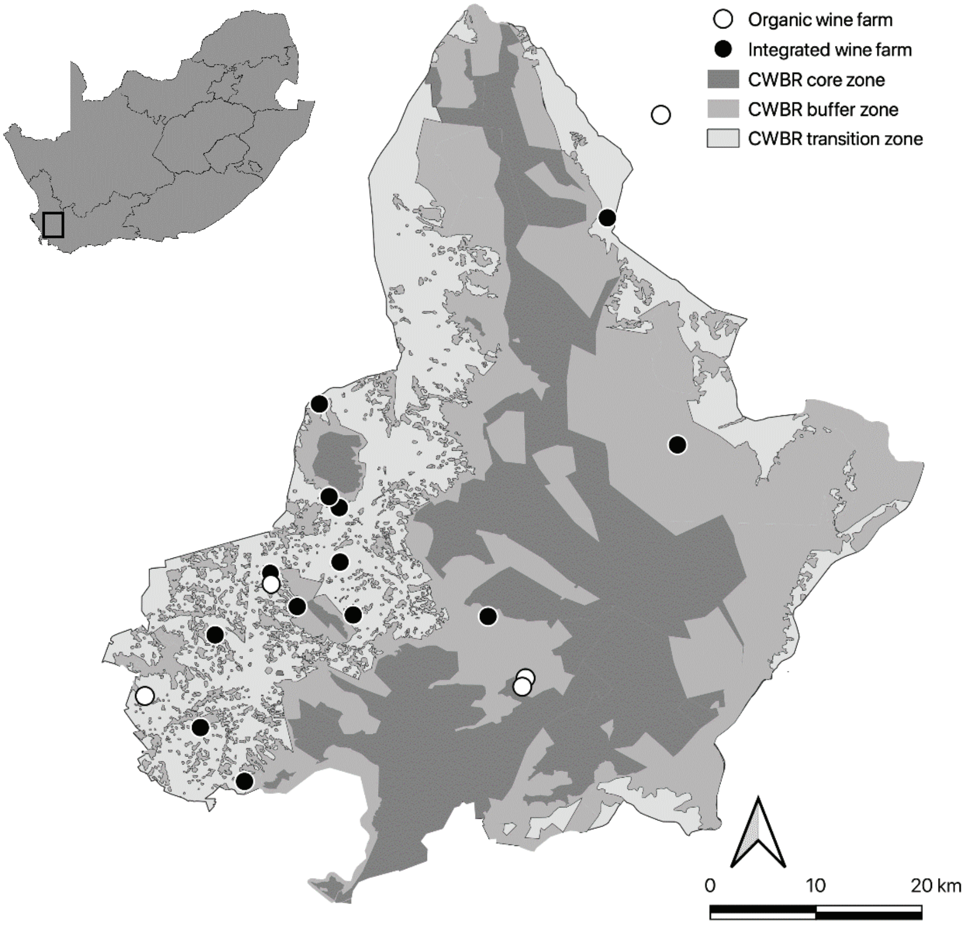

Figure 2.1: Locations of the organic and integrated wine farms across the Cape Winelands Biosphere Reserve in South Africa.

2.3.2 Arthropod collection

At each vineyard, arthropods were sampled in three crop positions: on the soil surface, on the cover crops, and on the vines. Ground-dwelling arthropods were collected using four pitfall traps (300 ml plastic jar with a 6 cm diameter opening) in each vineyard (Woodcock, 2005). Each pitfall trap was prepared with 200 ml of 75% ethylene glycol solution with two added drops of detergent to break the surface tension. At each vineyard, four pitfalls, one at each corner of a 1

m^2 quadrat, were sunk into the ground until the brim of the trap was level with the soil surface. Two of the pitfalls were positioned in the inter-row, and two in the vine row. Pitfalls were left open for one week per season. Samples were washed with water and preserved in 75% ethanol for later sorting and identification.

Arthropods on cover crops and vines were collected using a vacuum sampler (Swart et al., 2017). A Stihl SH56C-E vacuum shredder was used as vacuum sampler by attaching a 30 cm-long fine mesh bag onto the 10 cm diameter opening of the vacuum pipe. One sample consisted of two hundred insertions of the vacuum pipe into the vegetation along a walked transect in each vineyard. Each cover crop sample was taken within a single inter-row, < 10 m away from either side of the pitfall trap array, whereas each vineyard sample was split equally across two vine rows on either side of the pitfall trap array, < 10 m away from the pitfall traps. Each sample was stored in a plastic bag at -10°C for later sorting and identification. Where cover crops or vine foliage were absent due to management practices or seasonal variation, the vacuum pipe was brought close to the soil surface in the inter-row, or pushed onto the vine so as to remain consistent with sampling effort throughout the sampling period.

Spiders (Araneae), beetles (Coleoptera), and true bugs (Hemiptera) were extracted from samples. We focused on these taxonomic groups because they were the most abundant and speciose taxa in the samples. In addition, they represent a range of feeding guilds and would potentially vary in their responses to environmental variables. All specimens were initially assigned to morphospecies (Oliver & Beattie, 1996), and then identified to the finest taxonomic level possible. Adult spiders were identified to genus level, and where possible to species level by a taxonomic expert (Prof. A. Dippenaar-Schoeman, Agricultural Research Council). Juvenile spider identification is challenging, and therefore any juveniles that could not be identified to species level, or for which the accurate morphospecies classification could not be confirmed, were excluded from the dataset to prevent overestimation of species richness. Excluded juvenile spiders represented 12% of the original total spider abundance. Juveniles included in data analysis represented 33% and 34% of total spider morphospecies richness and abundance, respectively. Beetle morphospecies were assigned to family level by a taxonomic expert (Prof. F. Roets, Stellenbosch University). For bugs, morphospecies data were used in analyses due to a lack of taxonomic expertise.

All specimens were classified into one of three functional feeding guilds, namely detritivores, herbivores, and predators. All spiders were classified as predators. Beetle guild classification was based on the primary feeding mode at family level according to Scholtz & Holm (2012). Five bug families/subfamilies that are commonly sampled in the region, Reduviidae, Anthocoridae, Phymatidae, Asopinae, and Nabidae are primarily predatory, and morphologically easily recognisable (Scholtz & Holm 2012). Morphospecies belonging to any of these groups were classified as predators, and the remaining morphospecies were classified as herbivores without family level identifications, as most other bug taxa in the region are herbivorous (Scholtz & Holm 2012). Although there may be some exceptions where taxa within families vary in feeding mode, this classification should be accurate for most morphospecies. Spider reference specimens are kept in the National Collection of Arachnida in the National Museum, Pretoria, and beetle and bug specimens in the Stellenbosch University Entomological Museum.

2.3.3 Environmental variables

During each sampling event, environmental variables were recorded in two 1 m^2 quadrats in each vineyard, close to where arthropod sampling occurred. One quadrat was placed in the vine row, and one in the inter-row. Within each quadrat, we recorded the average of three soil moisture and pH measurements taken with a Yieryi VT-05 soil detector, as well as the average of three soil compaction measurements, taken with a DICKEY-john soil compaction tester. In addition, we estimated volume of plant litter, which consisted of all plant litter originating from the vines and cover crops within each quadrat compacted into a measuring jug. Furthermore, in each quadrat we measured average vegetation height, counted the number of plant species (mostly a mixture of spontaneous cosmopolitan weed species i.e. *Hypochaeris radicata*, *Plantago lanceolata*, and *Oxalis* species, and sown cover crops i.e. triticale and legumes), and visually estimated the percentage herbaceous vegetation and grass cover within the quadrats. Environmental data for the two quadrats in each vineyard were averaged for each site.

To account for possible effects of landscape context, the composition of the surrounding landscape in a 1 km radius around the centre of each site was quantified by digitizing land cover based on a raster layer of South Africa which was compiled by National Geo-spatial Information (http://www.ngi.gov.za) under the Department of Rural Development and Land Reform. The layer was compiled by means of satellite imagery and surface reflectance data products with Landsat 8 OLI/TIRS Level-2 at a spatial resolution of 30 m. Total area for each class in the buffer was calculated using zonal statistics in the GIS application CapeFarmMapper, a product of the Western Cape Department of Agriculture (https://gis.elsenburg.com/apps/cfm/). Classes were natural/semi-natural vegetation, cultivated areas, water bodies and infrastructure. Total area of natural/semi-natural vegetation was used as a measure of landscape complexity for each site, as it was highly negatively correlated with total cultivated area (Spearman's R = -0.81), and both measures have been used extensively in the literature to represent landscape complexity.

2.3.4 Management variables

Management data for each farm was collected for the 2015/2016 season for each sampled vineyard. Each farm made available their insecticide, herbicide, and fungicide application records, as well as information on tillage frequency and method. Most inputs were applied early in the growing season (September-January), except for herbicides which were applied primarily during the winter period (July-August). Tillage was done between May and September. To standardise the different application rates of insecticides, herbicides, and fungicides applied between vineyards, chemical compounds were first coded according to the South African IPW scheme's Integrated Production (IP) coding of all products (products used by the focal vineyards are listed in Appendix E). Chemicals are categorised by IPW into low risk (1), medium risk (2), medium to high risk (4), and high risk (8) (http://www.ipw.co.za). IPW assigns risk codes to agrochemicals based on human health and safety risks, as well as numerous laboratory and field toxicology tests (typically LC50, LD50, EC50, or IOBC and OEPP/EPPO classifications). The risks pertain to the impact of an agrochemical on the environment (water and soil) and organisms (avian, fish, aquatic organisms, and soil organisms), and impact on beneficial insects (bees, wasps, predatory mites, beetles, and lacewings). A ratio was calculated for spray intensity by dividing the amount of a chemical used (L ha^{-1}) into the registered dosage (L ha^{-1}) for each chemical applied (http://www.ipw.co.za). A score (a) was then calculated for each of the chemicals applied to each vineyard by multiplying the IP code (b), the intensity ratio (c) and the total number of applications (d) for the 2015/2016 season ($a = b \times c \times d$). Scores ranged from 0 to 253.33 for insecticides, from 0 to 25.16 for herbicides, and from 0 to 358.95 for fungicides.

Similarly, tillage intensity across farms were standardised using frequency of tilling per season and whether the implement used inverted the soil profile. The total number of tilling events for the 2015/2016 season for each vineyard was multiplied by either 1 (where the soil profile was not inverted) or by 2 (where the soil profile was inverted, due to the greater disturbance effect of inversion tillage (Soane et al. 2012)). Tillage category ranged from 0 to 6.

2.3.5 Statistical analyses

It was not possible to obtain information on the exact timing of management practices for all vineyards, and thus we were unable to relate seasonal differences in management practices to our seasonal arthropod data. We therefore used the overall management scores for the 2015/2016 period, together with environmental data averaged over the two sampling events and arthropod data pooled for the two sampling events to assess the relationships across the study period.

All analyses were done using R version 3.6.3 (R Core Team, 2018). The effect of individual variables and that of overall farming regime was assessed in separate modelling procedures to prevent the exclusion of potentially influential variables that may be strongly associated with a farming regime. Model selection was used to determine the effect of individual environmental and management variables on arthropod morphospecies richness and evenness of the overall assemblage (the sum of the three focal taxonomic groups), as well as richness and evenness partitioned into the three taxonomic groups, the three microhabitats, and the three feeding guilds. Evenness was calculated as Simpson's inverse index, using the *vegan* package (Oksanen et al., 2018). Correlated explanatory variables were identified by comparing Spearman's rho rank correlation coefficients using the *Hmisc* package (Harrell, 2018). The cut-off r_s value for identifying correlated explanatory variables was 0.6 or -0.6. Soil pH was excluded from statistical analyses as it was correlated with soil moisture ($r_s = -0.75$). Soil moisture was selected to remain in the models, as it is more easily interpretable in terms of its potential effect on arthropods. A total of 12 explanatory variables were included in the models: soil compaction, soil moisture, volume of plant litter, vegetation height, number of plant species, percentage herbaceous vegetation cover, percentage grass cover, fungicide score, herbicide score, insecticide score, tillage category, and percentage natural/semi-natural habitat in the surrounding landscape. Soil compaction, soil moisture, and volume of plant litter were omitted from analyses associated with the vine microhabitat as these variables were not relevant to the vine microhabitat. All explanatory variables were scaled before model selection.

Linear mixed-effects models (LMMs) were created for response variables with a normal distribution (all morphospecies richness responses) and generalised linear mixed-effects models (GLMMs) with a binomial link function were created for response variables with a binomial distribution (all evenness responses, as these were proportional data) (Bolker et al. 2009; Zuur et al. 2009) in the *lme4* package (Bates et al., 2015). Normality was assessed with Shapiro-Wilks tests. Spatial autocorrelation was tested for using the Mantel test in the *ade4* package (Dray & Dufour, 2007). To account for spatial autocorrelation and the nested study design, farm identity was included as a random spatial variable in all models. Variance components of the candidate LMMs were estimated with maximum likelihood estimation to enable model comparisons (Zuur et al. 2009). Model selection was done using forward selection, and all models including the null model were ranked using the second-order Akaike information criterion (AIC_c) (Burnham & Anderson, 2002) in the *AICcmodavg* package (Mazerolle, 2017). Statistical significance of each variable in the best fit model was calculated using Type II Wald chi-square tests.

LMMs for morphospecies richness responses and GLMMs for evenness responses were fitted in the *lme4* package to test for the effect of farming approach on overall arthropod morphospecies richness and evenness, as well as richness and evenness partitioned into the three taxa, the three microhabitats, and the three functional feeding guilds. In addition, LMMs were created to test whether management and environmental variables differed between organic and integrated vineyards. These models all included overall farming approach (organic vs. integrated) as fixed factor and farm identity as random variable. Statistical significance was calculated using Type II Wald chi-square tests.

2.4 Results

A total of 21 151 arthropod individuals from 486 morphospecies were sampled. In terms of abundance, true bugs dominated the assemblages, while for morphospecies richness, beetles were the dominant taxonomic group (Appendix F). A total of 218 beetle morphospecies, 156 true bug morphospecies and 112 spider morphospecies were sampled. Herbivores were the most speciose feeding guild with 226 morphospecies, followed by 210 predator morphospecies, and 50 detritivores morphospecies. On the soil surface 316 morphospecies were sampled, 272 from the cover crops, and 159 from the vine foliage. The taxonomic list with assignment of morphospecies to feeding guilds is in Appendix A.

Of the environmental variables influencing morphospecies richness, herbaceous vegetation cover was important in all models, and had a consistent significant positive effect on morphospecies richness of the overall assemblage, as well as all the taxonomic groups, microhabitats, and feeding guilds (Table 2.1). Amount of plant litter was also frequently included in models, and positively influenced morphospecies richness of overall arthropods, true bugs, arthropods on the cover crops, and herbivores (Table 2.1). Percentage grass cover positively influenced arthropods on the vine foliage, and plant species richness positively influenced spider morphospecies richness. Soil moisture negatively influenced arthropods on the soil surface, and soil compaction positively influenced spiders (Table 2.1). No effect was detected for any of the agrochemical inputs, tillage, or surrounding landscape complexity on morphospecies richness.

Evenness of true bugs, herbivores, and predators were positively influenced by non-crop vegetation height (Table 2.2). Non-crop plant species richness positively influenced evenness of beetles and soil surface arthropods (Table 2.2). Soil compaction positively influenced spider evenness. Beetle and true bug evenness responded positively to soil moisture, whereas spider evenness showed a negative response to soil moisture (Table 2.2). Herbicide intensity positively influenced beetle evenness, and tillage intensity positively influenced detritivore evenness (Table 2.2).

The type of agrochemical inputs differed between farming regimes (Appendix E). Integrated vineyards received a broader range of synthetic inputs, primarily fungicides, with a lower number of herbicides and insecticides. Organic vineyards received only fungicides permitted within the organic certification schemes. However, the toxicity scores for most inputs across all vineyards were low, and variation between vineyards was high, as seen in the high standard deviations of the means (Table 2.3). Consequently, the only variable that differed significantly was herbicide intensity, which was higher in integrated vineyards (Table 2.3). Environmental variables also varied greatly across all vineyards, and there were no statistically significant differences. An overall farming approach (organic or integrated) had no influence on any of the morphospecies richness or evenness responses (Table 2.4).

Table 2.1: Test statistics from model selection showing the effect of management and environmental variables on arthropod species richness based on LMMs. Signs in brackets after the chi-square values indicate the direction of the relationship. (Compact = soil compaction, SMoist = soil moisture, Litter = plant litter, Height = plant height, PlantSp = plant species richness, HerbVeg = herbaceous plant cover, Grass = grass cover, Herbic = herbicide intensity, Insectic = insecticide intensity, Fungic = fungicide intensity, Tillage = tillage intensity, Landscape = landscape complexity).

	All arthropods	Taxonomic group			Microhabitat			Feeding guild		
		Spiders	Beetles	True bugs	Soil surface	Cover crop	Vine	Detritivores	Herbivores	Predators
Compact	—	20.27 (+)	—	—	—	—	—	—	—	—
SMoist	—	—	—	—	5.21 (-)	—	—	—	—	—
Litter	5.61 (+)	—	—	10.75 (+)	—	11.90 (+)	—	—	14.90 (+)	—
Height	—	—	—	—	—	—	—	—	—	—
PlantSp	—	9.6 (+)	—	—	—	—	—	—	—	—
HerbVeg	17.00 (+)	14.66 (+)	7.36 (+)	7.94 (+)	10.54 (+)	10.41 (+)	4.60 (+)	6.46 (+)	13.13 (+)	6.86 (+)
Grass	—	—	—	—	—	—	9.19 (+)	—	—	—
Herbic	—	—	—	—	—	—	—	—	—	—
Insectic	—	—	—	—	—	—	—	—	—	—
Fungic	—	—	—	—	—	—	—	—	—	—
Tillage	—	—	—	—	—	—	—	—	—	—
Landscape	—	—	—	—	—	—	—	—	—	—

Conditional R^2 values for mixed models are given per response variable: All arthropods (0.80), Spiders (0.71), Beetles (0.66), True bugs (0.70), Soil surface (0.70), Cover crop (0.86), Vine (0.41), Detritivores (0.58), Herbivores (0.79), and Predators (0.77).

Table 2.2: Test statistics from model selection showing the effect of management and environmental variables on Inverse Simpson's evenness based on GLMMs. Signs in brackets after the chi-square values indicate the direction of the relationship. (Compact = soil compaction, SMoist = soil moisture, Litter = plant litter, Height = plant height, PlantSp = plant species richness, HerbVeg = herbaceous plant cover, Grass = grass cover, Herbic = herbicide intensity, Insectic = insecticide intensity, Fungic = fungicide intensity, Tillage = tillage intensity, Landscape = landscape complexity).

	All	Taxonomic group			Microhabitat			Feeding guild		
	arthropods	Spiders	Beetles	True bugs	Soil surface	Cover crop	Vine	Detritivores	Herbivores	Predators
Compact	__	6.97 (+)	__	__	__	__	__	__	__	__
SMoist	__	5.22 (-)	4.47 (+)	3.19 (+)	__	__	__	__	__	__
Litter	__	__	__	__	__	__	__	__	__	__
Height	__	__	__	1.91 (+)	__	__	__	__	5.26 (+)	4.61 (+)
PlantSp	__	__	6.72 (+)	__	5.94 (+)	__	__	__	__	__
HerbVeg	__	__	__	__	__	__	__	__	__	__
Grass	__	__	__	__	__	__	__	__	__	__
Herbic	__	__	2.62 (+)	__	__	__	__	__	__	__
Insectic	__	__	__	__	__	__	__	__	__	__
Fungic	__	__	__	__	__	__	__	__	__	__
Tillage	__	__	__	__	__	__	__	6.06 (+)	__	__
Landscape	__	__	__	__	__	__	__	__	__	__

Conditional R^2 values for mixed models given per response variable: Spiders (0.44), Beetles (0.50), True bugs (0.47), Soil surface (0.55), Detritivores (0.45), Herbivores (0.39), and Predators (0.55).

Table 2.3: Means and standard deviations of environmental and management variables in organic and integrated vineyards, and Wald χ^2 value from LMMs testing for the effect of management regime. Values in bold indicate significant differences at $P < 0.05$. Number of vineyards included = 11 organic, 29 integrated, number of farms included = 5 organic, 13 integrated.

Variables	Variable details	Organic vineyards	Integrated vineyards	Wald χ^2
Soil compaction	Continuous, measured as pound force per square inch	238.99 ± 59.54	218.86 ± 61.05	0.58
Soil moisture	Continuous, relative unitless measure	5.33 ± 1.61	4.32 ± 1.82	0.96
Soil pH	Continuous, relative scale	6.49 ± 0.21	6.62 ± 0.21	1.39
Volume plant litter	Continuous, measured as millilitre	613.86 ± 408.22	956.34 ± 579.35	1.82
Vegetation height	Continuous, measured in centimetres	33.06 ± 10.87	41.14 ± 7.80	3.6
Plant species richness	Continuous, number of dominant species	4.77 ± 0.95	4.44 ± 0.91	0.93
Herbaceous vegetation cover	Continuous, measured as percentage cover	13.60 ±12.42	10.37 ± 10.30	0.65
Grass vegetation cover	Continuous, measured as percentage cover	40.22 ± 26.15	32.36 ± 21.19	0.48
Fungicide intensity score	Continuous, relative unitless measure	159.13 ±115.31	192.17 ± 61.46	0.89
Herbicide intensity score	Continuous, relative unitless measure	0.00 ± 0.00	7.60 ± 8.89	**6.78**
Insecticide intensity score	Continuous, relative unitless measure	0.00 ± 0.00	23.87 ± 64.70	0.69
Tillage intensity score	Continuous, relative unitless measure	3.09 ± 1.81	2.76 ± 1.68	0.13
Landscape complexity	Continuous, natural and semi-natural vegetation cover in a 1 km radius around each site in ha	111.99 ± 78.92	99.63 ± 43.87	0.2

Table 2.4: Test statistics from LMMs on the effect of the overall farming approach (organic or integrated) on arthropod morphospecies richness and evenness.

	Morphospecies richness		Evenness	
Response variable	χ^2	P	χ^2	P
Overall arthropods	0.01	0.97	0.01	0.91
Microhabitat				
Soil surface	0.56	0.46	0.66	0.41
Cover crop	0.61	0.44	3.15	0.07
Vine	0.01	0.90	0.04	0.84
Taxa				
Spiders	1.65	0.20	0.19	0.66
Beetles	0.23	0.63	0.23	0.63
True bugs	0.03	0.87	1.67	0.20
Feeding guild				
Detritivores	0.85	0.36	0.05	0.82
Herbivores	0.05	0.82	0.97	0.32
Predators	0.35	0.55	2.36	0.12

The visualisation of the individual data points shows that the variation among arthropod richness and evenness responses of overall arthropods, the three taxonomic groups, microhabitats, and feeding guilds in vineyards is high, even within the same management regime (Figures 2.2-2.5).

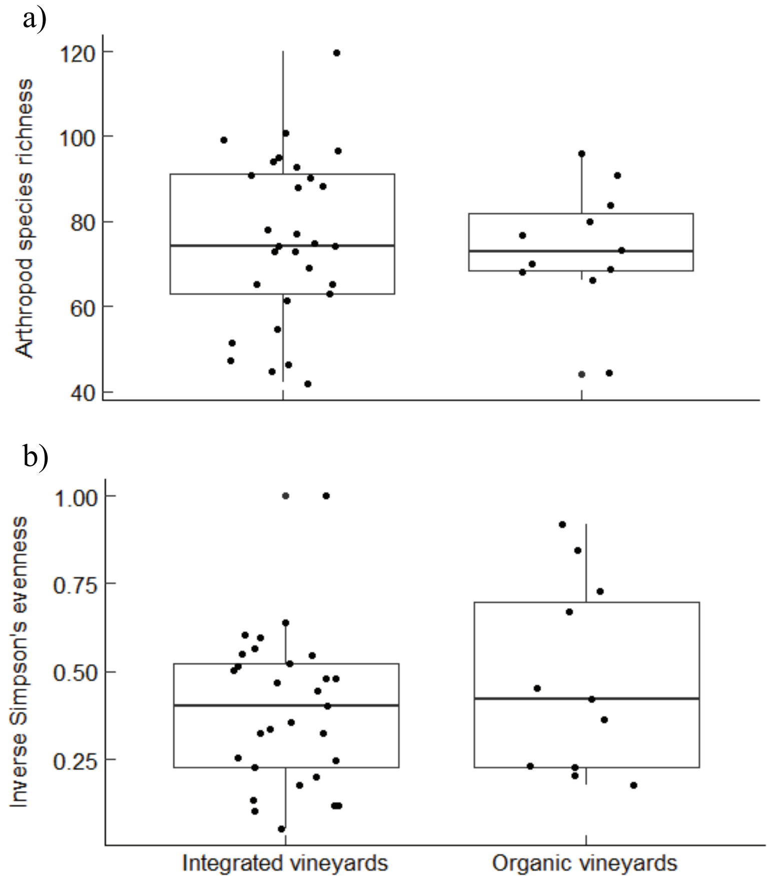

Figure 2.2: a) Morphospecies richness and b) evenness of overall arthropods in integrated and organic vineyards, with jittered points showing the values for individual vineyards.

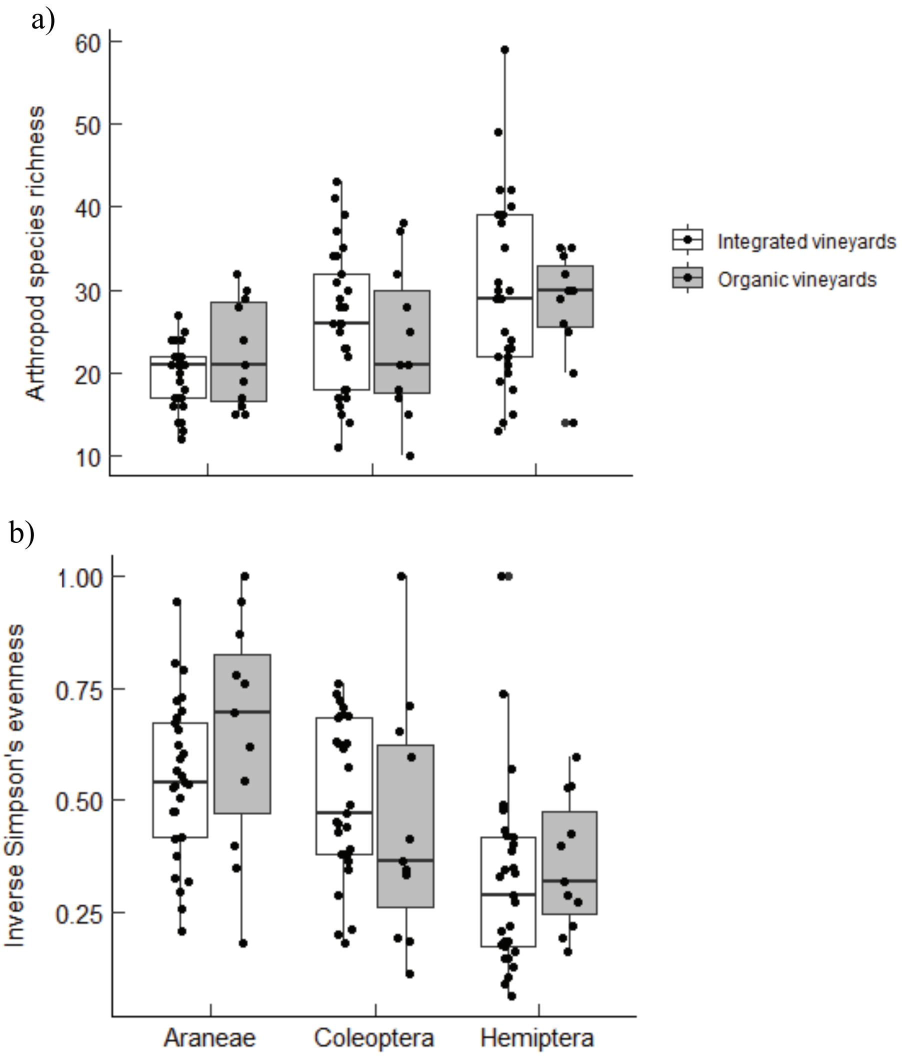

Figure 2.3: a) Morphospecies richness and b) evenness of the three arthropod taxonomic groups in integrated and organic vineyards, with jittered points showing the values for individual vineyards.

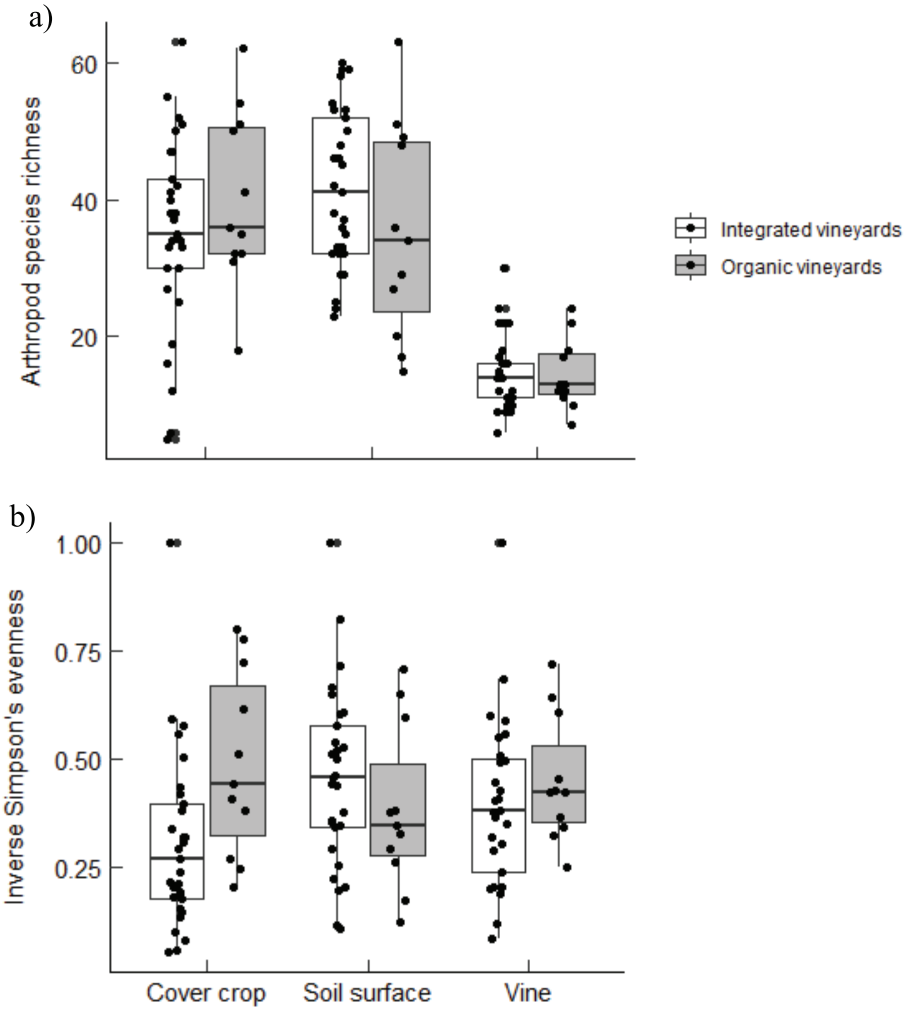

Figure 2.4: a) Morphospecies richness and b) evenness of arthropods in the three crop positions in integrated and organic vineyards, with jittered points showing the values for individual vineyards.

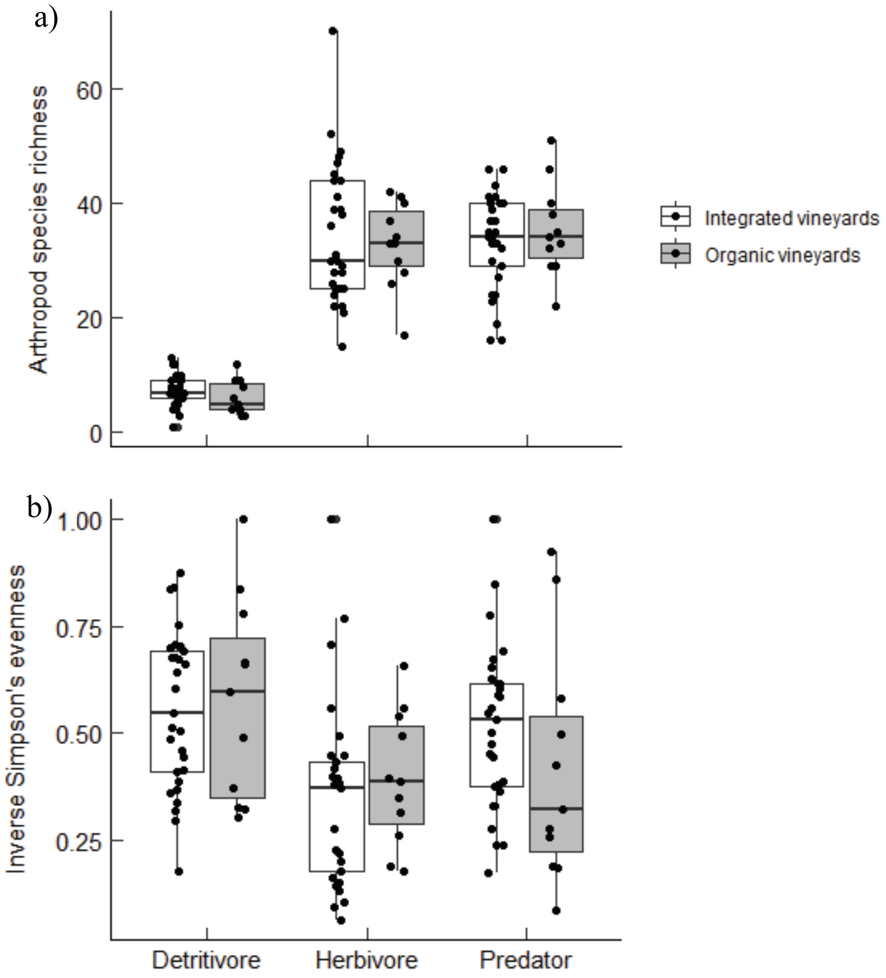

Figure 2.5: a) Morphospecies richness and b) evenness of the three arthropod feeding guilds in integrated and organic vineyards, with jittered points showing the values for individual vineyards.

2.5 Discussion

2.5.1 Effect of management practices and environmental variables

We expected arthropods in different taxonomic groups, microhabitats, and feeding guilds to vary in their response to the predictor variables, because different arthropod groups vary in their resource requirements and sensitivity to agricultural disturbances (Birkhofer et al., 2014; Fuller et al., 2005). In addition, different species can vary in their microhabitat preference in multi-strata vineyard agroecosystems (Shapira et al., 2018), and there may be unequal exposure of arthropods to disturbances in different vineyard microhabitats (Thomson & Hoffman, 2006).

However, there was a consistent, strong positive effect of vegetation-related variables on most of the responses. Percentage herbaceous vegetation cover influenced all the morphospecies richness responses positively. Plant litter positively influenced morphospecies richness of overall arthropods, true bugs, herbivores, and arthropods in the cover crops. Plant species richness promoted spider morphospecies richness, as well as evenness of beetles and soil surface arthropods. Furthermore, vegetation height positively influenced true bug, herbivore, and predator evenness, and grass cover promoted morphospecies richness of arthropods on the vines.

These findings correspond with results from recent global reviews showing that extensive vegetation management can significantly enhance biodiversity in vineyards (Paiola et al., 2020; Winter et al., 2018) and in other agricultural crops (Isbell et al., 2017; Lichtenberg et al., 2017). The effect can be attributed to the greater diversity of resources provided by diverse and dense non-crop vegetation, such as food and hosts, as well as greater structural complexity, refuge, and moderated microclimate in the crop fields (Danne et al., 2010; Landis et al., 2000) provided by both the live plants and plant residues. Increasing vineyard cover crop diversity can promote important service-providing arthropods in vineyards, such as natural enemies of pests (Sanguankeo & Leon, 2011; Shapira et al., 2018; Sommaggio et al., 2018), and species of conservation concern, such as wild bees (Kratschmer et al., 2019) and specialist butterflies (James et al., 2015). It is increasingly recognised as an important tool to enhance the biodiversity value of vineyards as a component of the overall landscape mosaic. An important benefit of perennial crops, such as vineyards and orchards, relative to annual crops, is that the permanence of the crop and the complex multi-strata design provide an opportunity for establishing longer lasting and diverse cover crops that can provide a range of micro-habitats (Simon et al. 2010) and resources for longer periods of the year (Pfiffner et al., 2019).

We did not detect any negative effects of agrochemical inputs on arthropods in this study. This was unexpected, considering the pervasive detrimental effect of synthetic agrochemicals which has been demonstrated globally (Desneux et al., 2007; Geiger et al., 2010). In our study locations, most vineyards were managed sensitively in terms of chemical inputs. Most agrochemicals used were rated either as 1 (low risk) or 2 (medium risk) by the IPW coding scheme. During the 2015/2016 season, there were only seven reported applications of pesticides rated as 4 (medium to high risk) across all farms. This suggests that the types of compounds used and intensity at which they are being applied in our study area, have a relatively low impact on our focal arthropods under field conditions, at least in terms of their immediately visible impacts on populations (see Bruhl & Zaller, 2019; Desneux et al., 2007). A limitation relating to the pesticide effects, is that we were unable to relate the precise timing of management practices to our arthropod responses. The time lag between chemical applications and our arthropod sampling, considering the short activity period of the pesticide, may be an additional reason for the lack of effect detected.

An additional trend observed here is that agronomic disturbances benefitted certain arthropod responses, which has also been documented for arthropods in Swiss vineyards (Bruggisser et al. 2010). Beetle evenness was promoted by herbicide intensity, detritivores responded positively to increased soil tillage, and spider morphospecies richness and evenness was positively associated with increased soil compaction. Many species that use agricultural fields can be well-adapted to these disturbances (Phalan et al. 2011). The increase in evenness may be due to the low level of disturbance enabling the coexistence of species with different competitive abilities (Connell, 1978).

2.5.2 Effect of overall farming approach

Globally, organic farming plays an important role in mitigating the ongoing loss of biodiversity (Hole et al., 2005; Tuck et al., 2017), although effects can vary among taxa and systems (Birkhofer et al., 2014; Fuller et al., 2005). In this region, there have also been mixed results, with some studies showing overall positive effects (Gaigher & Samways, 2010, 2014) or varied effects of organic farming on different taxa (Kehinde & Samways, 2012). A possible reason for the lack of effect detected here, is that organic vineyards are situated in a landscape where non-organic farming is still the dominant practice and there is spillover of management from neighbouring farms. This was proposed for the lack of effect of organic farming on pollinator diversity in Italian vineyards (Brittain et al., 2010). The proportion of organic farms in a landscape can enhance field-scale arthropod diversity and work best as an area-wide management strategy (Holzschuh et al., 2008; Inclán et al., 2015). Alternatively, the lower background disturbance levels and greater structural complexity in perennial crops compared to annual crops may mediate the effect of farming practices, leading to lower contrast between organic and non-organic farming regimes (Bruggiser et al., 2010).

Based on our model selection results, our findings are likely due to integrated production strategies that are already environmentally sensitive relative to conventional systems. With the modernisation of farming in response to environmental concerns, strongly driven by both the local National Biodiversity Strategy and Action Plan (NBSAP) alongside retailer pressure arising from greater consumer awareness, integrated and organic farming may have converged in terms of their protection of arthropod diversity. Notably, we observed great variation in management practices among vineyards within the same management regime, as well as large variation in arthropod responses. Other studies have also demonstrated the diversity of management styles that can occur within the same management system (Gosme et al., 2012; Puech et al., 2014), and have shown that variation among individual practices can play a more significant role than overall farming regime in structuring arthropod assemblages (Marliac et al., 2016). This suggests that the binary classification of farms as organic vs. non-organic based on certification status, does not necessarily reflect its potential influence on biodiversity in all agroecosystems or regions, as it does not take the nuances of individual farmer practices into account. An additional consideration is that, due to the limited availability of organic farms in the region, our sample size for organic vineyards was relatively low, which meant that we could not conclusively demonstrate a lack of effect. Larger datasets may provide a better opportunity to test for differences in future assessments.

2.6 Conclusion

We demonstrated clear benefits of vineyard cover cropping for arthropod diversity in this region, which corresponds with global recommendations for improving vineyard sustainability (Paiola et al., 2020; Winter et al., 2018). Furthermore, diversifying vegetation in vineyards may have broader benefits such as biological pest control, recycling of nutrients, regulating microclimate and hydrological processes, and reducing soil erosion (Garcia et al., 2018). Increasing non-crop vegetation cover and diversity can therefore be an effective multi-functional practice in vineyards, and feasible to implement, considering that cover cropping is widely practiced in vineyards worldwide. Further assessment of cover crop characteristics that benefit arthropod diversity under local conditions, and that minimise disservices such as competition with vines, will be important to develop targeted recommendations. In addition, the continued careful integrated use of agrochemicals, as opposed to more intensive use, will be important to promote the efficacy of other agroecological practices (Simon et al. 2010). In turn, putting these practices into positive conservation action also helps improve the buffer and transition zones of biosphere reserves, as in the case of the CWBR here.

2.7 References

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Chapter 3: Permeability of edges between vineyards and natural areas for arthropods in the Cape Floristic Region

3.1 Abstract

Complex landscape mosaics are characterised by high densities of edges between adjacent biotopes. A better understanding of edge effects and species spillover between natural and transformed areas enables us to manage landscape mosaics for optimal biodiversity conservation. I assessed arthropod spillover patterns across vineyard-fynbos edges in the Cape Floristic Region (CFR) of South Africa, where biodiversity-rich fynbos remnants often border on structurally complex vineyards. Selected arthropod taxa (spiders, beetles, and true bugs) were categorised according to biotope affiliation (crop-associated, fynbos-associated, or ubiquitous), based on patterns of habitat fidelity and specificity of each species. Overall species richness and assemblage patterns were assessed along transects across vineyard-fynbos edges, and were assessed separately for three vegetation layers (ground, cover crop, and vines). Environmental and management drivers of species richness of the three biotope affiliations were determined per biotope. Differences between vegetation layers in promoting spillover was also assessed. Arthropod species richness did not differ along vineyard-fynbos transects for ground and lower vegetation layers, but was significantly lower in vines than in fynbos vegetation. However, for all layers, arthropod assemblages differed significantly between vineyards and fynbos, suggesting limited assemblage-level spillover. There was limited spillover of fynbos-associated species from fynbos into vineyards. Variables relating to increased inter-row vegetation cover in vineyards significantly promoted crop-associated and ubiquitous arthropod species richness. Crop-associated arthropod richness demonstrated small-scale spillover from vineyards into fynbos. Ubiquitous species, which represents the subset that shows spillover in both directions, was associated with increased soil moisture in fynbos. None of the vegetation layers facilitated spillover. No factors were identified that would enhance spillover of fynbos-associated species from fynbos into vineyards. However, I recommend that vineyards in the CFR are managed to promote a diverse cover crop as this increased crop-associated and ubiquitous species richness in vineyards.

Keywords: Arthropod, assemblage structure, edges, environmental drivers, microhabitat, species richness, spillover, vegetation layers.

3.2 Introduction

Agricultural intensification, which leads to habitat loss and fragmentation, is one of the major threats to biodiversity today (Fletcher et al., 2018; Haddad et al., 2015; Pereira et al., 2010; Rands et al., 2010; Wilcove et al., 1986). Habitat loss and fragmentation decrease biodiversity and may cause local extinctions of fauna and flora due to processes associated with isolation (Haddad et al., 2015). Decreased functional connectivity combined with a loss of diversity can cause a system to reach a threshold-level of irreversible change in its resilience (Swift et al., 2004). Resilience is the capacity of a system to absorb disturbances and adapt to, or reorganise after disturbances (Bengtsson et al., 2003). Due to disturbances being intrinsic to all ecosystems, it is important to maintain a high diversity of species, as it is the diversity in responses to disturbances that is critical to ensure ecological resilience (Bengtsson et al., 2003). There is a need to improve landscape connectivity as this will reduce extinction rates and help maintain ecosystem services (Haddad et al., 2015), as well as a strong need for insurance reserves in managed landscapes (Bengtsson et al., 2003). Resilience may potentially be increased by maintaining landscape mosaics that consist of different sets of ecosystems (Jackson et al., 2007).

In landscape mosaics, edges exist where two different biotopes meet. The effects of edges on different organisms have long been the focus of many ecological studies (Baldissera et al., 2004; Fagan et al., 1999; Gaigher et al., 2015; Griggs, 1914; Hadjicharalampous et al., 2002; Harris, 1988; Pryke & Samways, 2012; Rand et al., 2006; Šálek et al., 2015; Wiens, 1976). As described by Murcia (1995), there are three types of edge effects that influence fragments or patches: 1) abiotic effects such as environmental changes as a result of proximity to a structurally different matrix (e.g. Inclán et al., 2015), 2) direct biological effects which include changes in species abundance and distribution due to physical conditions near the edge (e.g. Ng et al., 2018), and 3) indirect biological effects due to species interactions at edges (e.g. Ewers et al., 2013).

Edge effects are one of the most studied ecological processes, and are becoming increasingly important as habitat loss and fragmentation progresses (Rand et al., 2006; Ries et al., 2017). It is necessary to gain a broader understanding of edge effects on ecological processes to understand the impact that habitat loss and fragmentation have on specific ecosystems (Haddad et al., 2015; Ries et al., 2017). Due to the large variation in responses of different taxa (Ewers & Didham, 2005; Pryke & Samways, 2012) and site-specificity, there are still no clear-cut general patterns of how species will react to certain edges (Murcia, 1995).

There is an ever-increasing demand for a better understanding of factors that affect species richness of individual taxa in farmlands (Šálek et al., 2015). This is a major challenge as individual taxa respond differently to edges (Pryke & Samways, 2012) and topography is likely to be a major factor in determining site-specific characteristics of insects (Morris, 2000). Edge responses are key in furthering our understanding of landscape-level dynamics and understanding how the spatial patterning of landscapes influences species abundance and distribution (Ries et al., 2004). Furthermore, patches (which by definition edges feature strongly) can act as reserves when there are low levels of disturbance (Gaigher et al., 2015; Tscharntke et al., 2007), and are important in determining the extent of spillover of functionally important species (Tscharntke et al., 2005a ; Tscharntke et al., 2007).

Tscharntke et al. (2005b) show that the abundance, diversity, and functioning of beneficial arthropods in cropping systems are greatly influenced by landscape structure over a range of spatial scales, and arthropod diversity increases with an increase in diversity and area of non-cultivated habitats surrounding crop fields (Rand et al., 2006). Patch preservation is especially important in landscapes where high-value crops and biodiversity-rich natural land coincide (Fairbanks et al., 2004), and the potential for the conversion of natural land to expand agriculture is high (Viers et al., 2013), such as with viticulture in the CFR. It is therefore important to consider how different species react to different edges between natural, artificial, or cropland patches, as conservation efforts could maintain patches with edges that facilitate spillover of organisms, and which translates into resilience and enhanced agroecosystem function.

Terrestrial habitat patches are often surrounded by a mosaic of complex land cover types which may differ in their resistance to species' movement among patches due to physical constraints such as vertical vegetation structure, light environment, and temperature (Cadenasso et al., 2003; Ricketts, 2001). Permeable, or softer (Stamps et al., 1987), edges would facilitate landscape connectivity (Haddad, 1999), decrease negative effects associated with isolation by enabling arthropods to move through the landscape, and provide improved access to alternate resources. The challenge here is that connectivity may differ among different or the same species depending on the landscape and time (Kindlmann & Burel, 2008).

Extensive research has been done on arthropod spillover from natural areas into adjacent cropland, with far less literature on spillover in the opposite direction (Blitzer et al., 2012) and the potential impact that consumers of alternate resources may have on remaining natural habitats (Tscharntke, et al., 2005a). Rand & Louda (2006) found that cropping systems are potential high-density sources of generalist predatory beetles, and that spillover from agricultural habitats can influence insect dynamics i.e. abundance and potential impact of generalist predators in remnant natural areas. In turn, McKone et al., (2001) found that corn-rootworm beetles started feeding on pollen of native sunflowers after resources within maize fields became desiccated, and consequently reduced seed set in native sunflowers and other flowering composites. Furthermore, Thorbek & Bilde (2004) found that generalist predators such as spiders, carabid, and staphylinid beetles left arable fields in response to a range of management practices which may result in aggregations of predators in surrounding natural habitats. Spillover in both directions may be expected as many herbivorous agricultural pests and natural enemies are polyphagous and share both habitats (Symondson et al., 2002). Rand et al. (2006) suggested that more empirical work on the spillover of arthropods in the opposite direction should be done to gain a better understanding on how fragmentation impacts insect predator-prey interactions. This knowledge would be critical in the CFR as remnant patches of fynbos in the agricultural matrix hold high-biodiversity value (Gaigher et al., 2015; Theron et al., 2020).

There have been some studies on the effect of adjacent natural vegetation and management practices as drivers of species diversity or communities associated with vineyards in the CFR (Gaigher et al., 2015, 2016; MacLaren et al., 2019; Topp & Loos, 2019). However, there is little research on site-specific drivers that could influence spillover in both directions between natural areas and vineyards. Environmental drivers act as filters that sort species according to their response traits, which in turn results in the functional structure of communities that drives ecosystem functioning (Lavorel et al., 2013). Identifying such drivers would thus hold great benefits to conservation in terms of increased permeability in the landscape, and to viticulture in the CFR, in terms of resilience, ecosystem services, and agroecosystem function.

The CFR is a hyper-diverse global biodiversity hotspot on the southern tip of Africa, where fire is a major environmental driver. The CFR has a Mediterranean-type climate, covering an area of 90 000 km^2, with considerable transformation to agriculture and urbanisation, as well as being impacted by invasive alien vegetation (Cowling et al., 2003; Rebelo et al., 2006). The CFR supports around 9 383 plant species, of which 68% are endemic (Goldblatt & Manning 2000; Manning & Goldblatt, 2012; Rebelo et al., 2006), and with an arthropod diversity matching that of plant species (Procheş & Cowling, 2006). The CFR has largely been transformed into an urban-agricultural matrix, the Cape Winelands, where viticulture is the dominant practice. South Africa is the tenth top wine producing country in the world, making the coexistence of the remaining CFR biodiversity and production associated with the Cape Winelands crucial, as the natural diversity is irreplaceable, yet the revenue generated by wine production is essential for the development of the region.

The Cape Winelands Biosphere Reserve (CWBR) is situated within the CFR and was designated in 2007 by the International Coordinating Council of the UNESCO Man and the Biosphere Programme, covering a land area of 322 032 ha. Vines (*Vitis vinifera*) are a major crop in the CFR, with 88 366 ha under cultivation, comprising 96% of South Africa's wine grape vineyards (SAWIS, 2019), which dominates large areas in the transition and buffer zones of the CWBR. It is essential that vineyards in the CWBR are managed sensitively, as vineyards can contribute to biodiversity which provides ecosystem services (Paiola et al., 2020), i.e. pest control and pollination, and in turn will benefit wine production (Viers et al., 2013).

Vines are perennial crops where disturbances are less frequent than in annual crops. They have a complex structure and are multi-layered, providing opportunities for biodiversity conservation in the vineyard in that management practices can be adapted so as to provide, for example, alternate resources such as shelter, and increasing arthropod diversity through mulching (Addison et al., 2013; Thomson & Hoffmann, 2007) or cover cropping (Sáenz-Romo et al., 2019). On the other hand, studies in the CFR have shown the importance of maintaining remnant patches of fynbos within the production landscape as it supports high spider species richness and species turnover rates between patches (Theron, 2017), as well as retaining parasitoid diversity (Gaigher et al., 2015). This reinforces the conservation value of remnant patches to biodiversity in the CFR, regardless of patch size (Theron, 2017).

Arthropods are good bioindicators of changes in the natural environment due to their high responsiveness (McGeogh, 2007; McGeoch et al., 2011). Many arthropods disappear from a local area that has become unsuitable for them (Thomson et al., 2004) through, for example, an event such as physically clearing natural vegetation. This means that they only occur in remnant patches of natural or semi-natural vegetation following such an event. They are usually one of the first animal groups to respond to changes in the natural environment (McGeogh, 2007) and their short generation times (Gerlach et al., 2013) make them ideal organisms to use as bioindicators of the health of a system (Anderson et al., 2011; Paoletti et al., 1999; Paoletti et al., 1991; Rainio & Niemelä, 2003).

One of the major challenges for understanding how biodiversity is affected by habitat structure and ecological processes such as edge effects, is the great variation in the uniqueness of sites combined with taxa responding differently to different stimuli or factors. Consequently, using three arthropod taxa, I investigated arthropod species richness and assemblage patterns across vineyards and fynbos edges, as well as potential environmental and management drivers to gain a comprehensive understanding of edge effects in CFR vineyards.

3.2.1 Aim

To undertake an in-depth assessment of arthropod spillover patterns across vineyard-fynbos edges in terms of species richness, assemblage structures, and associated environmental and/or management drivers of spillover.

3.2.2 Objectives

1. Assess whether overall arthropod species richness and assemblage structure differ at different distances from the vineyard-fynbos edge in three vegetation layers (ground, cover crop, and on the vines). Additionally, arthropod assemblage structure was determined for five microhabitats in the two biotopes (two in the fynbos and three in the vineyard). This will reveal overall arthropod distribution patterns across the edges and show whether the arthropod assemblage differs between individual microhabitats.

2. To test which environmental and/or management variables drive species richness of crop-associated, fynbos-associated, and ubiquitous arthropod species in vineyards and fynbos, in both directions across the edge between the two biotopes. If drivers for fynbos-associated arthropods in vineyards can be identified, management can focus on these drivers to improve edge permeability in the agricultural landscape. Drivers for crop-associated arthropods in fynbos should be considered in conservation efforts of fynbos or remnant patches, as these drivers may have deleterious effects on the adjacent natural arthropod populations.

3. To assess the composition of crop-associated, fynbos-associated, and ubiquitous species richness and abundances among the different vegetation layers in vineyards and fynbos. This will determine whether certain species groupings are proportionately more diverse or abundant in certain microhabitats.

3.3 Materials and methods

3.3.1 Study sites and sampling design

A total of 11 vineyards adjacent to natural vegetation (henceforth “fynbos”) were used as sample units across 11 commercial wine farms. Vineyard blocks ranged in size from 1.25 to 6.1 ha. Farms were selected to represent a range of management practices and localities throughout the CWBR (Figure 3.1). Two of the 11 vineyards were located on organically certified farms, with a mean vineyard block size of 1.96 ha. Certification was done by Ceres and Ecocert. The remainder of the vineyards were managed according to the guidelines of the Integrated Production of Wine Scheme of South Africa (IPW, 2018a). The mean size of vineyard blocks on integrated farms were 3.70 ha. For this chapter, the spillover effect between vineyards and adjacent fynbos was assessed using transects spanning from within the vineyard blocks across their edges and into the adjacent fynbos. A transect consisted of six plots, of which three were in the vineyard, and three in the fynbos, at 10 m, 50 m, and 100 m distances away from the edge between the two biotopes. Sampling was undertaken over two seasons,

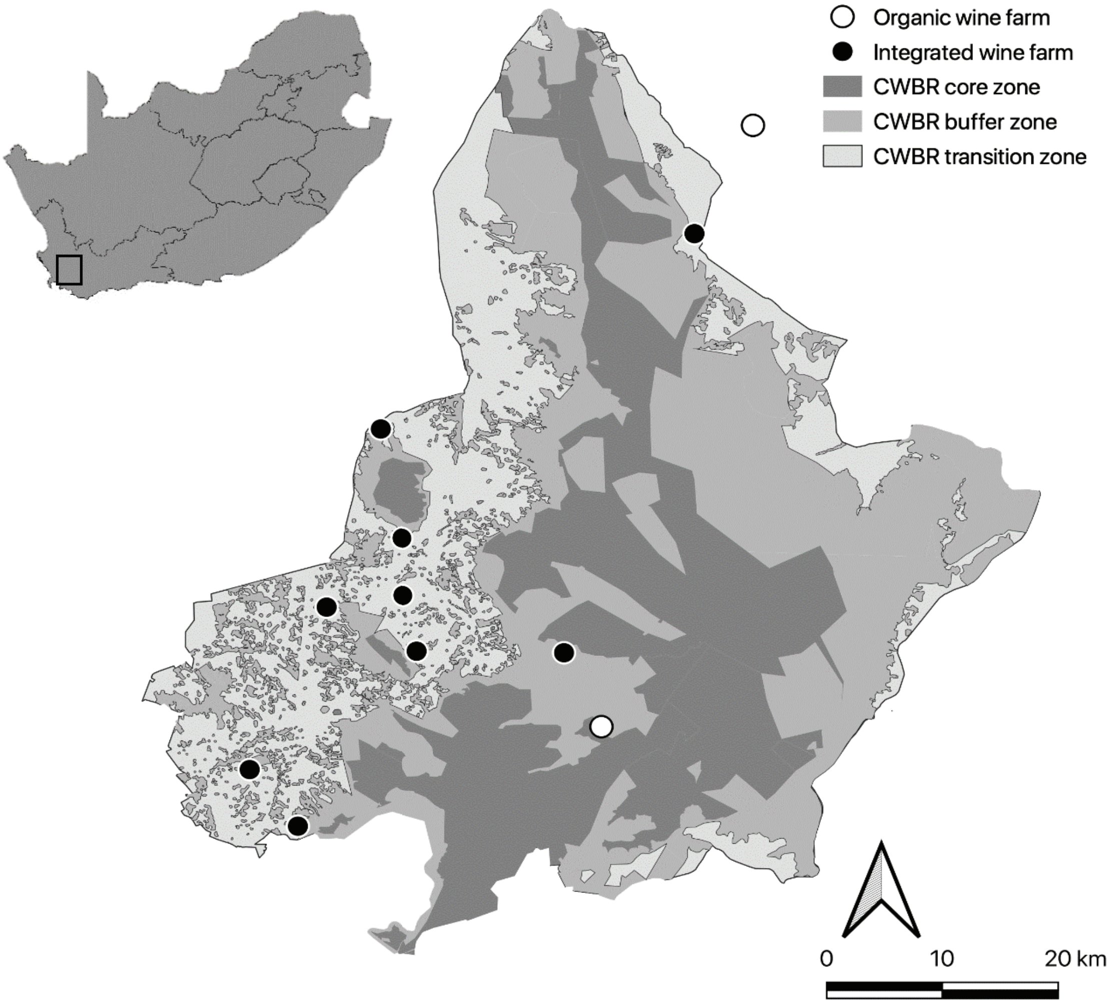

Figure 3.1: A map of farms used within the Cape Winelands Biosphere Reserve in South Africa.

May 2016 (autumn, post-harvest), and October 2016 (spring, early in the growing season when fruits were setting).

3.3.2 Arthropod collection

At each vineyard plot, arthropods were sampled in three layers namely on the ground, on the cover crops, and on the vine foliage. Fynbos vegetation in this study region does not have distinct stratification, and so arthropods were only sampled in two layers: on the ground and on the vegetation. Ground-dwelling arthropods were collected using four pitfall traps (300 ml plastic jars with 6 cm diameter openings) at each of the six plots on each transect (Woodcock, 2005). This added up to 264 pitfall traps and 66 pitfall samples (each pitfall trap array was pooled) per sampling period. Each pitfall trap was prepared with a 200 ml solution of ethylene glycol preservative and water (3:1) with two added drops of dishwashing liquid to reduce surface tension. At each plot, the four pitfall traps, one on each corner of a 1 m^2 quadrat, were sunk into the ground until the brim of the trap was level with the soil surface. In vineyards, the pitfall trap array was always placed with two pitfalls in the vine row and two in the inter-row. Pitfalls were left open for one week before they were retrieved and taken back to the laboratory, and all the pitfall trapping was completed over a period of 82 days. Samples were washed with water, and then preserved in a 75% ethanol solution for later sorting and identification.

Arthropods on cover crops, vines, and fynbos vegetation were collected using a vacuum sampler. A Stihl SH56C-E vacuum shredder was used as vacuum sampler by attaching a 30 cm-long fine mesh bag onto the 10 cm diameter opening of the vacuum pipe. The bag then acts as a net for arthropods and debris during the vacuuming process. This method is effective for sampling vegetation-dwelling arthropods in this region (Swart et al., 2017). One vacuum sample, at each vineyard plot, consisted of two sets of 100 insertions of the vacuum pipe into the vegetation along a walked transect. Each cover crop sample was taken within a single inter-row, < 10 m away from either side of the pitfall trap array, whereas each vine sample was split equally across two vine rows on either side of the pitfall trap array, < 10 m away from the pitfall trap array. Sampling of arthropods on the fynbos consisted of two sets of 100 insertions into the fynbos, within a 10 m radius around the pitfall trap array. The first set of 100 insertions were done in one half of the 10 m radius circle and the second set of 100 pokes in the remaining half of the circle. Each sample was stored in a clear, labelled plastic bag (250 mm × 360 mm) and preserved at -10°C for later sorting and specimen identification. Where cover crops, vine foliage or fynbos were absent, due to management practices, seasonal variation, or natural distribution, the vacuum pipe was brought very close to the soil surface or pushed onto the vine as to remain consistent with sampling effort throughout the sampling periods.

3.3.3 Arthropod identification

All spiders (Araneae), beetles (Coleoptera), and true bugs (Hemiptera) were extracted from samples and were identified to morphospecies (Oliver & Beattie, 1996) using a Leica MZ75 stereomicroscope (Leica Microsystems, Germany). Spiders, beetles, and true bugs were used as study species as they were the most abundant in samples and represent three feeding guilds (detritivores, herbivores, or predators among the various species), which maximises the range of responses to various changes in the environment. Ground beetles (Goulet et al., 2004; Rainio & Niemelä, 2003), spiders (Pearce & Venier, 2006), and bugs (Gerlach et al., 2013) have been described as good bioindicators of habitat types, environmental quality, and biodiversity studies. Spider reference specimens, including juveniles, were identified by a specialist, at least to genus, and some to species. Spider specimens are deposited in the National Collection of Arachnida in the National Museum, Pretoria. Due to the inclusion of juvenile spiders in the dataset which are difficult to link to adult morphospecies, it is possible that the spider morphospecies estimate is slightly inflated. This is considered in the interpretation of the results. The beetle reference specimens were classified in to morphospecies and identified by a specialist to family level, and beetles were classified into broad feeding guilds based on family and mouthpart morphology. True bugs were classified as predators based on morphologically easily recognisable families/subfamilies i.e. Reduviidae, Anthocoridae, Phymatidae, Asopinae, and Nabidae (Scholtz & Holm 2012). The remaining true bug morphospecies were classified as herbivores without family level identification as most other bug taxa in the region are herbivorous (Scholtz & Holm 2012). The beetle and bug reference collections are stored in the Stellenbosch University Entomological Museum.

3.3.4 Environmental variables

Environmental variables were collected in two separate quadrats of 1 m^2 at each vineyard and fynbos plot in all transects. In the vineyard, one quadrat was in the vine row, and one in the inter-row. In fynbos, the 1 m^2 pitfall array served as one quadrat with the second quadrat placed randomly at a distance no further than 3 m away from the pitfall array. Environmental variables recorded for each quadrat were soil moisture (using a Yieryi VT-05 soil detector), soil compaction (using a DICKEY-john soil compaction tester), volume of plant litter (using a 3 L measuring jug), vegetation height, number of dominant plant species, and additionally, for vineyards only, the percentage herbaceous vegetation cover and percentage grass cover was recorded. Herbaceous plants and grasses, as ground cover, are not typically associated with the fynbos biome (Rebelo et al., 2006) and were therefore not recorded in fynbos plots. The volume of plant litter was measured in the field by compacting all the plant litter from a quadrat into the measuring jug. For soil compaction and vegetation height, a minimum of three measurements was taken per quadrat. Environmental data for the two quadrats at each plot were averaged.

3.3.5 Management data

Management data for each farm were collected for the 2015/2016 season for the specific vineyards in which sampling occurred. Each farm made available their insecticide, herbicide, and fungicide records, as well as tillage frequency and intensity. To standardise the different application rates of insecticides, herbicides, and fungicides applied between vineyards, chemical compounds were first coded according to the Integrated Production of Wine (IPW) scheme's Integrated Production (IP) coding of all products document (IPW, 2018b). Chemicals are categorised by IPW into low risk (1), medium risk (2), medium to high risk (4), and high risk (8). IPW assign risk codes to agrochemicals based on human health and safety risks, as well as numerous laboratory and field toxicology tests (typically LC50, LD50, EC50, or IOBC and OEPP/EPPO classifications). The risks pertain to the impact of an agrochemical on the environment (associated water and soil risks) and organisms (avian, fish, aquatic organism, and soil organism risks), as well as impact on beneficial organisms i.e. bees, predatory mites, beetles, lacewings, and wasps. A ratio was calculated for spray intensity by dividing the amount of a chemical used (L ha^{-1}) into the registered dosage (L ha^{-1}) for each chemical applied. A score (a) was then calculated for each of the chemicals applied to each vineyard by multiplying the IP code (b), the intensity ratio (c) and the total number of applications (d) for the 2015/2016 season ($a = b \times c \times d$).

Similarly, tillage intensity across farms were standardised by taking into account the frequency of tilling per season, and whether or not the implement used inverted the soil profile. The total number of tilling actions for the 2015/2016 season for each vineyard was multiplied by either 1 (where the soil profile was not inverted) or by 2 (where the soil profile was inverted, due to the greater disturbance effect of inversion tillage (Soane et al. 2012)). Tillage category ranged from 0 to 6.

3.3.6 Statistical analyses

Arthropod data for the two sampling seasons were pooled for analyses, and environmental data were averaged. Univariate analyses were done in R (R Core Team, 2018), and multivariate analyses were done in PRIMER 6 version 6.1.13 (Clarke & Gorley, 2006) & PERMANOVA+ version 1.0.3 (Anderson et al., 2008) from PRIMER-e. To determine patterns across the fynbos-vineyard edge for species that are strongly associated with vineyards, fynbos, or both, arthropod species were assigned to one of three groups: crop-associated, fynbos-associated, and ubiquitous species, based on arthropod indicator species for the two biotopes, which were identified using the *indicspecies* package (Cáceres & Legendre, 2009). The test interprets a matrix of species and the biotope in which they were sampled, and then makes use of abundances to statistically weigh species as significant indicators of the specified biotope, in this case vineyards (crop-associated), fynbos (fynbos-associated), or both (ubiquitous). Arthropod species that were classified as being statistically significant indicators of a biotope, or of both biotopes in the case of ubiquitous species, were used in analyses. Results included were from statistical analyses of the significant indicator species subset only (singletons and doubletons excluded), as analyses on the overall dataset (singletons and doubletons included) had very similar outcomes. Due to similar results for both datasets, I decided to only include results for significant indicator species.

3.3.6.1 Patterns of arthropod species richness and assemblage structure across vineyard-fynbos edges

As the total vacuum sampling intensity differed between fynbos (200 insertions on the vegetation) and vineyards (200 insertions on the vine, and 200 on the cover crop = 400 insertions on vineyard vegetation), arthropod data were combined for the models in order to keep sampling effort consistent for the two biotopes as follows: 1) vineyard ground layer data from pitfall traps (VinGr) were combined with the fynbos ground layer data (FynGr), into an overall ground layer (G-G), 2) vineyard cover crop data from the vacuum samples (VinCC) were combined with those from the fynbos foliage layer (FynUp), into a cover crop-fynbos vegetation layer (CC-Up), and 3) vine foliage data from vacuum sampling (VinUp) was also combined with the fynbos foliage layer, into a vine-fynbos vegetation layer (Up-Up). Response variables were tested for normality using the Shapiro-Wilk test of normality in the *stats* package (R Core Team, 2018), and spatial autocorrelation was tested for using the Mantel test in the *ade4* package (Dray & Dufour, 2007). Due to some response variables having spatial autocorrelation, a random spatial variable was included for all response variables during model selection, namely 'Farm' (Figure 3.1). The *lme4* package (Bates et al., 2015) was used to assess species richness patterns across the vineyard-fynbos edge, and to test whether species richness differed significantly among plot locations on the transect. This was done separately for the three vegetation layers (G-G, CC-Up, and Up-Up). Linear mixed-effect models were used for response variables with normal distribution, and generalised linear mixed-effect models with a log link function were used for response variables with a Poisson distribution (Bolker et al., 2009). Tukey post-hoc comparisons were performed for each of the vegetation layers to test for significant differences between plot locations along the transect.

Differences in arthropod assemblage structures between plot locations along the transect were tested for each of the three vegetation layers (G-G, CC-Up, and Up-Up). In addition, differences in overall arthropod assemblage structures for all five microhabitats (VinGr, VinCC, VinUp, FynGr, and FynUp), were tested. Response variables were square-root transformed to reduce the influence of abundant species before creating resemblance matrices using Bray-Curtis similarity metric. Permutational multivariate analyses of variances (PERMANOVAs) (Anderson, 2001; McArdle & Anderson, 2001) were used to test for differences between arthropod assemblage structures at each plot location on a transect. The

PERMANOVA design was created with fixed ('Plot location') and random ('Farm') (Figure 3.1) factors. A PERMANOVA was also used to test for differences in arthropod assemblage structures between the five microhabitats (VinGr, VinCC, VinUp, FynGr, and FynUp). The PERMANOVA design was created with fixed ('Biotope layer') and random ('Farm') factors. These models were permutated 9 999 times based on the unrestricted raw data.

3.3.6.2 Environmental and management drivers of crop-associated, fynbos-associated, and ubiquitous arthropod species in vineyards and fynbos

Model selection was used to determine which individual environmental and management variables significantly influenced crop-associated, fynbos-associated, and ubiquitous arthropod species richness in vineyards, and which individual environmental variables influenced crop-associated, fynbos-associated, and ubiquitous arthropod species richness in fynbos. Vineyard variables influencing fynbos-associated species, and fynbos variables influencing crop-associated species were of primary interest, as these would be variables directly influencing spillover of species strongly associated with one biotope into the other biotope. Correlated explanatory variables were identified by comparing Spearman's rho rank correlation coefficients in a matrix created using the *Hmisc* package (Harrell Jr, 2018). The cut off r_s value used for identifying correlated explanatory variables was set at 0.6 or -0.6. Soil pH, fungicide score, and herbicide score were removed from statistical analyses as these variables were correlated with relative soil moisture ($r_s = 0.81$ in vineyards, and $r_s = 0.84$ in fynbos), number of plant species ($r_s = 0.6$), and insecticide score ($r_s = 0.6$), respectively. Relative soil moisture and insecticide score was preferred, as it is more important to the questions being posed, and the number of plant species was preferred as this variable was present in both biotopes. A total of 10 explanatory variables (in vineyards), and 6 explanatory variables (in fynbos), were used for statistical analyses (variables with asterisks were included in models for both biotopes):

soil compaction (psi)*, soil moisture (relative scale of 1-8)*, volume of plant litter (ml)*, vegetation height (cm)*, number of plant species*, % herbaceous vegetation, % grass vegetation, insecticide score, and tillage category. In addition to the measured variables, plot location along the transect (10 m, 50 m, and 100 m) was included in the candidate models, as distance from the edge was expected to influence species richness.

All continuous explanatory variables were scaled before model selection using the *base* package (R Core Team, 2018). Candidate models for crop-associated, fynbos-associated, and ubiquitous response variables were created using linear mixed-effects models as all data were normally distributed. Model selection was done using forward selection, and ranking candidate models using the second-order Akaike information criterion (AIC_c) value in the *AICcmodavg* package (Mazerolle, 2017). The information criterion used was AIC_c as $N/K < 40$ (where N = sample size, and K = number of parameters) (Burnham & Anderson, 2002). A model of explanatory variables was then created for each response variable based on the best model, and each variable in the model was tested for statistical significance by using Type II Wald chi-square tests in the *car* package (Fox & Weisberg, 2019), and dispersion was calculated. Statistically significant continuous explanatory variables were then visualised as scatterplots and categorical variables as boxplots using the *VGAM* package (Yee, 2015).

3.3.6.3 Composition of crop-associated, fynbos-associated, and ubiquitous arthropod species in different vegetation layers in vineyards and fynbos

Pearson's Chi-squared tests of independence were performed to test for significant differences between ratios of crop-associated, fynbos-associated, and ubiquitous species richness and abundances in each of the microhabitats associated with each biotope. This was done to determine whether arthropod species with different biotope associations occurred disproportionately more in certain microhabitats. In terms of assessing spillover, the microhabitat in vineyards supporting the highest proportion of fynbos-associated species, and the microhabitat in fynbos supporting the highest proportion of crop-associated species was of main interest.

3.4 Results

A total of 29 720 arthropod individuals (351 species) were sampled of which 8 460 individuals (42 species) were crop-associated, 6 884 individuals (49 species) were fynbos-associated, and 14 376 individuals (260 species) were ubiquitous.

3.4.1 Patterns of arthropod species richness and assemblage structure across vineyard-fynbos edges

There were significant differences in arthropod species richness among plot locations along transects in the G-G ($\chi^2 = 478.55$, $p < 0.001$), the CC-Up ($\chi^2 = 494.56$, $p < 0.01$), and the Up-Up layers ($\chi^2 = 429.91$, $p < 0.001$) (Figure 3.2).

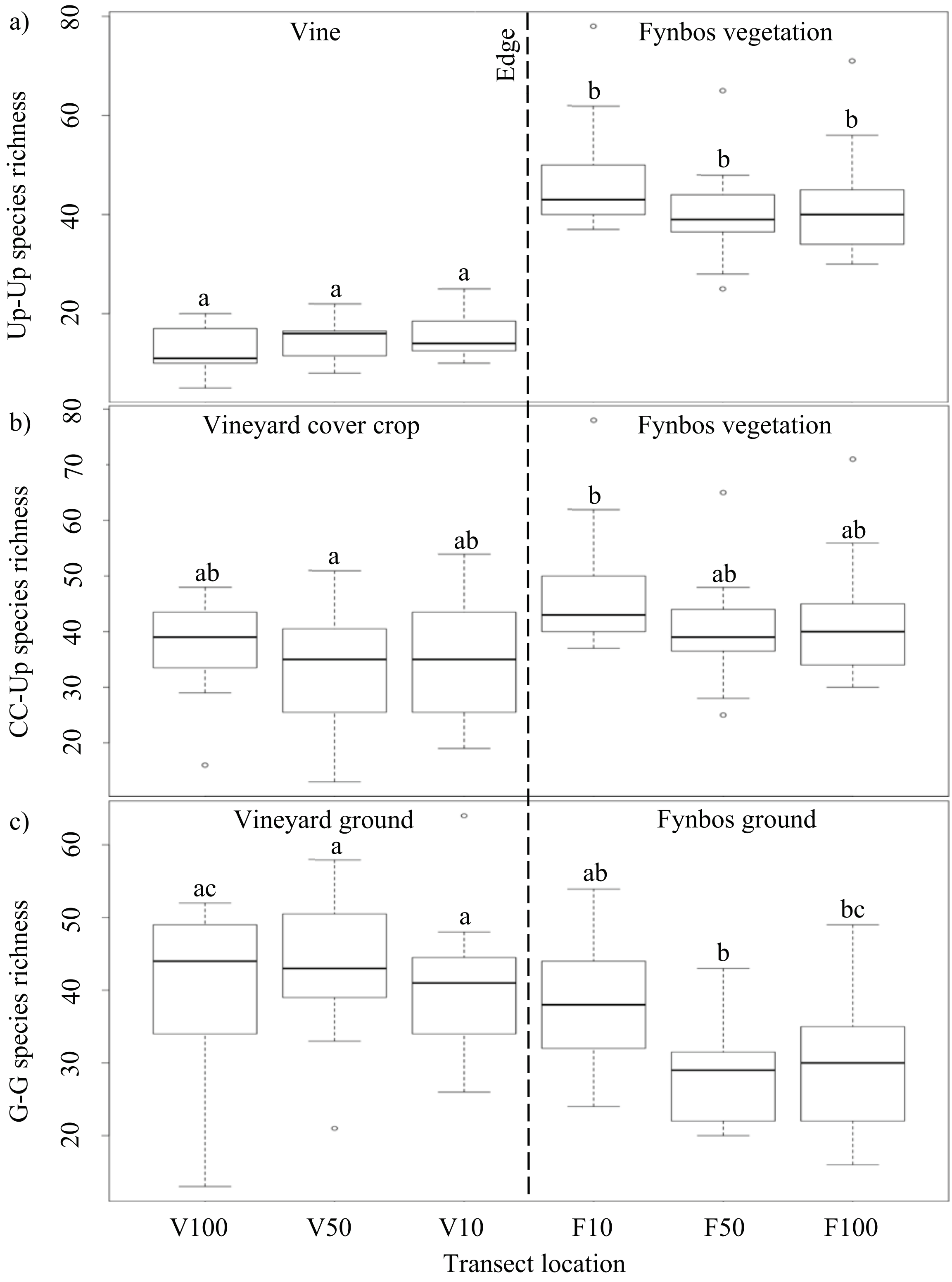

Figure 3.2: Overall arthropod species richness at different plot locations along transects spanning the edges between vineyards and fynbos. Transects were split into three vegetation layers: a) Up-Up, b) CC-Up, and c) G-G. Medians with letters in common are not significantly different. Conditional R^2 values for mixed models were: Up-Up (0.82), CC-Up (0.40), and G-G (0.43).

Arthropod species richness in the Up-Up layer was significantly higher in all fynbos plots compared to all vineyard plots, but did not differ among fynbos locations or among vineyard locations (Figure 3.2a). Arthropod species richness in the CC-Up layer did not differ between any of the plot locations, except that species richness was significantly higher in fynbos 10 m plots compared to vineyard 50 m plots (Figure 3.2b). Arthropod species richness in the G-G layer did not differ among any of the vineyard and 10 m fynbos plots. Arthropod species richness was significantly lower in fynbos 100 m plots compared to vineyard 10 m and 50 m plots. Additionally, arthropod species richness in the G-G layer was significantly lower in fynbos 50 m plots compared to arthropod richness in each of the vineyard plots (Figure 3.2c).

Plot location along the transect had a significant effect on the arthropod assemblage structures in each of the three vegetation layers: G-G (Pseudo-F = 2.17, $p < 0.001$) (Table 3.1), CC-Up (Pseudo-F = 3.15, $p < 0.001$) (Table 3.2), and Up-Up layers (Pseudo-F = 4.69, $p < 0.001$) (Table 3.3).

Table 3.1: PERMANOVA post-hoc comparison showing arthropod assemblage structures in the G-G layer, at specific plot locations along transects spanning the edges between vineyards and fynbos.

G-G	V50	V10	F10	F50	F100
V100	0.80	1.06	1.87***	1.93***	2.09***
V50		0.88	1.78***	1.93***	2.05***
V10			1.86***	1.93***	2.14***
F10				1.20	1.03
F50					1.03

Results are given: The t-value followed by the level of significance. Significance levels are based on p-values where ≤ 0.05 '*', ≤ 0.01 '**' and ≤ 0.001 '***'.

The G-G layer arthropod assemblages were significantly different in all vineyard plots compared to all fynbos plots, but there were no differences among vineyard assemblages or among fynbos assemblages (Table 3.1).

Table 3.2: PERMANOVA post-hoc comparison showing arthropod assemblage structures in the CC-Up layer, at specific plot locations along transects spanning the edges between vineyards and fynbos.

CC-Up	V50	V10	F10	F50	F100
V100	1.11	0.95	1.79***	2.03***	2.08***
V50		1.26*	1.84***	2.21***	2.24***
V10			1.69***	2.04***	2.05***
F10				1.23*	1.17
F50					1.07

Results are given: The t-value followed by the level of significance. Significance levels are based on p-values where ≤ 0.05 ‘*’, ≤ 0.01 ‘**’ and ≤ 0.001 ‘***’.

The CC-Up layer arthropod assemblages were significantly different between all vineyard plots compared to all fynbos plots. Assemblage structure mostly did not differ among vineyard plots or among fynbos plots, except that within vineyard cover crops, the arthropod assemblage was significantly different in 50 m plots compared to 10 m plots. Also, within fynbos, the arthropod assemblage was significantly different in 50 m plots compared to 10 m plots (Table 3.2).

Table 3.3: PERMANOVA post-hoc comparison showing arthropod assemblage structures in the Up-Up layer, at specific plot locations along transects spanning the edges between vineyards and fynbos.

Up-Up	V50	V10	F10	F50	F100
V100	0.94	1.11	2.36***	2.48***	2.45***
V50		0.87	2.54***	2.67***	2.55***
V10			2.44***	2.72***	2.57***
F10				1.23*	1.17
F50					1.07

Results are given: The t-value followed by the level of significance. Significance levels are based on p-values where ≤ 0.05 ‘*’, ≤ 0.01 ‘**’ and ≤ 0.001 ‘***’.

The Up-Up layer arthropod assemblages were significantly different between all vineyard plots compared to all fynbos plots. Assemblage structure mostly did not differ among vineyard plots or among fynbos plots, except that within fynbos the arthropod assemblage was significantly different in 50 m plots compared to 10 m plots (Table 3.3).

Arthropod assemblage structures in each of the five microhabitats (VinGr, VinCC, VinUp, FynGr, and FynUp) were significantly different from each other (Pseudo-F = 18.36, $p < 0.001$) (Table 3.4).

Table 3.4: PERMANOVA post-hoc comparison showing arthropod assemblage structures in five microhabitats within two biotopes (vineyards and fynbos).

Biotope layer	VinUp	FynUp	VinGr	FynGr
VinCC	4.30***	3.40***	5.07***	4.45***
FynGr	4.81***	4.32***	2.62***	
VinGr	5.43***	5.17***		
FynUp	4.43***			

Results are given: The t-value followed by the level of significance. Significance levels are based on p-values where ≤ 0.05 ‘*’, ≤ 0.01 ‘**’ and ≤ 0.001 ‘***’.

3.4.2 Environmental drivers of crop-associated, fynbos-associated, and ubiquitous arthropod species in vineyards and fynbos

In vineyards, crop-associated and ubiquitous arthropod species richness were positively correlated to the mean vegetation height (Appendix G) and the percentage of herbaceous vegetation (Appendix H) respectively (Table 3.5). Fynbos-associated arthropod species richness was positively correlated to the number of plant species, with marginal significance ($\chi^2 = 3.54$, $p = 0.059$). None of the other variables in vineyards significantly influenced arthropod richness.

In fynbos, crop-associated arthropod species richness was negatively correlated to mean soil compaction, volume of plant litter, and vegetation height. Furthermore, crop-associated arthropod species richness differed significantly among plot locations along the transect.

Table 3.5: Univariate results from model selection showing effect of environmental and management variables on the richness of crop-associated, fynbos-associated, and ubiquitous arthropod species in vineyards and fynbos.

	Crop-associated species in vineyard	Fynbos-associated species in vineyard	Ubiquitous species in vineyard	Crop-associated species in fynbos	Fynbos-associated species in fynbos	Ubiquitous species in fynbos
Soil compaction				5.73*(-)		
Soil moisture				♦		4.18*(+)
Volume plant litter				8.91**(-)		
Vegetation height	6.06*(+)		♦	14.82***(-)	♦	
# Plant species		3.54•(+)	♦		5.97*(+)	♦
Transect location		♦	♦	21.37***(10 m > 50 m & 100 m)	♦	6.96*(10 m > 50 m & 100 m)
% Herbaceous vegetation			4.96*(+)			
% Grass vegetation			♦			

Statistically significant variables are given: The type II Wald chi-square value, followed by the level of significance and the direction of relationship in brackets. Significance levels are based on p-values where ≤ 0.05 ‘*’, ≤ 0.01 ‘**’ and ≤ 0.001 ‘***’. Marginally significant variables are indicated with ‘•’, and variables that formed part of the best model but had no statistical significance are indicated with ‘♦’. Conditional R^2 values for mixed models in vineyards as per response variable: Crop-associated (0.67), Fynbos-associated (0.43), and Ubiquitous (0.66). Conditional R^2 values for mixed models in fynbos as per response variable: Crop-associated (0.74), Fynbos-associated (0.51), and Ubiquitous (0.65). The insecticide score and tillage variables had no significant effect on any of the response variables and were therefore omitted from this table. Environmental variables that were not present in fynbos plots were greyed out.

Crop-associated arthropod species richness was significantly higher in fynbos 10 m plots compared to fynbos 50 m ($z = -2.83$, $p = 0.01$) and 100 m ($z = -3.63$, $p < 0.001$) plots (Appendix I). Fynbos-associated arthropod species richness was positively correlated to the mean number of plant species present in fynbos. Ubiquitous arthropod species richness was positively correlated to relative soil moisture and differed significantly among plot locations along the transect. Ubiquitous arthropod species richness was significantly higher in fynbos 10 m plots compared to fynbos 50 m ($z = -3.25$, $p < 0.01$) and 100 m ($z = -2.39$, $p < 0.05$) plots (Appendix I). Additionally, see Appendix I for the distribution of crop-associated, fynbos-associated, and ubiquitous arthropod species richness across the complete transects.

Mean soil compaction at plot locations was higher in interior fynbos plots compared to all vineyard and fynbos 10 m plots. Mean soil moisture and volume plant litter was higher in vineyards compared to fynbos. Mean vegetation height and number of plant species was higher in fynbos than vineyards (Table 3.6).

Table 3.6: Mean and standard deviation of environmental variables per plot location for transects spanning the edges between vineyards and fynbos.

Plot location	Soil compaction (psi)	Relative soil moisture	Plant litter (ml)	Vegetation height (cm)	# Plant species
V100	221.59 ± 51.94	4.52 ± 2.18	907.73 ± 632.59	37.14 ± 11.18	4.41 ± 0.67
V50	235.08 ± 37.53	4.82 ± 1.91	1007.84 ± 560.35	39.97 ± 14.94	4.57 ± 0.82
V10	239.78 ± 41.26	4.52 ± 1.68	784.77 ± 474.44	38.42 ± 10.73	4.48 ± 0.54
F10	224.02 ± 91.02	3.39 ± 2.05	369.55 ± 257.46	77.02 ± 41.08	6.18 ± 1.54
F50	280.54 ± 19.04	3.74 ± 2.03	531.93 ± 399.52	57.13 ± 23.21	7.98 ± 2.05
F100	264.85 ± 26.79	3.10 ± 1.92	828.64 ± 965.44	83.03 ± 36.58	6.95 ± 1.66

3.4.3 Composition of crop-associated, fynbos-associated, and ubiquitous arthropod species in different vegetation layers in vineyards and fynbos

Crop-associated, fynbos-associated, and ubiquitous arthropod ratios, in terms of species richness, were not significantly different between microhabitats in vineyards ($\chi^2 = 5.18$, $p = 0.27$), or between microhabitats in fynbos ($\chi^2 = 3.79$, $p = 0.15$) (Figure 3.3). Crop-associated, fynbos-associated, and ubiquitous arthropod ratios, in terms of abundance, were significantly different between microhabitats in vineyards ($\chi^2 = 531.18$, $p < 0.001$), and between microhabitats in fynbos ($\chi^2 = 634.78$, $p < 0.001$) (Figure 3.4).

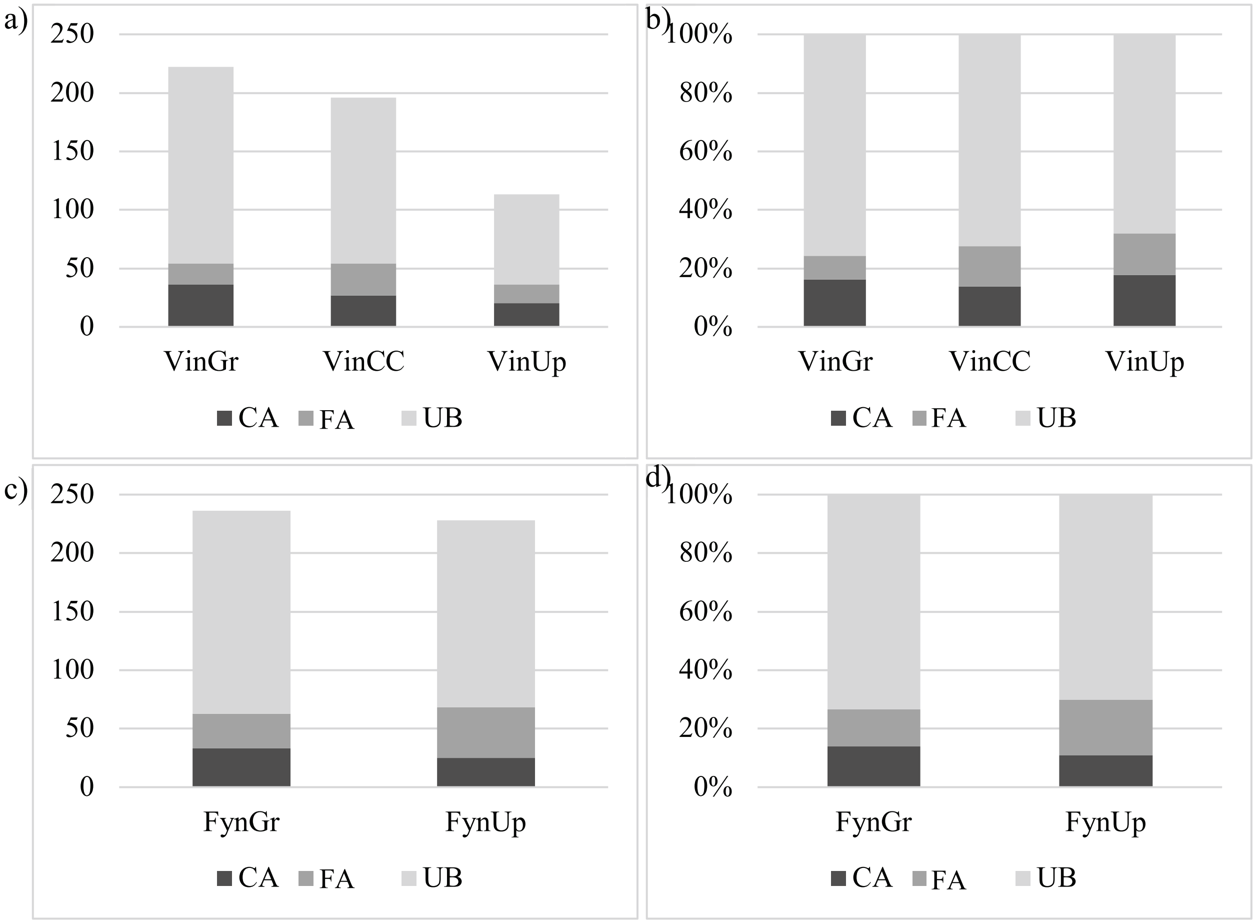

Figure 3.3: The composition of crop-associated (CA), fynbos-associated (FA), and ubiquitous (UB) arthropod species richness as number of species (a & c), and as a percentage of the total number of species (b & d), for three microhabitats in vineyards (a & b), and two microhabitats in fynbos (c & d).

In vineyards, overall, crop-associated, and ubiquitous arthropod species richness was highest on the ground, followed by cover crops, and then vine foliage. Fynbos-associated arthropod species richness was highest on the cover crops, followed by the ground and then vine foliage. In fynbos, slightly more overall, crop-associated, and ubiquitous arthropod species occurred on the ground compared to fynbos foliage. Fynbos-associated arthropod species richness was higher in fynbos foliage compared to on the ground.

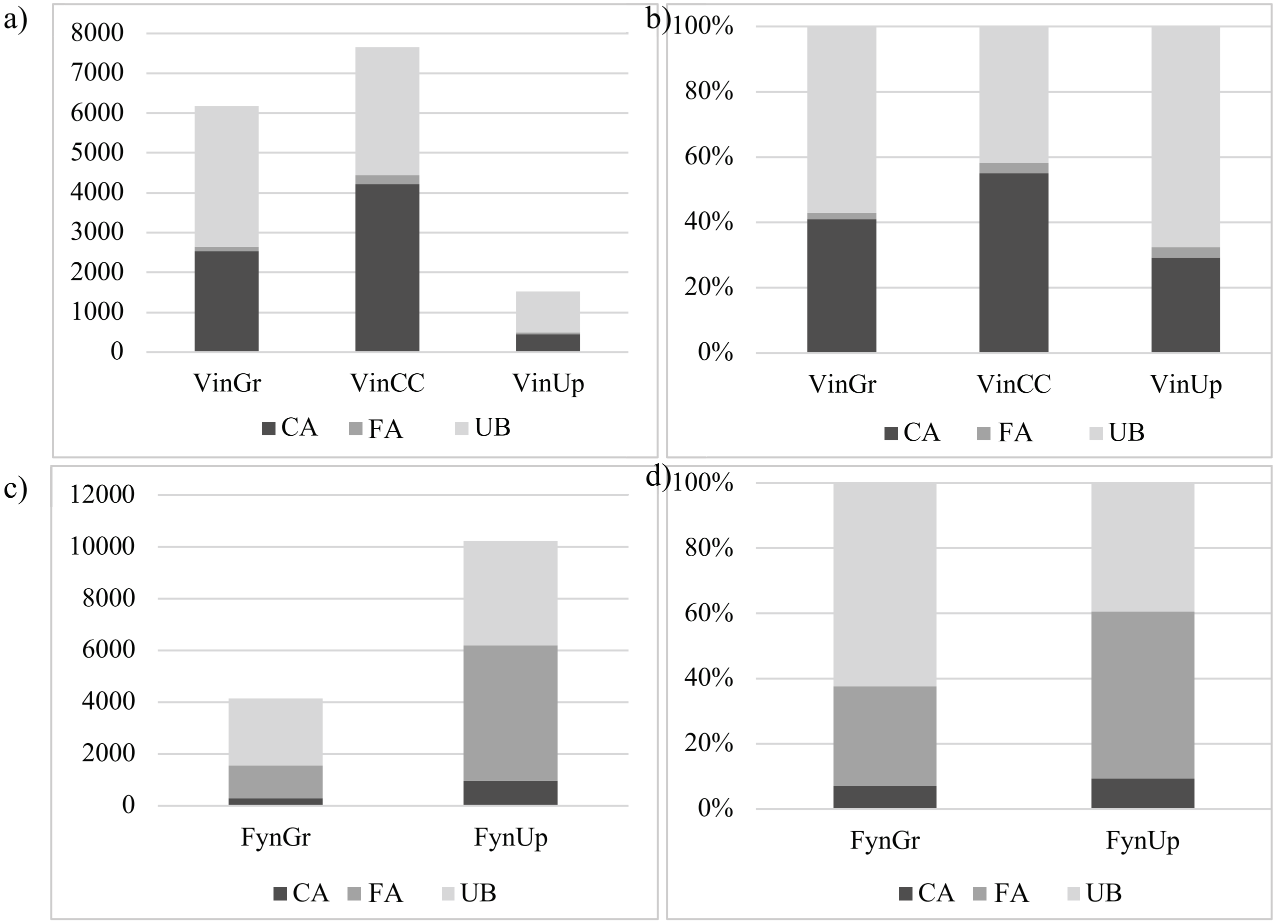

Figure 3.4: The composition of crop associated (CA), fynbos-associated (FA), and ubiquitous (UB) arthropod species abundances (a & c), and as a percentage of the total abundance (b & d), for three microhabitats in vineyards (a & b), and two microhabitats in fynbos (c & d).

In vineyards, highest abundances of overall, crop-associated, and fynbos-associated arthropods occurred on the cover crops, followed by the ground, and then vine foliage. The cover crops in vineyards supported a higher percentage of crop-associated arthropods compared to the other vegetation layers. In fynbos, highest abundances of overall, crop-associated, fynbos-associated, and ubiquitous arthropods occurred on fynbos foliage, followed by the ground. The fynbos vegetation supported a higher percentage of fynbos-associated arthropods compared to the ground layer.

3.5 Discussion

3.5.1 Patterns of arthropod species richness and assemblage structure across vineyard-fynbos edges

Generally, differences in arthropod species richness were more pronounced between plot locations in the upper vegetation layers than between those in the lower vegetation or ground layers of vineyards and fynbos. In the G-G layers, arthropod species richness was significantly higher in vineyards compared to fynbos interior, while in the CC-Up layers richness was similar in vineyards and fynbos. This may be due to vegetation structure (Franin et al., 2016), habitat complexity (Benton et al., 2003), and habitat heterogeneity (Langellotto & Denno, 2004) being similar in the CC-Up layers. In the Up-Up layers arthropod species richness was significantly higher at all fynbos plots compared to all vineyard plots. This may be due to a combination of factors i.e., major differences in vegetation structure, habitat complexity, and habitat heterogeneity between vines and fynbos plants, disturbances associated with vineyard management i.e. tractor activity, pruning, harvesting, etc., and vines being seasonal and only having foliage from spring until autumn. Perennial crop systems may also be disrupted by pesticide applications which make refuge outside of the treated area critical (Landis et al., 2000). Populations which may have taken an entire growing season to establish in a crop, may actively emigrate to adjacent natural areas when declines in resource availability occurs, whether the decline in resources is due to temporal variations or management activities (Rand et al., 2006). The steep gradient between arthropod richness on vines and fynbos plants, and the distinct arthropod assemblages that occurred in vines and cover crops, highlights the importance of managing for complex cover crops to support additional arthropod species and provide refuge during times of disturbances or temporal variations.

Crop-associated arthropod richness was significantly higher in the fynbos 10 m plots compared to fynbos interior, which might indicate that fynbos edges provide alternate resources for vineyard arthropod species living close to the edges, which can be used during periods when resources in vineyards are under stress (Rand et al., 2006). Alternate resources include floral nectar, pollen, prey/host species, and shelter (Evans & England, 1996; Gurr et al., 2017; Hickman et al., 1995; Tylianakis et al., 2004). Important alternate resources can increase natural enemy abundance, activity, or impact near crop field edges compared to field interiors (Rand et al., 2006). Farmland-forest edges typically host species associated with adjoining habitats and edge specialists, and which benefit from light, microclimate, and hydrological conditions that are unique to the edge environment (Šálek et al., 2015). Exploiting resources in both biotopes would be advantageous to the survival of arthropods. Predatory arthropods living close to alternate resources experience increased longevity and fecundity, which in turn, may increase population growth rates and explain the higher densities of predators near the edges (Rand et al., 2006), and here could be reflected in the higher species richness of crop-associated and ubiquitous arthropods near the edges. An alternative explanation for this pattern could be that crop-associated species do not disperse very far into natural habitat (e.g. Rand et al., 2006).

Despite the similarities in species richness along the transects for some of the vegetation layers, arthropod assemblage structure in each of the vegetation layers was significantly different between all vineyard and fynbos plots. This result is in line with Gaigher et al. (2015) who reported that natural sites and vineyards had very different parasitoid assemblage structures. The abrupt change in arthropod assemblages between vineyards and fynbos is evidence that large-scale spillover at the assemblage level did not occur between the two biotopes here. Although many of the sampled species, i.e. ubiquitous species, use both biotopes, this distinction between the biotopes at the overall assemblage level may be due to strong preferences of crop associated arthropods to remain in vineyards, and non-crop associated arthropods to remain in fynbos. Certain predator groups have a strong preference for remaining in natural systems (Baldissera et al., 2004; Martin & Major, 2001), while others have a strong preference for remaining in cropping system (Duelli et al., 1990; Orr et al., 2000).

3.5.2 Environmental drivers of crop-associated, fynbos-associated, and ubiquitous arthropod species richness in vineyards and fynbos

None of the environmental variables measured acted as significant drivers for fynbos-associated arthropod species richness in vineyards, hence nothing could be inferred relative to possible adjustments to management practices to improve spillover in vineyards. However, fynbos-associated arthropod species richness was positively correlated with number of plant species present in vineyards, with marginal significance. Neither of the management variables measured had significant effects on crop-associated, fynbos-associated, or ubiquitous arthropod species richness. Management variables not having any negative effects on arthropod species richness could be an indication that the farms in the present study were sensitively managed, and that the IPW guidelines for number of insecticide applications and dosages applied for specific products are within acceptable limits.

Vineyard environmental variables that enhanced vineyard arthropod richness for the other arthropod groups were all cover crop related variables i.e. percentage of herbaceous vegetation, mean vegetation height, and number of plant species. Symondson et al. (2002) recorded predator groups i.e. spiders, carabid, staphylinid, and coccinellid beetles as important in suppressing crop pests, and are known to use herbaceous habitats extensively. Shapira et al. (2017) found that arthropod abundance and richness within taxa in vineyards in Israel were greater in herbaceous vegetation than on the vines. Butterfly and moth species richness has been seen to peak in taller vegetation (Pöyry et al., 2006), and more suitable niches and feeding resources occur in tall compared to short successional vegetation (Morris, 2000). Sanguankeo & León (2011) in California, Gaigher & Samways (2010) in the Cape Winelands of South

Africa, and Winter et al. (2018) in a meta-analysis of vineyards under a Mediterranean climate, all found a positive relationship between non-crop plants and arthropod diversity, as well as beneficial effects of non-crop plants on biodiversity and ecosystem services. Therefore, even though non-crop vegetation did not enhance spillover of fynbos-associated species, the positive effect on crop-associated and ubiquitous species has important positive implications for agroecosystem functioning.

In fynbos, crop-associated arthropod species richness was negatively correlated with most of the environmental variables that were measured i.e. mean soil compaction, mean volume of plant litter, and mean vegetation height. This could be due to more favourable conditions for crop-associated arthropods in vineyards i.e. the lower soil compaction and higher volume of plant litter. Crop-associated arthropods, being adapted to a vineyard environment, may have a strong preference to remain in the vineyard environment (Duelli et al., 1990; Orr et al., 2000) rather than the fynbos environmental variables negatively affecting arthropod species per se. Crop-associated arthropod species richness was significantly influenced by the plot location on the transects in fynbos, with significantly higher species richness at fynbos 10 m plots compared to fynbos 50 m and 100 m plots. This shows that spillover of crop-associated arthropods did occur from vineyards to fynbos, although mostly limited to the edge, and that spillover could be facilitated by environmental variables such as mean soil compaction that was similar for vineyards and fynbos 10 m plots. Fynbos-associated arthropod species richness was positively correlated to the mean number of plant species in fynbos and was not significantly influenced by the plot location along the transects in fynbos. Fynbos-associated arthropod richness not being affected by plot location on the transects is a positive result, indicating that vineyard management activities did not affect fynbos-associated arthropod species in the surrounding fynbos within 100 m of the edge. Ubiquitous arthropod species were positively correlated to relative soil moisture in fynbos, and was significantly influenced by plot location along the transects, with species richness being significantly higher in fynbos 10 m plots compared to fynbos 50 m and 100 m plots. Ubiquitous arthropod species richness being positively correlated to soil moisture in fynbos, and also being significantly higher at the fynbos 10 m plot locations, could be an indication that ubiquitous arthropods are benefitting from and using water originating from vineyard irrigation, as mean soil moisture was higher in vineyards compared to fynbos.

Results here, where spillover from fynbos to vineyards was limited, has implications for fynbos-associated arthropod species in remnant patches, and in the long-term, may have negative effects on populations through ecological relaxation (Kuussaari et al., 2009). One reason for most fynbos-associated arthropods not spilling over into vineyards, may be because fynbos vegetation and remnant patches are ancient compared to the native vegetation or semi-natural vegetation referred to in the many studies on arthropods in European farmlands (Andersson et al., 2014; Caprio et al., 2015; Hendrickx et al., 2007; Muneret et al., 2018; Weibull et al., 2003). Fynbos patches in these agricultural landscapes are true remnants that have been relatively undisturbed both through historical and recent times (Linder, 2005). Many arthropod groups in fynbos are highly adapted to, and have developed specialist relationships with fynbos vegetation during the process of coevolution (Augustyn et al., 2013; Wright & Samways, 2000), and this might be why fynbos-associated arthropods prefer to remain in fynbos. Some arthropod groups have a strong preference for, and remain in, natural systems (Baldissera et al., 2004; Martin & Major, 2001). Here, due to the lack of evidence that environmentally friendly farming can ensure the conservation of fynbos-associated arthropod species, it becomes critical to preserve remnant patches of natural vegetation in order to maintain an important component of arthropod diversity (Theron et al., 2020). The preservation of remnant patches should therefore be incorporated in farmland conservation planning.

3.5.3 Composition of crop-associated, fynbos-associated, and ubiquitous arthropod species in different vegetation layers in vineyards and fynbos

The composition of crop-associated, fynbos-associated, and ubiquitous arthropod species among the different microhabitats were explored to determine whether certain arthropod groups are more prevalent in certain microhabitats. If a greater proportion of fynbos-associated arthropod species occurred in one of the vineyard microhabitats, or a larger proportion of crop-associated arthropod species occurred in one of the fynbos microhabitats, it would have been an indication that that specific microhabitat could facilitate the spillover of the respective arthropod group. For example, a flowering weed layer enhances pollinator spillover from natural vegetation into orchards (Carvalheiro et al., 2011). However, there were no significant differences in proportion of crop-associated, fynbos-associated, and ubiquitous arthropod species richness among the different microhabitats in each biotope, showing that certain microhabitats are not preferentially used by certain species groupings. For example, the proportion of crop-associated arthropod species, in terms of richness, which occurred in each of the vegetation layers in vineyards, was equal to the proportion of fynbos-associated, and the proportion of ubiquitous arthropod species richness that occurred in these three vegetation layers. The same was true for the proportions of arthropod species richness of the three arthropod groups in fynbos microhabitats.

Proportions of arthropod abundances among microhabitats in vineyards, and among microhabitats in fynbos, were significantly different. Most arthropods in vineyards were crop-associated and ubiquitous individuals which mostly occurred on the cover crops, followed by the ground and then vine foliage. The proportion of crop- and fynbos-associated arthropods were equal on the cover crops, and most individuals on vine foliage were ubiquitous arthropods. In fynbos, most arthropod individuals were on fynbos foliage.

Similar ratios of arthropod species richness in microhabitats and arthropod assemblages being significantly different in each of the microhabitats, is evidence that vineyards hold the potential to support a wide range of arthropod species, with different niche requirements, at fairly high abundances. Rosas-Ramos et al. (2019) highlighted the importance of maintaining different types of ecological infrastructures (woodland hedges, rosaceous hedges, grass strips, flower strips) across vineyard agroecosystems as the abundance, richness, and distribution of functionally important families are determined by features characterising the different types of infrastructures.

3.6 Conclusion

No significant environmental or management drivers that would facilitate arthropod spillover from fynbos to vineyards were identified. This means that no suggestions can be made on possible practices that would improve spillover into vineyards. These results suggest that for highly stenotopic species associated with remnant vegetation, softening of the agricultural matrix may not be an effective solution for increasing landscape permeability. Instead, we may need to focus on the retention of remnant stepping-stone habitats or conservation corridors, and maintain remnant patches close to each other.

In contrast, cover crop related variables did improve species richness of crop-associated and ubiquitous arthropods, with evidence for the potential of vineyards to support a wide range of arthropod species in high abundance. The range of ubiquitous arthropod species may have been somewhat inflated through including juvenile spiders. However, as these morphospecies were mainly in the ubiquitous species category, their pattern of occurrence would have been consistent across most sites. These results for the CFR, contrast with studies reporting spillover of native arthropods from European semi-natural areas to croplands, with spillover of fynbos-associated species from fynbos to vineyards being negligible. Spillover of ubiquitous arthropods is possible in both directions across the vineyard-fynbos edge as this group of arthropods were most likely generalist species (Blitzer et al., 2012) with a broad range of prey species (Thorbek & Bilde, 2004) and habitat requirements (Brouat et al., 2004; Rainio & Niemelä, 2003). Nevertheless, there was limited spillover from the vineyards into the fynbos. Spillover from vineyards to fynbos is poorly studied, and it is not clear how this will affect adjacent fynbos populations. Use of biological control involving releases of so-called 'specialised' natural enemies for the control of specific agricultural pests can spillover and attack native species in adjacent natural habitats (Tscharntke et al., 2005a), and predator spillover from high densities to areas with lower densities are to be expected (Rand et al., 2006). This is important, as spillover from vineyards into fynbos might have deleterious effects on native diversity, whereas the aim for the management of Cape Winelands vineyards should be to conserve as much fynbos as they can in order to conserve the natural arthropod population in fynbos or remnant patches. I suggest that more studies at a finer-scale need to be done in the CFR/CWBR in order to determine specific environmental and management drivers of specific beneficial arthropod species across edges between vineyards and fynbos, as farm managers or viticulturists could benefit from spillover of such arthropods in the fynbos-vineyard direction. Even if spillover in the fynbos-vineyard direction only occurs during brief periods each year, such periods may be associated with enhanced predator activity in vineyards. Additional assessments are needed to determine how spillover in the vineyard-fynbos direction affects native arthropod communities and population dynamics, especially for farms where biological control is applied, and where fynbos remnants are small and subject to greater edge effects (Ewers et al., 2007).

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Chapter 4: Assessing local- and landscape-scale effects on vineyard arthropod biodiversity in the Cape Winelands Biosphere Reserve

4.1 Abstract

Understanding the effects of agricultural practices on farmland biodiversity requires a landscape perspective, as local-scale processes can be mediated by the structure of the surrounding landscape. Here, I assess the extent to which landscape complexity (proportion of natural vegetation in the surrounding landscape) interacts with local-scale variables (percentage herbaceous vegetation in the cover crop, and farming approach, i.e. organic vs. integrated) to influence vineyard arthropod biodiversity in the Cape Winelands Biosphere Reserve (CWBR). Responses were assessed for overall arthropods sampled, as a whole, and subsets of the overall arthropods that were divided into three categories based on habitat specialisation i.e. arthropods with a high affinity to 1) vineyards, 2) fynbos (natural vegetation), or 3) both systems. Contrary to expectation, there was no interaction between the effects of landscape complexity and either of the local-scale variables on any of the species richness response variables. However, overall and ubiquitous arthropod species richness was enhanced by percentage herbaceous vegetation in cover crops in all landscape contexts. Landscape complexity influenced fynbos-associated arthropod assemblages through an increase in surrounding source habitat. Furthermore, interactions between the effects of landscape complexity and farming approach (organic vs. integrated) significantly influenced the assemblage structures of all arthropod categories, suggesting that integrated vineyards are more similar in arthropod assemblage composition despite different landscape complexities, whereas they diverge in organic vineyards. The positive effect of increased herbaceous vegetation cover on vineyard arthropod species richness is robust and consistent across different landscapes, and can be recommended to farmers in different zones of the BR. Further assessment is needed to understand the effect of organic farming on landscape-scale biodiversity.

Keywords: Arthropod biodiversity, agroecosystem, assemblage structure, fynbos, landscape complexity, landscape scale, local scale, species richness.

4.2 Introduction

Agricultural intensification, with its associated changes in the landscape, emerged as a serious threat to biodiversity in the 20th century (Robinson & Sutherland, 2002). Major land-use changes include habitat loss and fragmentation due to agricultural expansion (Fletcher et al., 2018; Haddad et al., 2015; Pereira et al., 2010; Rands et al., 2010; Wilcove et al., 1986), and conversion of complex natural ecosystems into simplified, managed ecosystems with generally higher resource use, application of pesticides, and agricultural output (Tscharntke et al., 2005a).

Over the past few decades there has been increased recognition of the importance of spatial scale for population dynamics (Holt, 2002; Muneret et al., 2019; Ries et al., 2004). The distribution and abundance of populations and their biotic interactions depend on processes at spatial scales larger than the local habitat patch, and patterns of diversity and interactions are influenced by factors at both the local- and landscape-scale (Tscharntke et al., 2005b). Different species experience their surroundings at different spatial and temporal scales owing to different traits i.e. body size, life history, and resource requirements (Schmidt et al., 2007; Steffan-Dewenter et al., 2002). Local communities assemble from the regional species pool and pass through a series of filters that act on different spatial scales (Lawton, 1999). These environmental filters differ in composition, configuration, and structure, and affect species richness (Robertson et al., 1990; Weibull et al., 2000), composition of communities, and their functional structure due to species-specific ecological traits (Burel et al., 1998; Lessard et al.,

2011) such as body size and trophic guild (Tscharntke & Brandl, 2004). Therefore, connectivity in the landscape is important to allow the entire species pool to access local sites so that sorting can occur (Leibold et al., 2004).

Higher landscape heterogeneity is associated with higher abundance and diversity of various taxa in agroecosystems (Chaplin-Kramer et al., 2011; Rusch et al., 2016a). Natural habitats provide important resources i.e. food, alternate hosts, and refuge to species colonising crop fields, and some of the negative impacts of intensive crop management can be offset by complex, high-diversity landscapes, but not by simple landscapes (Tscharntke et al., 2005a). Indeed, there can be mediating effects of the landscape on local-scale management practices. According to the intermediate landscape complexity hypothesis, benefits of local biodiversity-friendly management practices are expected to be small in extremely simplified and in complex landscapes compared to landscapes of intermediate complexity (Rusch et al., 2017). The lack of positive effects of local management efforts on biodiversity are expected in complex landscapes where diversity is already high everywhere, whereas in extremely simplified landscapes there is insufficient biodiversity to colonize crop fields to translate any positive efforts of local management into significant biodiversity increases (Rusch et al., 2017). Therefore, positive effects of local management efforts on biodiversity are expected to be revealed best in intermediate landscape complexities, but this hypothesis lacks empirical validation and studies in perennial cropping systems are scarce (Rusch et al., 2017). Managers will benefit from identifying interactions between local and landscape variables to determine the most effective context for implementing conservation measures, which will greatly assist in best practice decision-making.

The effects of both landscape complexity (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Rusch et al., 2016b) and local management i.e. organic farming and in-field diversification (Lichtenberg et al., 2017), and their interactions, have mostly been studied in the Northern

Hemisphere (Tuck et al., 2014) on annual crops (Thomson & Hoffmann, 2013). Perennial systems vary greatly from annual systems in terms of temporal dynamics and disturbance regimes (Bruggisser et al., 2010; Rusch et al., 2015) which can lead to different effects on biodiversity composition (Rusch et al., 2017). Little is known about these effects on perennial crops (Thomson & Hoffmann, 2013) in Mediterranean regions (Lichtenberg et al., 2017).

There is a stark contrast between the natural remnant fynbos vegetation in the Cape Floristic Region (CFR) farmland areas and the natural or semi-natural vegetation in European farmlands. Fynbos is dominated by fine-leaved sclerophyllous shrubs (53.2%), has a large number of geophytes (17.4%), very few tree species (2.4%), and a very low number of annuals (6.7%) (Goldblatt & Manning, 2002). Fynbos has also been relatively undisturbed historically and in more recent times (Linder, 2005), and has high plant and arthropod species turnover (van Schalkwyk et al., 2019). On the other hand, in Europe, human pressures on the natural environment is high, with 51.4% of the European Union's territory consisting of urban, industrial, and agricultural land, and 97% of its forests under management (García-Feced et al., 2014). In Europe, semi-natural vegetation in agricultural land is broadly divided into two core groups, 1. large areas of semi-natural vegetation which include semi-natural grasslands, agro-forestry areas, or traditional orchards, and is described as high nature value farmland (Paracchini et al., 2008), and 2. small unfarmed features which include natural and anthropogenic components such as hedgerows, buffer strips, field margins, or woodlots (IEEP & Alterra, 2010).

Vineyards are a perennial Mediterranean crop of major economic importance. To optimise wine production, vineyards are usually managed intensively, which has a negative effect on biodiversity and ecosystem services, although cover crops in the inter-rows enhance biodiversity and ecosystem services (Winter et al. 2018). Furthermore, extensive inter-row vegetation management and increased floral resource availability in vineyards strongly promotes species richness, abundance, and functional traits of wild bees (Kratschmer et al. 2019).

Organic farming is an additional local-scale factor important globally for biodiversity. Both organic farming and higher in-field diversity enhances arthropod abundance of rare taxa which increases richness and facilitates ecosystem services (Lichtenberg et al. 2017), as was found in the CFR (Chapter 2).

The CFR is a hyper-diverse global biodiversity hotspot, renowned for its exceptional level of plant endemism and landscape-level species turnover (Goldblatt & Manning, 2000; Manning & Goldblatt, 2012; Rebelo et al., 2006). The CFR is under constant pressures from land transformation and increasing population density (Fairbanks et al., 2004). It has largely been transformed into an urban-agricultural matrix, the Cape Winelands, of which viticulture is the dominant agricultural crop. My study was conducted on farms that are located in the CFR and surrounded by remnant natural vegetation, ranging from 2.5% to 54.4% of natural remnant vegetation in a 1 km buffer area surrounding each farm. A great amount of remnant vegetation remains in the farmlands of the CFR (Cox & Underwood, 2011), making coexistence of conservation and wine production crucial, especially as the natural diversity is irreplaceable yet revenue from wine production is essential for regional development.

The CWBR is situated within the CFR and was designated in 2007 by the International Coordinating Council (ICC) of the United Nations Educational, Scientific, and Organisation's (UNESCO) Man and the Biosphere (MAB) Programme and covers a land area of 322 032 ha. The biosphere reserve consists of zones with different levels of utilisation. The inner core zone consists of formally protected natural vegetation, the buffer zone consists of low intensity land use, and the outer transition zone consists of more extensive development (Fig. 4.1). The vine (*Vitis vinifera*) is a major crop in the CFR, with 88 366 ha under cultivation, comprising 96%

of South Africa's wine grape vineyards (SAWIS, 2019), dominating large areas in the transition and buffer zones of the CWBR. Wine farms in different parts of the biosphere reserve are therefore situated in greatly different landscape contexts with much variation in the level of transformation surrounding them. There is a major contrast between managed vineyards, consisting mostly of vines and weeds associated with cover crop management, and the surrounding fynbos which is mainly nutrient deficient and sclerophyllous in nature.

A limited number of studies have assessed the interaction between local-scale vineyard practices and the surrounding landscape in this region (see Kehinde et al. 2018; Kehinde & Samways, 2012), and in European landscapes (see Buchholz et al., 2017; Kratschmer et al., 2019). Kehinde et al. (2018) found that bee abundance responded positively to increased flower density at higher proportions of uncultivated land surrounding vineyards in the CFR, and Kehinde & Samways (2012) showed that bee abundance increased with increasing proportion of natural habitat surrounding organic but not conventional vineyards in the CFR. In European vineyards, there is an interaction between landscape compositional diversity and floral resource availability, where diverse landscapes compensate for low floral resources for eusocial wild bees (Kratschmer et al. 2019). In contrast, strong effects of local management practices can sometimes outweigh landscape effects, such as soil management effects on soil biota in Austrian vineyards, which did not interact with the surrounding landscape in a substantial way (Buchholz et al., 2017).

One of the major challenges in understanding how biodiversity is affected by habitat structure and ecological processes is the great variation and uniqueness of sites combined with taxa responding differently to different stimuli or factors. For this study, I therefore assessed the species richness and assemblage structure of various arthropod taxa at a local scale, but taking into account the influence of the surrounding natural landscape-scale complexity to gain insight into the interacting effects of these factors in the CWBR.

4.2.1 Aim

To determine the relationship between landscape-scale variables and local-scale variables, and the effect that this relationship has on arthropod species richness and assemblage structure within vineyards in the CWBR.

4.2.2 Objectives

1. To determine the effect of landscape and local variables, and their interaction on arthropod species richness within vineyards. A significant interaction would indicate a mediating effect of the landscape on local-scale practices.

2. To determine the effect of landscape and local variables, and their interaction on arthropod assemblage structure within vineyards.

3. To assess how these relationships differ between different categories of arthropod species, that are expected to respond differently to factors at different spatial scales. The categories were crop-associated (i.e. vineyard-associated), fynbos-associated (i.e. natural habitat-associated), and species associated with both types of ecosystems (i.e. ubiquitous arthropods). This was also assessed for the overall arthropod dataset to include responses of species not in any of the three categories.

4.2.3 Hypotheses

1. Species richness and assemblage structure of crop-associated arthropods are determined by local-scale variables, as these arthropods are significant indicator species of vineyards, and are expected to utilise and respond to within-vineyard resources and conditions.

2. Species richness and assemblage structure of fynbos-associated arthropods are determined by the landscape-scale variables, as these arthropods are significant indicator species of fynbos and are expected to respond to the landscape complexity surrounding vineyards.

3. The overall and ubiquitous species richness and assemblage structures will be determined by an interaction between the local- and landscape-scale variables. This is predicted, as overall arthropods are arthropods that occur in both biotopes regardless of their association or affinity to any specific one of the biotopes, and the ubiquitous arthropods are significantly associated with both biotopes and seem to require resources available in both fynbos and vineyards. If there is an interaction, the positive effects of local-scale management will be most pronounced in intermediate complexity landscapes (Tscharntke et al., 2005a).

4.3 Materials and methods

4.3.1 Study sites and sampling design

A total of 40 vineyards were used as sampling units, spread across 18 commercial wine farms. Farms were selected to represent a range of management practices and localities throughout the CWBR (Figure 4.1). Vineyard blocks ranged in size from 1 – 14.4 ha. Eleven of the 40 vineyards were located on organically certified farms, with a mean vineyard block size of 2.82 ha. Certification was undertaken by Ceres[1], Demeter[2], and Ecocert[3]. The remainder of the vineyards were managed according to the guidelines of the Integrated Production of Wine Scheme of South Africa (IPW) (IPW, 2018). The mean size of vineyard blocks on integrated farms was 4.21 ha. Where more than one vineyard block was selected on a single farm, the vineyard blocks were spaced 170-1360 m apart to avoid pseudoreplication. Sampling was

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[1] http://www.ceres-cert.co.za
[2] https://www.demeter.net
[3] https://www.ecocert.com/en/home

conducted at the centre of blocks to minimise edge effects (> 20 m away from the edge). Sampling was undertaken over two seasons, May 2016 (autumn, post-harvest), and October 2016 (spring, early in the fruit setting season).

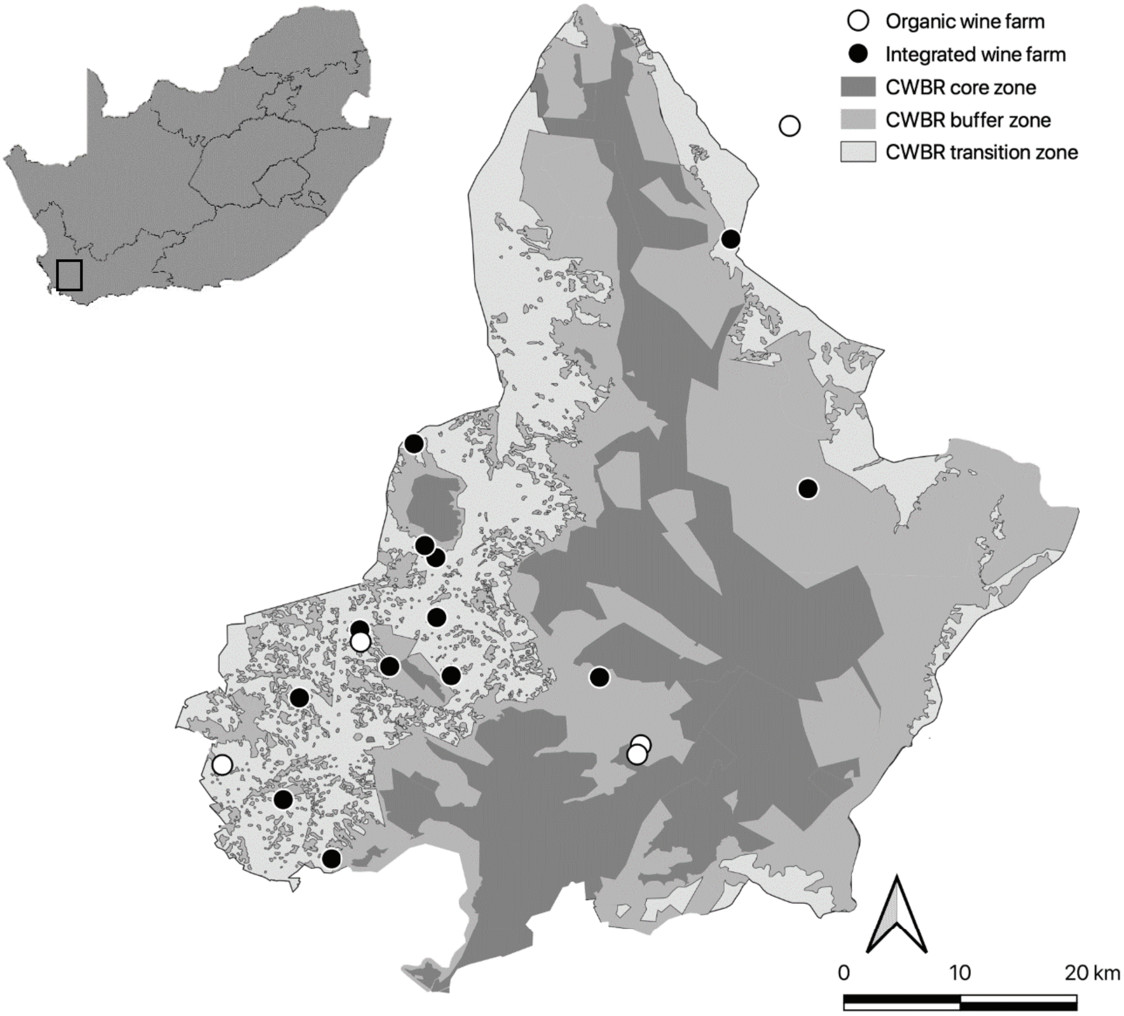

Figure 4.1: A map of farms used within the Cape Winelands Biosphere Reserve. See Appendix K for detailed site information.

4.3.2 Arthropod collection

At each plot, ground-dwelling arthropods were collected using four pitfall traps (300 ml plastic jars with 6 cm diameter openings) (Woodcock, 2005). This added up to 160 pitfall traps and 40 pitfall samples (each pitfall trap array was pooled) per sampling period. Each pitfall trap contained 200 ml solution of ethylene glycol preservative and water (3:1) with two added drops of dishwashing liquid to reduce surface tension (Woodcock, 2005). At each plot, the four pitfall traps, one on each corner of a 1 m^2-quadrat, were sunk into the ground until the brim of the trap was level with the soil surface. The pitfall trap array was always placed with two pitfall traps in the inter-row and the remaining two in the vine row. Pitfalls were left open for one week before they were retrieved and taken back to the laboratory. All pitfall trapping was completed over a period of 82 days. Samples were washed with water and preserved in a 75% ethanol solution for later sorting and identification.

Arthropods on cover crops and vines were collected using a vacuum sampler. A Stihl SH56C-E vacuum shredder was used as vacuum sampler by attaching a 30 cm-long fine mesh bag onto the 10 cm diameter opening of the vacuum pipe. The bag then acts as a net for arthropods and debris during the vacuuming process. This method is effective for sampling vegetation-dwelling arthropods in the area (Swart et al., 2017). One vacuum sample, at each plot, consisted of two sets of 100 insertions of the vacuum pipe into the vegetation along a walked transect. Each cover crop sample was taken within a single inter-row, < 10 m away from either side of the pitfall trap array, whereas each vine sample was split equally across two vine rows on either side of the pitfall trap array, < 10 m away from the pitfall trap array. Each sample was stored in a clear labelled plastic bag (250 mm × 360 mm) and preserved at -10°C for later sorting and specimen identification. Where cover crop or vine foliage were absent, due to management practices or seasonal variation, the vacuum pipe was brought very close to the soil surface, or pushed onto the vine to remain consistent with sampling effort throughout the sampling periods.

4.3.3 Arthropod identification

All spiders (Araneae), beetles (Coleoptera), and true bugs (Hemiptera) were extracted from samples and were identified to morphospecies level (Oliver & Beattie, 1996) using a Leica

MZ75 stereomicroscope (Leica Microsystems, Germany). Spiders, beetles, and true bugs were used as study taxa as they were the most abundant in samples and represent three feeding guilds (herbivores, predators, or detritivores among the various species), which maximises the range of responses to various changes in the environment. Spiders are sensitive responders to vineyard mosaic in the study area (Gaigher & Samways, 2014; Theron et al., 2020). Ground beetles (Carabidae) (Goulet et al., 2004; Rainio & Niemelä, 2003), spiders (Pearce & Venier, 2006), and bugs (Gerlach et al., 2013) are good bioindicators of habitat types, environmental quality, and for biodiversity studies. Spiders and beetles are species-rich groups in agricultural landscapes, and vary in their life-history strategy, degree of specialisation, and can be important for biological control (Östman et al., 2001; Weibull et al., 2003).

Spiders, including juveniles, were identified by a specialist to genus, and some to species, and a large proportion of the juvenile spider reference specimens that were identified to genus level could be confirmed as distinct morphospecies. Spider specimens are deposited in the National Collection of Arachnida in the National Museum, Pretoria. The beetle reference specimens were identified by a specialist to family level, and beetles and true bugs were classified into broad feeding guilds (see Scholtz & Holm 2012). Easily recognisable true bug families/subfamilies (e.g. Reduviidae, Anthocoridae, Phymatidae, Asopinae, and Nabidae) were classified as predators with the remaining morphospecies classified as herbivores, without family level identification, as most other bug taxa in the region are herbivorous (Scholtz & Holm 2012). The beetle and bug reference collections are stored in the Stellenbosch University Entomological Museum.

4.3.4 Local-scale variable

The local-scale variable, *% herbaceous vegetation* (comprising a mixture of spontaneous cosmopolitan weed species i.e. *Hypochaeris radicata*, *Plantago lanceolata*, and *Oxalis* species, and sown cover crops i.e. legumes), was recorded in two separate quadrats of 1 m^2 at each plot. One quadrat was placed on the vine row, and one in the inter-row. Local-scale data for the two quadrats at each plot were averaged. The local-scale variable *Organic* or *Integrated* is based on whether plots occurred on farms that were certified organic, or not.

4.3.5 Landscape-scale variable

The online application CapeFarmMapper version 2.2.2.1 was used to calculate the area land cover of natural vegetation (henceforth "fynbos"), in a buffer area with a radius of 1 km, surrounding each plot. A buffer area with a 1 km radius was used as this distance has been shown to be ecologically important for mobile arthropods (Rusch et al., 2017; Thies et al., 2005; Winqvist et al., 2011). Percentage natural area surrounding vineyards (henceforth "landscape complexity") was used. Chaplin-Kramer et al. (2011) described percentage natural habitat as a more consistent metric of landscape complexity compared to percentage crop and percentage non-crop. CapeFarmMapper is a product of the Western Cape Department of Agriculture (WCDoA), developed by a team of geographic information science technologists. The product was designed to assist with spatial information queries and decision-making in agricultural and environmental management in the Western Cape (WCDoA, 2019).

A point was drawn at each plot location, and a buffer area of 1 km was then created around each point. Zonal statistics for the created buffer areas were calculated from a land cover raster layer of South Africa which was compiled by National Geo-spatial Information (NGI, 2017) under the Department of Rural Development and Land Reform. The layer was compiled by means of satellite imagery and surface reflectance data products with Landsat 8 OLI/TIRS Level-2. The positional accuracy of topographical data captured did not exceed 3 m (horizontal) of its true ground position at the 95% confidence interval (Semoli et al., 2019). The total area of fynbos (natural sclerophyllous vegetation) was calculated within each buffer by using zonal statistics, and was cross-checked manually by confirming that raster layer pixels corresponded to the actual landscape features in satellite images.

4.3.6 Statistical analyses

Arthropod data for the two sampling seasons were pooled for analyses, and vegetation data were averaged. Univariate and multivariate analyses were done in R (R Core Team, 2018), and multivariate data were visualised in PRIMER 6 version 6.1.13 (Clarke & Gorley, 2006) & PERMANOVA+ version 1.0.3 (Anderson et al., 2008) from PRIMER-e. The overall arthropod species richness and abundance datasets, as well as subsets of significant indicator species richness and abundances were used in analyses, as one of the objectives here is to assess how patterns of arthropod species richness and assemblage structures differ depending on different categories of arthropod species within vineyards. The subsets were extracted from the complete dataset of the previous chapter, where arthropods were sampled in both biotopes (fynbos vs. vineyard) and identified as being significant indicators of vineyards (crop-associated), fynbos (fynbos-associated), or both biotopes (ubiquitous) using the *indicspecies* package (Cáceres & Legendre, 2009). The test interprets a matrix of species and the biotope in which they were sampled, and then makes use of abundances to statistically weigh species as significant indicators of the specified biotope. Here, the subsets include crop-associated, fynbos-associated, and ubiquitous species that were sampled in vineyard interiors only. Species that were infrequently sampled (often singletons and doubletons) were not included in any of these three categories, but were included in the overall arthropod category. Sampling effort was visualised as a species accumulation curve based on the overall abundance of species sampled, and species accumulation curves for each of the three categories of arthropods, based on abundances. Species accumulation curves were created in Primer 6 & PERMANOVA+.

4.3.6.1 Effect of local and landscape variables on arthropod species richness within vineyards

Response variables were tested for normality using the Shapiro-Wilk test of normality in the *stats* package (R Core Team, 2018), and spatial autocorrelation was tested for using the Mantel test in the *ade4* package (Dray & Dufour, 2007). Due to some response variables having spatial autocorrelation, a random spatial variable was included for all response variables during model testing, namely 'Farm' (Figure 4.1). The continuous landscape variable was converted to categories by dividing the continuous data into three levels of landscape complexity based on the percentage of natural area within the 1 km buffer area for each plot, where: $x \leq 18\%$ = '*Low*', $x > 18\%$ and $\leq 36\%$ = '*Intermediate*', and $x > 36\%$ = '*High*'. Cut-off percentages for categories were determined by considering a histogram of the number of plots representing the range of percentages of natural area. Landscape complexity was categorised in order to create interaction graphs, in the case of significant interactions between local and landscape variables, and to reduce the possible number of outcomes to a more manageable amount for interpretation. The *lme4* package (Bates et al., 2015) was used to assess main effects and interactions of the local and landscape variables on each response variable. Two separate sets of models were created including either of the two different local-scale variables assessed (herbaceous vegetation cover and overall farming approach) and are referred to further on as the HerbVeg models and the FarmApp models. Linear mixed-effects models were used for response variables with normal distribution, and generalised linear mixed-effects models with a log link function were used for response variables with a Poisson distribution (Bolker et al., 2009).

4.3.6.2 Effect of local and landscape variables on arthropod assemblages within vineyards

Main effects and interactions of the local- and landscape-scale variables were assessed for their effect on assemblage structures. Here, I also created two separate sets of models including either herbaceous vegetation cover or farming approach as the local-scale variable. The *mvabund* package in R (Wang et al., 2019) was used to create multivariate space based on the abundance of each species. The manyglm function was then used to fit generalised linear models to the high-dimensional multivariate abundance data with a negative binomial link function (O'Hara & Kotze, 2010). Models were tested for significant main effects and/or interactions using analyses of deviance, where the p-value was calculated using 999 resampling iterations via PIT-trap resampling to account for correlation in testing.

Canonical analyses of principal coordinates (CAPs), for multivariate response variables that had significant main effects and/or interactions in R, were created in Primer 6 & PERMANOVA+ as available packages for visualising mvabund do not allow for easy interpretation of multivariate interactions. Abundance matrices were square root transformed to reduce the influence of abundant species before creating resemblance matrices using Bray-Curtis similarity metric. The local-scale variable was made categorical by categorising the continuous data into two levels based on the presence of herbaceous vegetation for each plot, where: $x < \text{mean}(x)$ = '*Low*' and $x > \text{mean}(x)$ = '*High*'. The categorical local and landscape variables were then combined to create a six-level factor for each response, and CAPs models were permutated 9 999 times. CAPs, used to interpret assemblage structure, may have exaggerated separation of sites as CAP tests are constrained analyses based on PERMANOVA which have been criticised to behave unreliably when analysing unbalanced designs. PERMANOVA may be too liberal when a smaller group has greater dispersion, or overly conservative when a larger group has greater dispersion (Anderson & Walsh, 2013).

4.4 Results

An overall total of 21 550 individual arthropods comprising 554 morphospecies were sampled. The Chao2 predictor estimated 811.7 ± 48.83 species, and the Jackknife2 predictor estimated

869.8 species (Appendix J). From this, 42 species (9 546 individuals) (Chao2: 42 ± 0.89 and Jackknife2: 43.93 species, Appendix J) were crop-associated, 36 species (643 individuals) (Chao2: 37.33 ± 1.85 and Jackknife2: 38.15 species, Appendix J) were fynbos-associated, and 223 species (10 003 individuals) (Chao2: 291.6 ± 25.45 and Jackknife2: 395.59 species, Appendix J) were ubiquitous. For a detailed list of the local variables and surrounding landscape complexity for each farm, see Appendix K.

4.4.1 Effect of local and landscape variables on arthropod species richness within vineyards

In the HerbVeg models, no interactions were found between the effects of herbaceous vegetation cover and landscape complexity on overall species richness, or any of the three arthropod categories (Table 4.1). The only significant main effects were that overall and ubiquitous arthropod richness were positively influenced by the percentage herbaceous vegetation that was present in the cover crop of vineyards (Figures 4.2 and 4.3). In the FarmApp models, there were also no interactions between the effect of overall farming approach and the surrounding landscape, and neither of the main effects had an effect on arthropod species richness of any of the arthropod categories (Table 4.1). I ascertained whether surrounding landscape complexity and % herbaceous vegetation varied between organic and integrated vineyards to avoid associated bias. By running a lmm with landscape complexity (area of natural vegetation) as a function of farming approach, I detected no significant difference ($P = 0.08$) in landscape complexity surrounding organic vineyards (81.31 ha ±18.14 ha) and integrated vineyards (76.10 ha ± 9.32 ha). Similarly, a lmm with % herbaceous vegetation as a function of farming approach detected no significant difference ($P = 0.41$) in the prevelance of herbaceous vegetation in the cover crops of organic vineyards (13.60% ± 3.74%) and integrated vineyards (10.37% ± 1.91%).

Table 4.1: Univariate results showing the effects of local (% herbaceous vegetation and organic farming) and landscape variables (landscape complexity) on the overall species richness, and species richness of three arthropod categories for the HerbVeg and FarmApp models.

HerbVeg model				
	Overall	Crop-associated	Fynbos-associated	Ubiquitous
Landscape complexity	0.52	0.26	1.51	0.46
% Herbaceous vegetation	9.38**(+)	1.04	0.88	18.04***(+)
(Interaction)	0.72	0.35	3.87	3.73
FarmApp model				
	Overall	Crop-associated	Fynbos-associated	Ubiquitous
Landscape complexity	1.71	0.32	1.11	0.07
Organic farming	0.02	0.86	1.60	0.01
(Interaction)	0.11	1.37	1.50	0.04

Statistics are given: The type II Wald chi-square values, followed by the level of significance and the direction of relationship in brackets. Significance levels are based on p-values where ≤ 0.05 '*', ≤ 0.01 '**' and ≤ 0.001 '***'. Conditional R^2 values for mixed models as per response variable in the HerbVeg model: Overall (0.73), Crop-associated (0.55), Fynbos-associated (0.09), and Ubiquitous (0.76). Conditional R^2 values for mixed models as per response variable in the FarmApp model: Overall (0.67), Crop-associated (0.57), Fynbos-associated (0.15), and Ubiquitous (0.62).

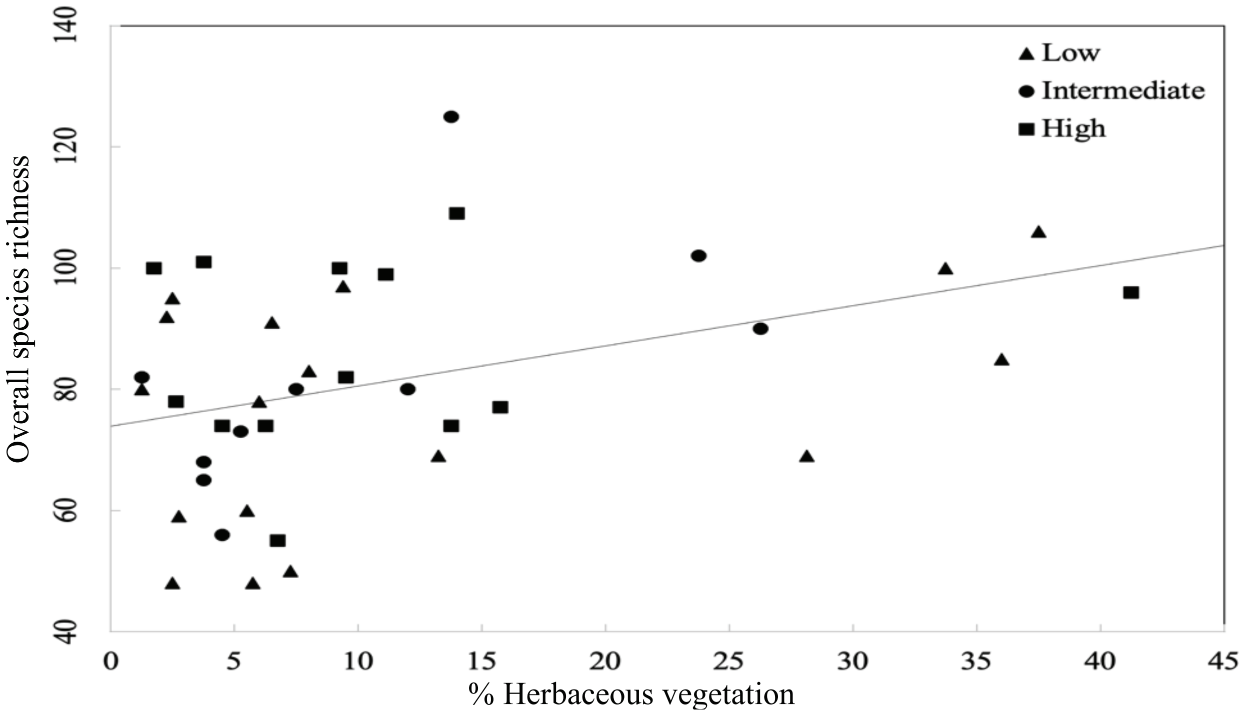

Figure 4.2: The positive relationship between overall arthropod species richness and the percentage of herbaceous vegetation present in the cover crop at low, intermediate, and high landscape complexities.

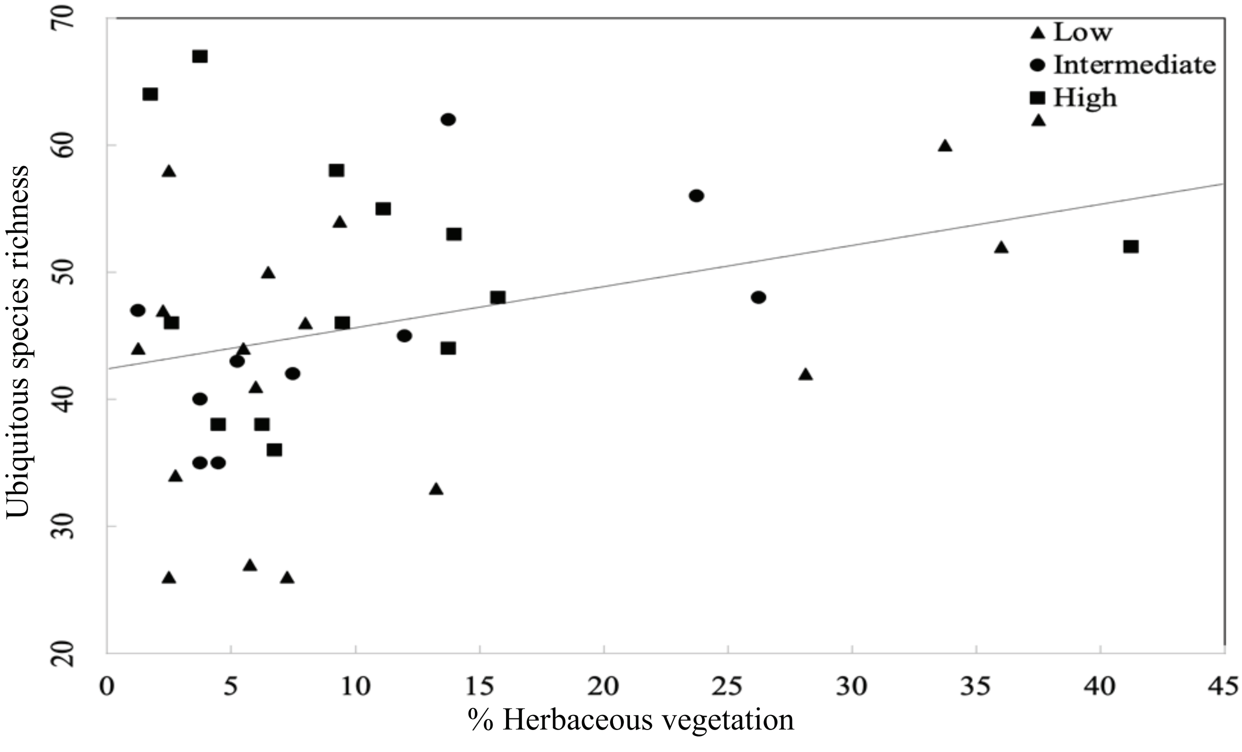

Figure 4.3: The positive relationship between ubiquitous arthropod species richness and the percentage of herbaceous vegetation present in the cover crop at low, intermediate, and high landscape complexities.

4.4.2 Effect of local and landscape variables on arthropod assemblage structure within vineyards

In the HerbVeg models, an interaction between percentage herbaceous vegetation and landscape complexity significantly affected the overall and ubiquitous arthropod assemblages in vineyards (Table 4.2), although it was not possible to determine the nature of this interaction through visual inspection of the graphs (Figures 4.4 and 4.5). Fynbos-associated arthropod assemblage structure within vineyards were significantly affected by landscape complexity alone (Table 4.2) (Figure 4.6).

In the FarmApp models, an interaction between organic farming and landscape complexity significantly affected the overall arthropod assemblage structure, and the assemblages of all three arthropod categories in vineyards (Table 4.2). For arthropods overall, and all three categories, there were major differences in different landscape contexts between the organic vineyards, whereas the effect of landscape context was less pronounced in integrated vineyards (Figures 4.7-4.10).

Table 4.2: Multivariate results showing effects of local (% herbaceous vegetation and organic farming) and landscape variables (natural complexity) on overall arthropod assemblage, and assemblages of the three arthropod categories in vineyards for HerbVeg and FarmApp models.

HerbVeg model				
	Overall	Crop-associated	Fynbos-associated	Ubiquitous
Landscape complexity	1546.50*	101.10	125.88**	648.80*
% Herbaceous vegetation	852.80**	62.20	49.30	353.90*
(Interaction)	790.80**	131.40	44.75	425.0*
FarmApp model				
	Overall	Crop-associated	Fynbos-associated	Ubiquitous
Landscape complexity	1546.50*	101.11	125.88**	648.80*
Organic farming	786.00**	64.08	41.03	345.70*
(Interaction)	805.50***	160.76**	64.52*	422.00***

Statistics are given: The type II Wald chi-square values followed by the level of significance. Significance levels are based on p-values where ≤ 0.05 ‘*’, ≤ 0.01 ‘**’ and ≤ 0.001 ‘***’. Conditional R^2 values for mixed models for all response variables in the HerbVeg model was $R^2 = 0.06$. Conditional R^2 values for mixed models as per response variables in the FarmApp model: Overall (0.06), Crop-associated (0.05), Fynbos-associated (0.07), and Ubiquitous (0.06).

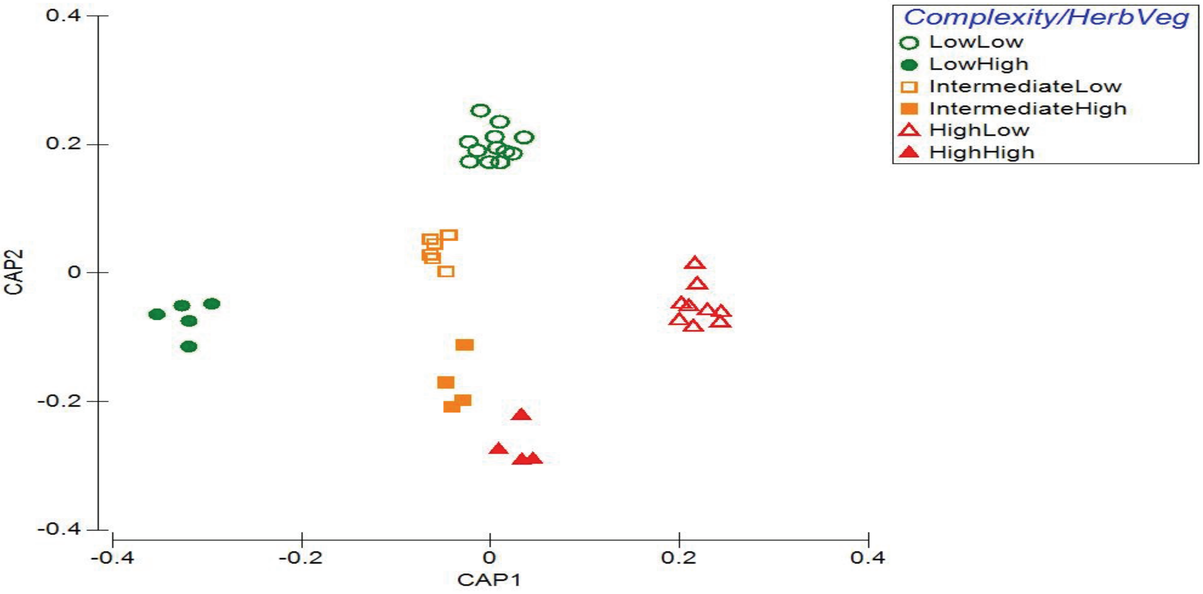

Figure 4.4: A canonical analysis of principal coordinates showing the differences in overall arthropod assemblage structures in different landscape complexities and with different levels of herbaceous vegetation cover.

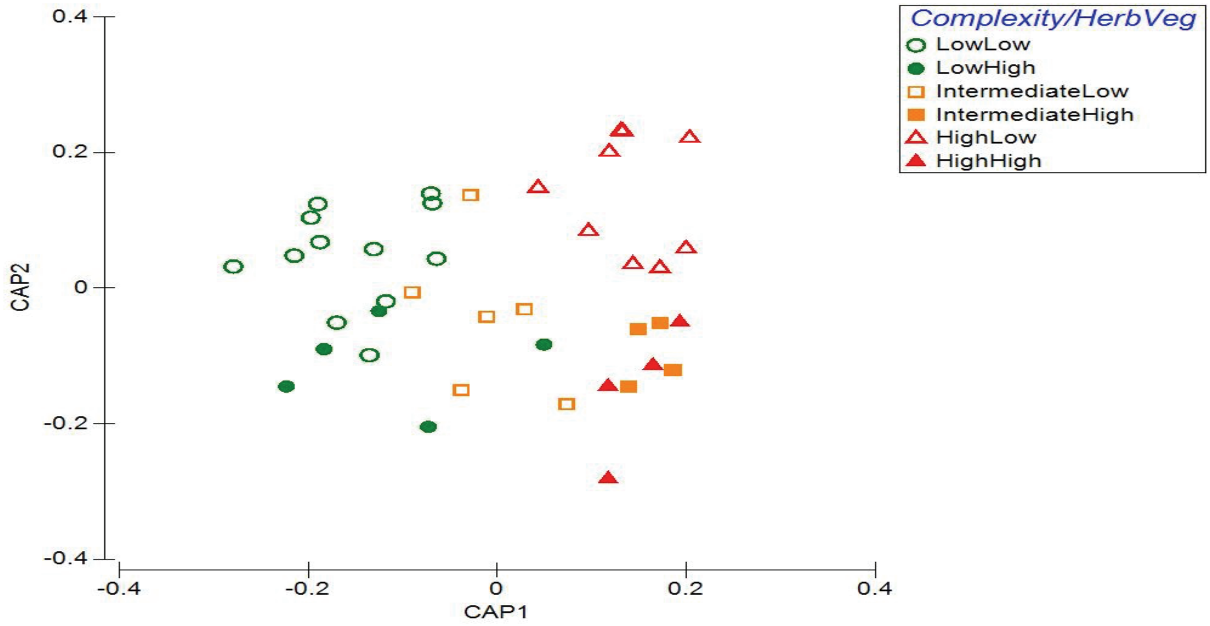

Figure 4.5: A canonical analysis of principal coordinates showing the differences in ubiquitous arthropod assemblage structures in different landscape complexities and with different levels of herbaceous vegetation cover.

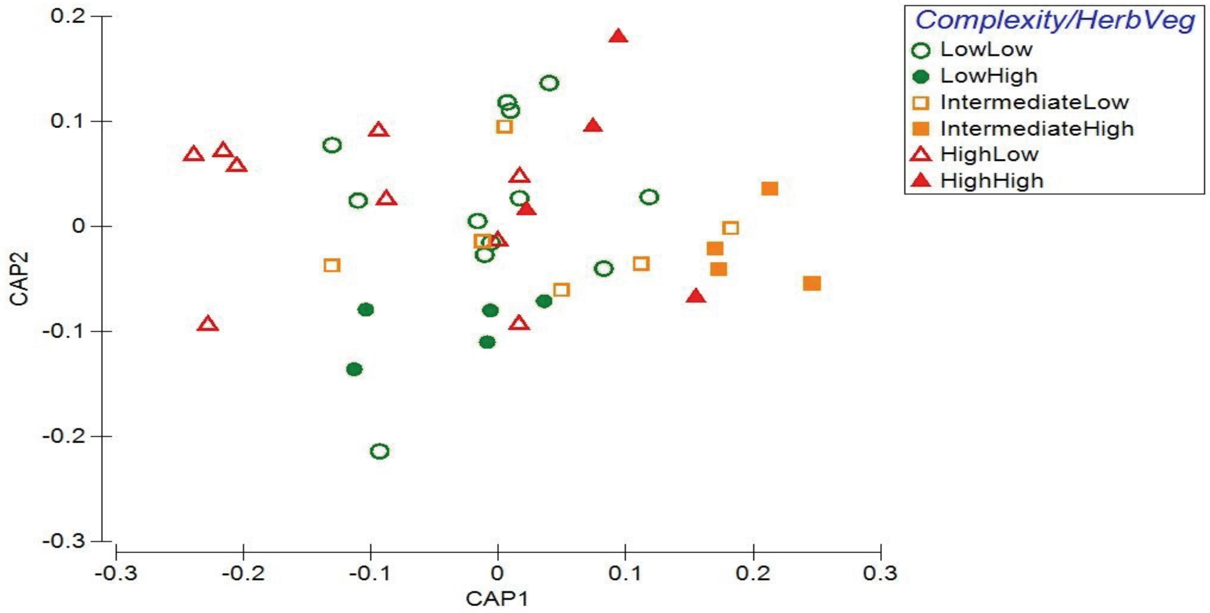

Figure 4.6: A canonical analysis of principal coordinates showing the differences in fynbos-associated arthropod assemblage structures in different landscape complexities and with different levels of herbaceous vegetation cover.

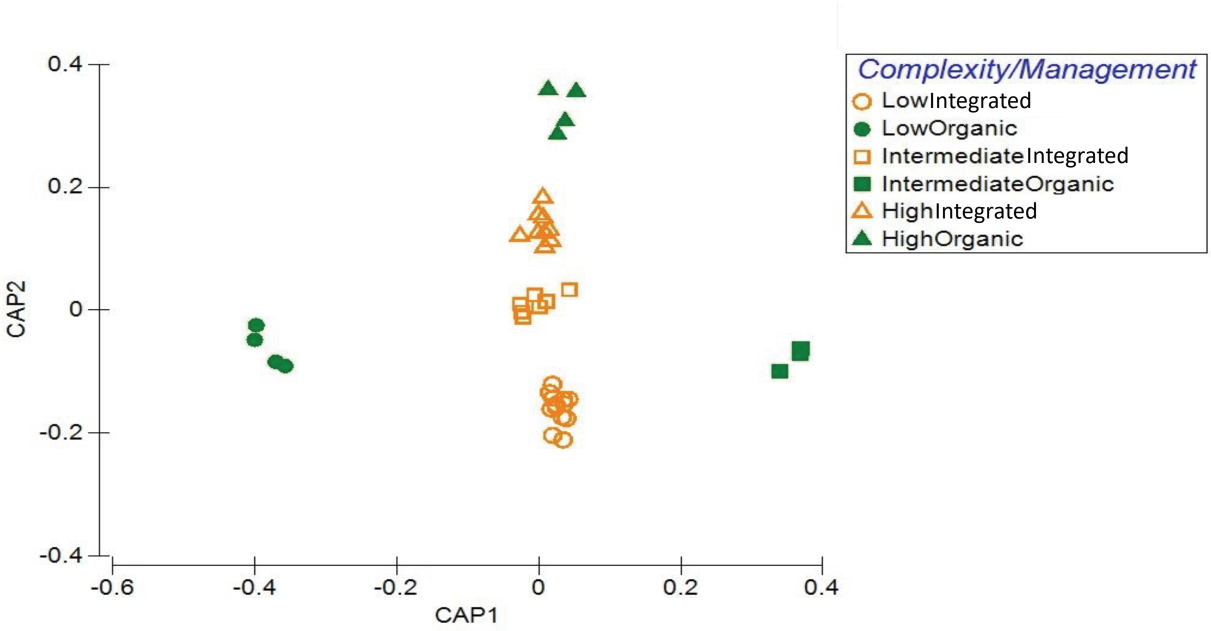

Figure 4.7: A canonical analysis of principal coordinates showing the differences in overall arthropod assemblage structures associated with different landscape complexities and in organic vs. integrated vineyards.

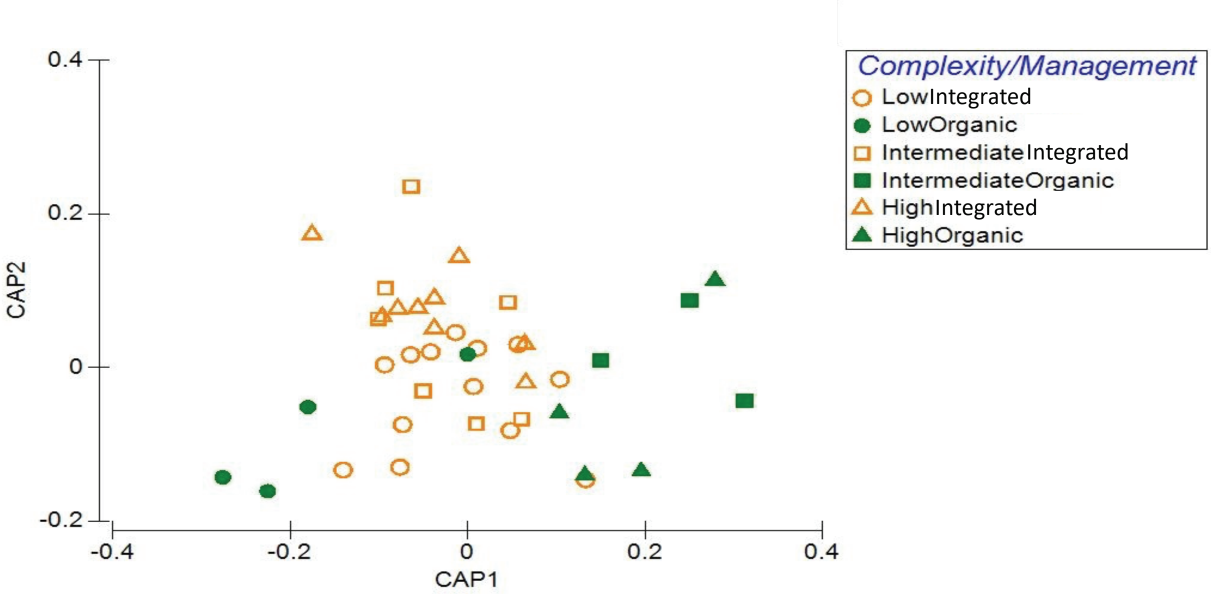

Figure 4.8: A canonical analysis of principal coordinates showing the differences in crop-associated arthropod assemblage structures in different landscape complexities and in organic vs. integrated vineyards.

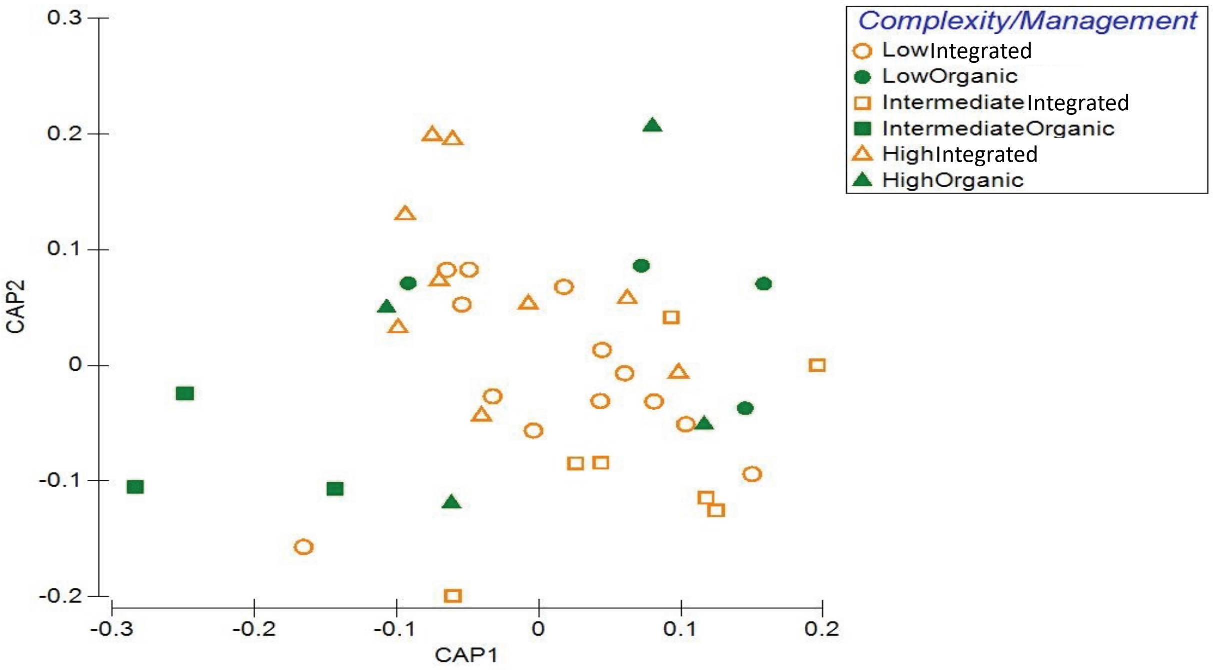

Figure 4.9: A canonical analysis of principal coordinates showing the differences in fynbos-associated arthropod assemblage structures associated with different landscape complexities and in organic vs. integrated vineyards.

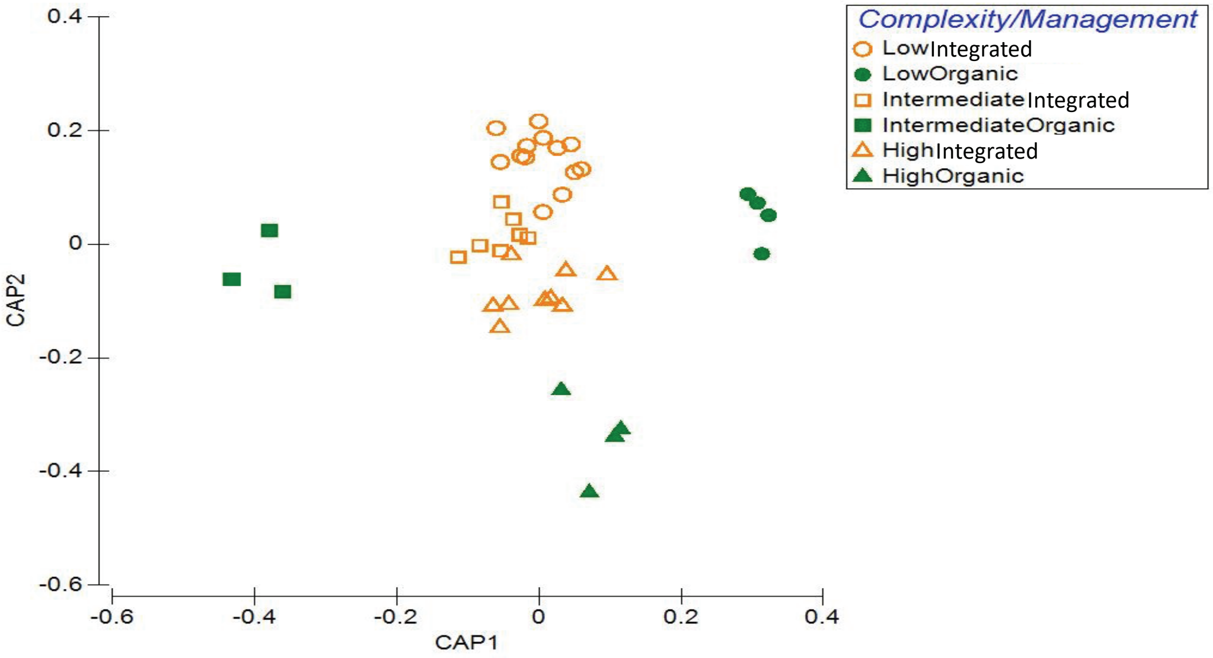

Figure 4.10: A canonical analysis of principal coordinates showing differences in ubiquitous arthropod assemblage structures associated with different landscape complexities and in organic vs. integrated vineyards.

4.5 Discussion

Surprisingly, none of the univariate results supported my hypotheses. There were no mediating effects of landscape complexity on the response of species richness to herbaceous vegetation within the cover crops, or to an organic farming approach. These results contrast with the main trends in the literature, which show that interactive effects of local and landscape variables on farmland biodiversity are common in many regions (Holzschuh et al., 2007; Muneret et al., 2018; Nicholson et al., 2017). The lack of interaction here could be due to strong segregation of arthropod assemblages between the vineyards and fynbos. Previous studies in this region have shown that arthropod spillover between fynbos vegetation and cultivated areas is lower than expected (Chapter 3; Gaigher et al., 2015; Gaigher & Samways, 2014; van Schalkwyk et al., 2020) possibly due to high contrast between these biotopes and the high level of specialisation of fynbos arthropods. This could mean that complementary habitat use between biotopes is less prevalent here than in older, more transformed agricultural regions, which would make an interaction between local- and landscape-scale variables less detectable.

Alternatively, the lack of interacting effects of landscape complexity and local-scale variables on arthropod richness may be due to biodiversity in the CFR vineyard landscapes already being relatively high, even in landscapes that were classified here as low complexity. Tscharntke et al. (2012) hypothesised that the positive effects of conservation management on farmlands in complex landscapes with a high proportion of non-crop habitat should be less observable than in simpler landscapes, as biodiversity and associated functioning is already high throughout complex landscapes. This has been demonstrated for some systems, for example, both Tuck et al. (2014) on the effect of organic farming on biodiversity, and Batáry et al. (2011) on agri-environmental management on pollinator species richness, found greater positive effects in simple compared to complex landscapes.

Study sites were located in the CFR, a biodiversity hotspot, which makes it possible that sites that were categorised as being surrounded by low natural complexity were more complex compared to high complexity sites as described in a number of other similar studies. Tscharntke et al. (2012) described a complex landscape as an area containing > 20% non-crop vegetation, and Purtauf et al. (2005), Roschewitz et al. (2005), Thies & Tscharntke (1999), and Vollhardt et al. (2008) all described a complex landscape as containing > 50% non-crop, semi-natural, or uncultivated land. Here, the minimum and maximum percentages of remnant fynbos vegetation in buffer areas were 2.5% and 54.4%, respectively, for the entire dataset, and percentage fynbos in landscapes classified as complex ranged from 36-54.4%. This estimate of non-crop vegetation included in the models can be considered to be conservative, as the estimate only included relatively undisturbed vegetation and did not include semi-natural vegetation. The minimum and maximum estimate would be 4.8-71% when semi-natural vegetation is included, and the range for complex landscapes would then be 47.3-71%. Therefore, it may have appeared as though arthropod species richness was unaffected by a landscape-local interaction as the landscape was complex throughout the study region.

Contrary to my expectations, local variables did not affect crop-associated arthropod species richness and the landscape variable did not affect fynbos-associated arthropod richness. These results could be an artefact of the arthropod categories that consisted of significant indicator species of the two biotopes. Several crop-associated species are generalist predators and are well adapted to vineyards, such as ground beetles (Symondson et al., 2002) and arable spiders (Schmidt et al., 2007), which thrive in vineyards regardless of local management (Schmidt et al., 2005). By contrast, fynbos-associated arthropods may contain many specialist species adapted to the surrounding natural fynbos, and therefore remain in fynbos (Baldissera et al., 2004; Martin & Major, 2001). This is likely the case here, as the number of fynbos-associated individuals sampled in vineyard interiors were relatively low.

Nonetheless, there was a significant main effect of herbaceous vegetation cover on overall and ubiquitous arthropod species richness, which were positively correlated to the percentage herbaceous vegetation present in cover crops. Ubiquitous species richness here may be slightly inflated due to the inclusion of juvenile spiders. However, this approach was consistent across sites, and is unlikely to influence the overall patterns. Various authors (Eckert et al., 2020; Lichtenberg et al., 2017; Sanguankeo & León, 2011; Winter et al., 2018) have underscored the importance of maintaining a diverse cover crop in perennial agricultural systems. This approach promotes farmland diversity through mechanisms such as providing alternate resources to arthropod species, many of which, in turn, are associated with economically important ecosystem services e.g. predation of crop pests (Vogelweith & Thiéry, 2017; Winqvist et al., 2011) and pollination (Garibaldi et al., 2016).

At the local-scale, species richness is typically positively correlated with habitat quality, which is usually measured as plant species richness (Kleijn et al., 2004) or abundance of plants needed for food and/or reproduction (Steffan-Dewenter & Tscharntke, 2001). Increased arthropod diversity in vineyards will increase the diversity of responses to disturbances, which is critical to ensure ecological resilience in all ecosystems, including agroecosystems which are generally associated with frequent disturbances. For example, following a more severe disturbance event, i.e. a required spot-treatment of insecticide due to a pest outbreak, a diverse cover crop may increase re-establishment rates of natural enemies and other beneficial arthropods in vineyards (Bengtsson et al., 2003).

However, in line with my hypotheses, interactions were found between herbaceous vegetation cover and landscape complexity on overall and ubiquitous assemblage structures. The interaction between organic farming and landscape complexity affected the assemblage structures of all three arthropod categories within vineyards, even the crop-associated and fynbos-associated species, which was not hypothesised.

Patterns on the ordination graphs of the HerbVeg models suggest that there is a relatively high species turnover between different landscape complexities, which may be linked to natural divergence of assemblages across different types of landscapes (Laurance et al., 2007; van Schalkwyk et al., 2019). However, interpreting the interactions with herbaceous vegetation cover, based on the graphs, was not possible. The nature of the mediating effect of landscape complexity on herbaceous vegetation cover therefore requires further in-depth study.

The interaction between landscape complexity and farming approach was relatively consistent between arthropod categories. Despite a relatively low amount of variation explained by the models, the CAP analyses provided insight into these results. The overall arthropod assemblage appears to converge among integrated vineyards and diverge among organic vineyards. Arthropod assemblages had more overlap in integrated vineyards regardless of the surrounding natural complexity, whereas arthropod assemblages in organic vineyards showed greater dissimilarity from each other, and from integrated vineyard assemblages, and these differences appear to depend on surrounding natural complexity. Conventional farming, which is associated with monocultures due to more frequent and intensive inputs, may cause arthropod assemblages to converge regardless of the surrounding natural complexity. Organic farming which is associated with more diverse cover crops, and less frequent and intensive inputs, could cause species assemblages to diverge through more specialised or localised species that differ across landscape contexts being able to utilise the organic vineyards more (Lichtenberg et al., 2017).

Organic farming interacted strongly with the surrounding landscape, i.e. proportion of fynbos and proportion of associated species in the species pool in the surrounding buffer, was reflected more clearly on organic farms. This pattern is obscured on integrated farms and could be due to a homogenising effect of integrated farming in terms of species turnover. Previous work in this region has shown that neither organic nor conventional vineyards homogenise flowervisitation networks relative to natural fynbos areas (Kehinde & Samways, 2014). However, additional in-depth study of other taxa will be important to determine whether this trend is consistent for other arthropods.

Finally, in the HerbVeg models, there was a main effect of natural complexity on the fynbos-associated arthropod assemblage structure. This conformed to the hypothesis and suggests that fynbos species occurrence in vineyards are influenced by the amount of suitable fynbos habitat in the surrounding landscape.

4.6 Conclusion

There was a strong positive effect of increased herbaceous vegetation in the cover crop of vineyards on overall and more generalist arthropod species. This is good for buffering ecosystem functioning against environmental changes and is a key measure for enhancing field-scale biodiversity in vineyards in this region (Chapter 2, Chapter 3). Maintaining high levels of herbaceous vegetation in vineyards can be recommended to local winegrowers regardless of the natural complexity surrounding their vineyards.

Organic farming did not improve species diversity at the local scale, even in different landscape contexts. However, there were strong interaction effects between organic farming and surrounding natural complexity. Furthermore, arthropod assemblage structures on organic farms better reflected the local natural pool of species, but were dependent on surrounding natural complexity. In contrast, arthropod assemblages on integrated farms converged, regardless of surrounding habitat complexity. This was likely due to homogenising effects of integrated farming on the landscape, leading to equalisation of associated arthropod composition.

There are benefits to farming vineyards organically, especially through a diverse cover crop, reduction of intensive inputs such as tilling, mineral fertilisers, pesticides, and other practices normally associated with conventional farming. In sum, organic farming allows within-vineyard arthropod assemblages to more closely represent the native arthropod species pool.

As CWBR wine farms are largely connected to each other and given the wide range of how arthropods respond at different spatial scales, effective management requires a coordinated effort among farmers to promote arthropod diversity. It would make little sense, from a biodiversity conservation perspective, for one farm to promote ecological intensification and another agricultural intensification. Furthermore, the organic approach ensures functional connectivity and landscape heterogeneity, meaning that there is mutual benefit in farms co-operating, and there is a vehicle for doing this, the IPW initiative.

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Chapter 5: Comparison of arthropod species turnover, functional diversity, and functional trait associations in natural vegetation and vineyards in a biodiversity hotspot

5.1 Abstract

Agriculture is a major contributor to habitat transformation, homogenising biological communities and reducing biodiversity at local and regional scales. Over time, biotic homogenisation causes regional biotas to become genetically, taxonomically, and functionally more similar, impacting the functioning and resilience of both natural and agricultural systems. Here, I used beta and functional diversity analyses, and trait-based multivariate analyses to determine whether viticulture has a homogenising effect on spider and beetle assemblages across two biotopes in a biosphere reserve in the Cape Floristic Region (CFR) biodiversity hotspot. Both systems supported high spider and beetle alpha diversity. However, spider species richness was significantly higher in natural fynbos compared to vineyards. Spider beta diversity did not differ between systems, but was significantly lower for beetles in vineyards, driven mostly by a less nested structure, rather than assemblage turnover. Spider functional evenness and divergence were similar between the two systems, but functional richness was significantly lower in vineyards. Beetle functional evenness and richness were similar between systems, though functional divergence was significantly lower in vineyards. Assemblage composition of both taxonomic groups was significantly altered by the biotope in which they occurred, due to associations of species with different traits with each biotope. The strongest positive associations were that of plant-dwelling spiders and small-bodied beetles with fynbos, and predatory beetles with vineyards. The strongest negative associations were that of common spiders and predatory beetles with fynbos. Although there was a strong shift in the assemblage between fynbos and vineyard, with some negative effects of vineyards on some of the diversity measures, my results indicate that vineyards are by no means depauperate in arthropod diversity and support the concept that sensitively managed agroecosystems can support species-rich assemblages at different spatial scales.

Keywords: Assemblage structure, beetles, beta diversity, functional diversity, fynbos, species traits, spiders, vineyards.

5.2 Introduction

Within biodiversity hotspots, such as the CFR in South Africa, biodiversity and ecosystem function remain under pressure due to habitat fragmentation and degradation through land-use change. This occurs despite high conservation priority, as only parts are legally protected and conservation implementation can be ineffective (Topp & Loos, 2019). Habitat transformation, and subsequently fragmentation, produces a wide range of effects which are complex, occurring across several spatial scales and levels of biological organisation. These changes alter ecological processes, changing the spatial configuration of vegetation, and influencing taxa and species at the level of the individual (Lindenmayer & Fischer, 2007). Habitat transformation leads to the loss of important habitats, and transformed areas typically have a lower conservation value and can be difficult to incorporate in conservation networks (Rouget et al., 2003).

Agriculture is a major contributor to habitat transformation in the CFR (25.9% of the CFR) and has transformed some diverse habitats following agricultural expansion (Rouget et al., 2003). Agriculture is known to have homogenising effects on biological communities, as it reduces biodiversity and affects the distribution of species at both local and regional scales (Clough et al., 2007; Ekroos et al., 2010; Flohre et al., 2011; Gabriel et al., 2006). Biotic homogenisation increases the genetic, taxonomic, and functional similarity of regional biotas over time (Olden & Rooney, 2006). The process not only removes native species and simplifies the system through reducing the diversity of resources and biological interactions (Cardoso et al., 2020a), but it also allows for secondary invasions from ecologically dominant alien invasive species (Roy et al., 2016). In turn, the loss of diversity can impact the functioning and resilience of natural systems which could have profound implications for humans and wildlife (Ponisio et al., 2016). From an agricultural point of view, reducing the size of the species pool may impact the stability of services (Winfree & Kremen, 2009) and, in turn, the reliability of crop yields (Garibaldi et al., 2013).

In order to do effective conservation management in an area, an understanding of the relationship between local and regional diversity dynamics, and mechanisms that drive changes in diversity from local to regional scales are essential (Kraft et al., 2011). A clear understanding of such processes will not only enable conservation planning to identify areas which are more likely to be homogenised should anthropogenic land use occur there, but it may also provide decision-making with relevant steps to improve the heterogeneity of already homogenised areas (Karp et al., 2012). Regional patterns of diversity are the sum of within-patch (alpha) and among-patch (beta) diversities. Many ecologists' focus have recently shifted away from the traditional focus on alpha diversity patterns to studying drivers of beta diversity patterns (Stier et al., 2016), as beta diversity patterns give insight into factors that generate species boundaries (Condit, 2002), facilitate regional diversity, and produce alternate community states (Fukami & Nakajima, 2011). Beta diversity in some cases is poorly related to alpha diversity, and to be a better indicator of overall biodiversity (Clough et al., 2007; Flohre et al., 2011). Beta diversity has a direct effect on ecosystem function and comprises two different processes: species replacement (turnover) which occurs when species at some sites are replaced by different species at other sites, and species richness difference (gain or loss) when assemblages at some sites are nested subsets of one another along spatial or environmental gradients (Baselga, 2010; Legendre, 2014). Different aspects of ecological processes can be analysed through partitioning beta diversity into its replacement and richness difference components, for example, the rate of replacement is a function of ecological tolerance or niche breadth of a species and the richness difference reflects the diversity of niches (Legendre, 2014). Partitioning beta diversity into its replacement and richness difference components has the potential to reveal more complex patterns in community assemblages than using the overall coefficients alone (Cardoso et al., 2014). It is important to assess these patterns in order to draw more accurate conclusions about the effects of agricultural transformation, as high total beta diversity in transformed sites may be driven by localised species losses instead of true turnover, which leads to regional diversity declines (Socolar et al., 2016) and biotic homogenisation at the regional scale.

A common approach when analysing the distribution of co-occurring species is to model each species separately as a function of the environmental variables, which allows modelling different species as having different environmental responses, but these models fail to show how and why species respond differently (Brown et al., 2014). Species traits, behaviours, physiology, and morphology can help define how and why species respond to the environment (Hooper et al., 2005; McGill et al., 2006). Functional diversity is a facet of biodiversity which quantifies the value and range of biological traits which interact with the abiotic and biotic environment (Wong et al., 2019), and influences organism performance and thus ecosystem function (Díaz & Cabido, 2001; Petchey & Gaston, 2006; Tilman, 2001). In short, functional diversity is the distribution of species and abundance of a community in niche space (Mason et al., 2005). It can be partitioned into functional richness, evenness, divergence, and dispersion indices (Laliberté & Legendre, 2010; Mason et al., 2005) in order to assess the distribution of species in functional space. Functional diversity is a driver of ecosystem processes such as ecosystem services and resilience (Diaz et al., 2007; Folke et al., 2004; Hooper et al., 2005), and can provide important information about functional responses to land-use change, including biotic homogenisation in terms of functional homogenisation. Furthermore, trait-based approaches can provide a more mechanistic understanding of assemblage response to land-use change by identifying characteristics of species that are either vulnerable to landscape transformation, or that benefit from it.

The CFR of South Africa is a global biodiversity hotspot which has been considerably transformed for agriculture and urbanisation, and is under pressure from alien invasive vegetation (Cowling et al., 2003). The CFR supports an exceptional plant diversity of 9 383 species, of which 68% are endemic (Manning & Goldblatt, 2012), with a similar diversity of certain arthropods (Janion-Scheepers et al., 2020; Kemp & Ellis, 2017; Procheş & Cowling, 2006). At larger spatial scales, the diversity of the CFR is exceptional, with complete species turnover between vegetation types and great floristic dissimilarity along transects ranging from hundreds of metres to hundreds of kilometres (Rebelo et al., 2006). The high regional richness of the CFR is a function of the high turnover within and between moderately rich communities (Cowling, 1990).

The major crop in the CFR is wine grapes, with vineyards covering an area of roughly 88 366 ha, comprising 96% of South Africa's wine grape vineyards (SAWIS, 2019). Due to the high potential of future vineyard expansions and the limited extent of natural habitat remaining outside protected areas (Viers et al., 2013), it is important to assess the impacts of viticulture on beta and functional diversity at larger spatial scales in the CFR. A large portion of the CFR has been designated as the Cape Winelands Biosphere Reserve (CWBR) under the Biosphere Reserve Model of UNESCO's Man and the Biosphere Program, which strives to integrate development and conservation (Pool-Stanvliet & Giliomee, 2013). However, there is a gap in the knowledge of arthropod distribution patterns in the CFR, as much of the previous work focussed on plant diversity and patterns of distribution (Born et al., 2006; Cowling &

Campbell, 1984; Goldblatt & Manning, 2000, 2002; Linder, 2005; Manning & Goldblatt, 2012; Rebelo et al., 2006; Rouget et al., 2003).

Earlier work has assessed the effect of vineyards on arthropod alpha diversity (Gaigher et al., 2015, 2016; Gaigher & Samways, 2010; Kehinde & Samways, 2012; Kehinde et al., 2018), and has assessed patterns and drivers of arthropod beta diversity (Janion-Scheepers et al., 2020; van Schalkwyk et al., 2019), insect-flower interactions (Adedoja et al., 2018; Kehinde & Samways, 2014a), and the homogenisation of vineyards on insect-flower interactions (Kehinde & Samways, 2014b). To my knowledge, no work has been done on the effect of vineyards on arthropod turnover and functional diversity, or on how species-specific traits differ between vineyards and fynbos. Therefore, the aim of this chapter is to use beta and functional diversity analyses and trait-based multivariate analyses as tools to determine whether viticulture has a homogenising effect on the assemblage structures of two arthropod taxa, spiders and beetles, within the CFR.

5.2.1 Objectives

1. To compare overall alpha and beta diversity, and its turnover and richness components, of spider and beetle assemblages between fynbos and vineyards.

2. To compare functional diversity, using functional richness, evenness, and divergence of spider and beetle assemblages in natural fynbos and vineyards.

3. To determine whether spider and beetle assemblage composition differs between fynbos and vineyards, and which species traits are driving differences between assemblages in the two systems.

5.3 Materials and methods

5.3.1 Study sites and sampling design

A total of 11 vineyards adjacent to natural vegetation (henceforth ‘fynbos’) were used as sample units across 11 commercial wine farms (located 6 to 79.6 km apart). Farms were selected to represent a range of management practices and localities throughout the CWBR (Figure 5.1). Vineyard block sizes ranged between 1.25 and 6.1 ha. Two of the 11 vineyards were located on organically certified farms and had a mean vineyard block size of 1.96 ha. Certification was done by Ceres and Ecocert. The remainder of the vineyards were located on integrated farms and managed according to the guidelines of the Integrated Production of Wine Scheme of South Africa (IPW) (IPW, 2018). The mean size of vineyard blocks on integrated farms was 3.70 ha. On each farm, plots were located on a transect spanning within vineyards to within adjacent fynbos. A transect consisted of six plots, of which three were in the vineyard, and three in the fynbos, at 10 m, 50 m, and 100 m from the edge between the two systems. Sampling was undertaken over two seasons, May 2016 (autumn, post-harvest), and October 2016 (spring, early in the growing season when fruit was setting).

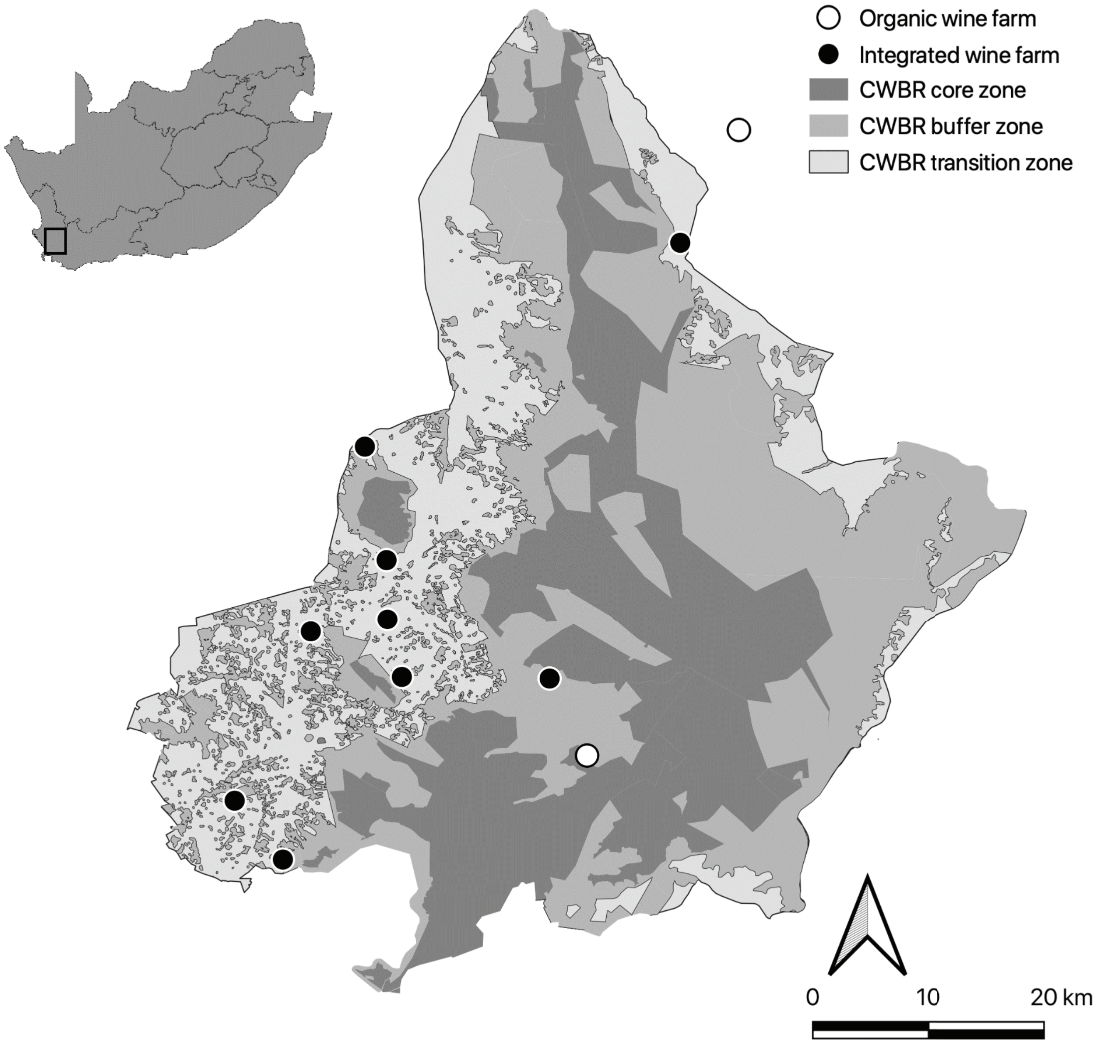

Figure 5.1: A map of farms used within the Cape Winelands Biosphere Reserve.

5.3.2 Arthropod collection

At each plot, arthropods were sampled on the ground and on the vegetation. In vineyards, vegetation sampling focused on the cover crops, as this has previously been shown to support the largest proportion of vineyard vegetation-dwelling arthropods compared to the vines (Chapter 3). Ground-dwelling arthropods were collected using four pitfall traps (300 ml plastic jars with 6 cm diameter openings) at each of the six plots on each transect (Woodcock, 2005). This added up to 264 pitfall traps and 66 pitfall samples (each pitfall trap array was pooled) per sampling period. Each pitfall trap was prepared with a 200 ml solution of ethylene glycol preservative and water (3:1) with two added drops of dishwashing liquid to reduce surface tension. At each plot, the four pitfall traps, one on each corner of a 1 m^2 quadrat, were sunk into the ground until the brim of the trap was level with the soil surface. In vineyards, the pitfall trap array was always placed with two pitfalls in the vine row and two in the inter-row. Pitfalls were left open for one week before they were retrieved and taken back to the laboratory. All the pitfall trapping was completed over a period of 82 days. Samples were washed with water, and then preserved in a 75% ethanol solution for later sorting and identification.

Arthropods on cover crops and fynbos vegetation were collected using a vacuum sampler. A Stihl SH56C-E vacuum shredder was used as vacuum sampler by attaching a 30 cm-long fine mesh bag onto the 10 cm diameter opening of the vacuum pipe. The bag then acts as a net for arthropods and debris during the vacuuming process. This method is effective for sampling vegetation-dwelling arthropods in this region (Swart et al., 2017). One vacuum sample, at each vineyard plot, consisted of two sets of 100 insertions of the vacuum pipe into the cover crop vegetation along a walked transect. Each cover crop sample was taken within a single inter-row, < 10 m away from either side of the pitfall trap array. Sampling of arthropods on fynbos consisted of two sets of 100 insertions into the fynbos, within a 10 m radius around the pitfall trap array. The first set of 100 insertions were done in one half of the 10 m radius circle and the second set of 100 insertions in the remaining half of the circle. Each sample was stored in a clear, labelled plastic bag (250 mm × 360 mm) and preserved at -10°C for later sorting and specimen identification. Where cover crops or fynbos were absent, due to management practices, seasonal variation, or natural distribution, the vacuum pipe was brought very close to the soil surface as to remain consistent with sampling effort throughout sampling periods.

5.3.3 Arthropod identification

All spiders (Araneae) and beetles (Coleoptera) were extracted from samples and were identified to morphospecies (Oliver & Beattie, 1996) using a Leica MZ75 stereomicroscope (Leica Microsystems, Germany). Spiders and beetles were used as study species as they were the most abundant in samples and represent three feeding guilds (detritivores, herbivores, or predators among the various species), which maximises the range of responses to various changes in the environment. Ground beetles (Goulet et al., 2004; Rainio & Niemelä, 2003) and spiders (Pearce & Venier, 2006) have been described as good bioindicators of habitat types, environmental quality, and biodiversity studies. Spiders have also been described as a species-rich group with high dispersal potential and varying degrees of habitat specialisation (Bell et al., 2005; Entling et al., 2007) which make them well suited for studying metacommunity dynamics (Schmidt et al., 2007). Beetle clades in European countries show a close relationship between ecological specialisation, dispersal ability, and compositional heterogeneity (Gómez-Rodríguez et al., 2015). Spider reference specimens were identified by a taxonomic specialist, at least to genus-level, and many to species-level, to reduce the inflation of spider species richness due to juvenile presence in field-collected samples. Where identification was done to genus-level, a large proportion of the reference specimens within a genus could still be classified as distinct morphospecies, even though the species names could not be assigned. Spider specimens are deposited in the National Collection of Arachnida in the National Museum, Pretoria. The beetle reference specimens were classified into morphospecies, identified by a specialist to family level, and categorised into functional feeding guilds based on the primary feeding mode of the family according to Scholtz & Holm (2012). The beetle reference collection is stored in the Stellenbosch University Entomological Museum.

5.3.4 Arthropod traits

Spider traits considered were mean body size, hunting mode (i.e. active hunter or web builder), preferred substrate (i.e. ground dweller or plant dweller), local abundance (based on the number of localities a species has been recorded in South Africa, where 1 is common [known from > 10 localities] and 3 is rare [known from 1 - 3 localities]), and endemicity (based on the extent of distribution of a recorded species, where 0 is cosmopolitan/introduced and 6 is endemic i.e. known from one locality only) as described in Dippenaar-Schoeman et al. (2010). Where body size was not available for a specific species, or a specimen was identified to genus-level only, the mean body size of the range of body sizes, as described in Dippenaar-Schoeman et al. (2010), for that genus was used. Among spiders, larger body sizes have been identified as a proxy for reproductive success (Bowden et al., 2015), and in arthropods, feeding guild has been identified as a proxy for trophic level and position in the food web, and that it determines the quality of resources which has an influence on species growth, reproduction, and survival (Moretti et al., 2017). Beetle traits considered were body length, feeding guild (predator, herbivore, or detritivore), and whether it was winged or wingless. Beetles' body lengths were measured from the tip of the head to the tip of the abdomen to the nearest tenth of a millimetre using hand-held calipers. Beetles were observed using a Leica MZ7s dissecting microscope (Leica Microsystems, Germany) to determine whether flying wings were present or absent. For each of the two taxa the finest available scale of body size and length measurements available were used, therefore spider body size was a continuous variable whereas beetle body length was a categorical variable. Beetle body lengths were categorised into small = 1 (0-0.33 cm), medium = 2 (0.34-0.66 cm), and large = 3 (> 0.66 cm) based on a histogram of body length distribution for all measured beetles. Body length was included as a trait as it may indicate prey type, prey size, and feeding rate, and may provide information on dispersal ability. Hunting strategy gives information about activity rates and foraging mode (Rusch et al., 2015), and flight ability may give insight into the dispersal ability of species. In general, higher trophic level species (Kruess & Tscharntke, 1994) with low dispersal abilities (Hendrickx et al., 2009), and highly specialised or endemic species (Kehinde & Samways, 2012) are more sensitive to disturbances. I therefore expect that the diversity of arthropods in the predatory feeding guild and less mobile arthropods will be negatively affected by vineyards in the landscape.

5.3.5 Statistical analyses

Arthropod data for the two sampling seasons were pooled for analyses. All statistical analyses were done using R (R core team, 2018) statistical software.

5.3.5.1 Alpha and beta diversity

For alpha diversity, arthropod data for vineyard plots across all transects were pooled and arthropod data for fynbos plots across all transects were pooled. This was done separately for spiders and beetles. The *BAT* package (Cardoso et al., 2020b) was used to calculate the alpha diversity of spiders and beetles within each biotope. The *lme4* package (Bates et al., 2015) was then used to create linear models with the alpha diversity of spiders and beetles as a function of biotope. For beta diversity, arthropod data for vineyard plots were pooled per transect and arthropod data for fynbos plots were pooled per transect, but not across farms (one transect per farm). This was done separately for spiders and beetles. The *BAT* package was used to calculate beta diversity (β_{Tot}) and its two components namely, replacement (β_{Rep}), and richness difference (β_{Ric}) using pairwise comparisons of Sørensen dissimilarity coefficients (Baselga, 2010; Ricotta & Pavoine, 2015). Normality of the three beta diversity components were tested by performing Shapiro-Wilk normality tests. Linear models were then created, using the *lme4* package, with the different beta diversity components as a function of biotope.

5.3.5.2 Functional diversity

Three primary indices of functional diversity (functional richness (F_{Ric}), evenness (F_{Eve}), and divergence (F_{Div})) were calculated using the *FD* package (Laliberté et al., 2014; Laliberté & Legendre, 2010), as these three indices meaningfully explain different aspects of functional diversity (Mouchet et al., 2010; Pakeman, 2011; Villéger et al., 2008). These three indices are complementary, and together describe the distribution of species and their abundances within functional space. F_{Ric} describes the amount of functional space occupied by an assemblage, F_{Eve} describes the regularity of species abundances in the functional space, and F_{Div} describes how far the most abundant species are from the centroid of the functional space (Mouchet et al., 2010). Linear models were then created with the three indices as a function of biotope.

5.3.5.3 Assemblage structure

The *mvabund* package (Wang et al., 2019) was used to assess the assemblage structures of spider and beetle species in multivariate space based on the abundance of each species within each of the two biotopes. The *manyglm* function was used to create linear models with species abundance in multivariate space as a function of biotope. Models were then tested for significance and accounted for correlations through 1000 resampling iterations via *pit.trap* resampling. To visualise the assemblage structures of spiders and beetles in the two systems in multivariate space, Bayesian ordination and regression analyses were performed on site-species abundance matrices using the *boral* package (Hui, 2016, 2020). Two ordinations were created to visualise the assemblage structure, 1) with the effect of biotope i.e. latent and explanatory variables included, and 2) excluding the effect of biotope i.e. latent variables only. This was done separately for spiders and beetles.

5.3.5.4 Fourth-corner analyses

Fourth-corner models were created using the *traitglm* function of the *mvabund* package. This function fits a model to predict abundance across several species/morphospecies as a function of biotope and traits, to describe the environment-trait interaction, i.e. how the environmental response across species/morphospecies varies as traits vary (Brown et al., 2014; Warton et al., 2015). Lasso penalty was used to reduce the effect of species/morphospecies with small numbers of individuals; the lasso penalty is recommended for predictive modelling (Osborne et al., 2000). This was done separately for spiders and beetles, and fourth-corner results were visualised using the *lattice* package (Sarkar, 2008).

5.4 Results

A total of 5662 individual spiders from 41 families comprising 121 genera and 244 distinct morphospecies (116 identified species and 128 morphospecies), and 9760 individual beetles from 36 families comprising 362 morphospecies were sampled.

5.4.1 Alpha and beta diversity

A total of 218 spider morphospecies were observed in fynbos and 167 morphospecies in vineyards, and 292 beetle morphospecies were observed in fynbos and 205 morphospecies in vineyards. There were significantly more spider species within fynbos compared to within vineyards (t-value = -3.21, $p < 0.01$), although beetle species richness was not significantly affected by the particular biotope (t-value = -0.86, $p = 0.4$) (Table 5.1). The β_{Rep} component of beta diversity contributed most of the weight to β_{Tot} for spiders and beetles within each biotope (Table 5.2).

Table 5.1: Means and standard deviation for spider and beetle alpha diversity within two biotopes. Significant differences are indicated with different letters.

Biotope	Spiders	Beetles
Fynbos	65.73 ± 11.23^{a}	61.27 ± 13.68^{c}
Vineyards	51.36 ± 9.1^{b}	47.55 ± 10.66^{c}

Table 5.2: The means of Sørensen dissimilarity coefficients for spiders and beetles within two biotopes. Fyn = fynbos and Vin = vineyards.

	β_{Tot}	β_{Rep}	β_{Ric}
$\text{Spider}_{\text{Fyn}}$	0.68	0.49	0.19
$\text{Spider}_{\text{Vin}}$	0.70	0.45	0.25
$\text{Beetle}_{\text{Fyn}}$	0.86	0.45	0.40
$\text{Beetle}_{\text{Vin}}$	0.71	0.41	0.30

For spiders the β_{Tot} (t-value = 0.7, p = 0.48) and β_{Rep} component (t-value = -1.77, p = 0.08) did not differ significantly between the two biotopes. However, the β_{Ric} component (t-value = 1.95, p = 0.053) of spiders was marginally higher among vineyards compared to among fynbos. For beetles, the β_{Tot} (t-value = -8.67, $p < 0.001$) and β_{Ric} component (t-value = -2.63, $p < 0.01$) was significantly lower among vineyards compared to among fynbos, however the β_{Rep} component (t-value = -1.34, p = 0.18) did not significantly differ between the two biotopes.

5.4.2 Functional diversity

For spiders the F_{Ric} was significantly lower in vineyards compared to fynbos (t-value = -2.46, p = 0.02) (Appendix L), while there were no significant differences between the F_{Eve} (t-value = 0.79, p = 0.43) and F_{Div} (t-value = 1.23, p = 0.22). For beetles, the F_{Div} was significantly lower in vineyards compared to fynbos (t-value = -2.5, p = 0.02) (Appendix M), while there were no significant differences between the F_{Ric} (t-value = 0.51, p = 0.61) and F_{Eve} (t-value = 1.76, p = 0.08).

5.4.3 Assemblage structure

The assemblage structures of both spiders ($\chi^2 = 19.19$, $p < 0.001$) and beetles ($\chi^2 = 19.91$, $p < 0.001$) were strongly influenced by the biotope (system) in which they occurred. Where the effect of biotope was included, there was a clear separation in the assemblage structure of both spiders (Figure 5.2a) and beetles (Figure 5.2c), and where the effect of biotope was excluded there was no clear separation in the assemblage structure of either spiders (Figure 5.2b) or beetles (Figure 5.2d). Additionally, there were clear family-level taxonomic differences between the two biotopes for spiders and beetles (Appendix N).

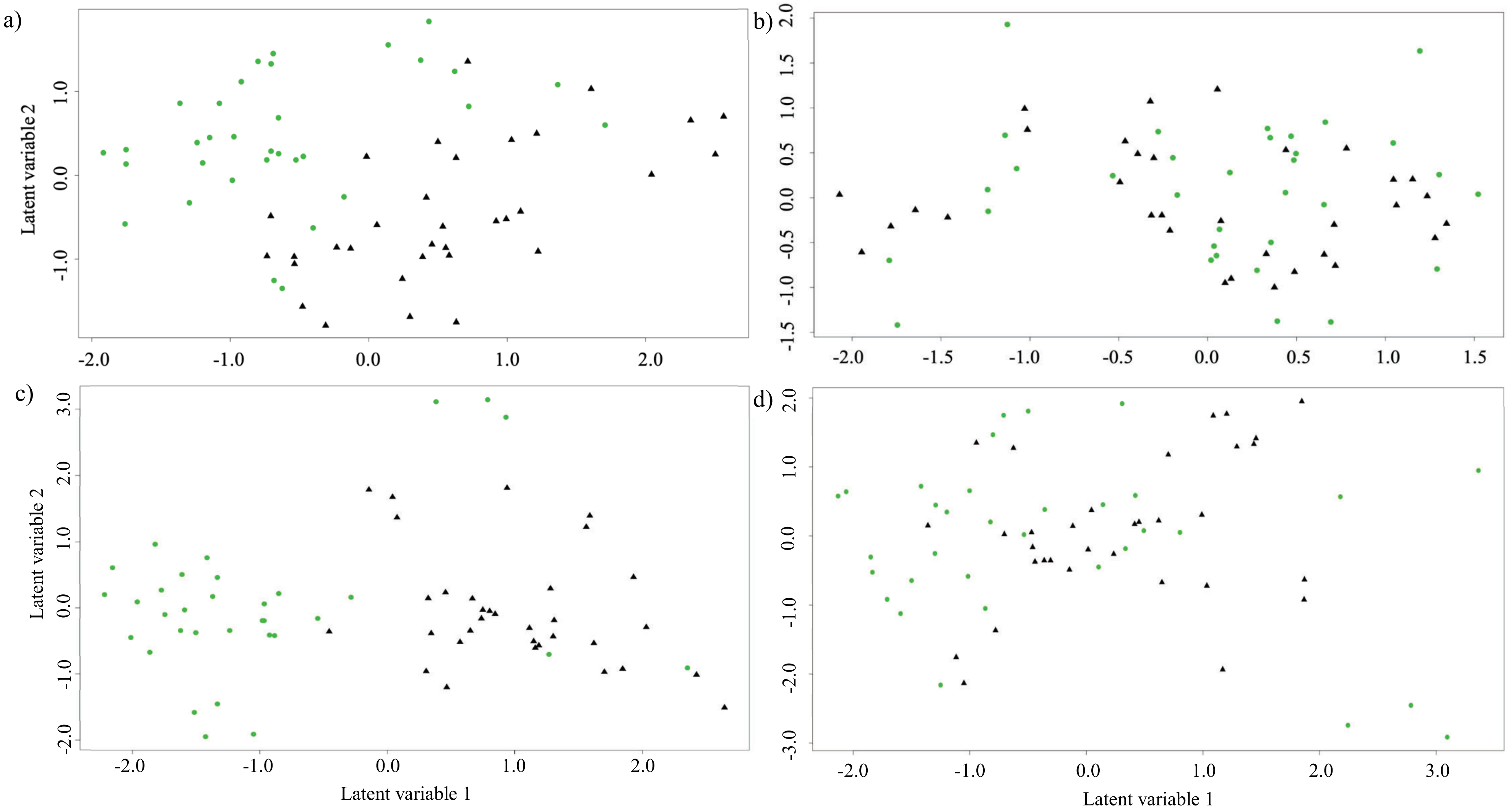

Figure 5.2: Bayesian ordination and regression analyses of the spider (a & b) and beetle (c & d) assemblage structure across vineyard (▲) and fynbos (●) sites with latent and explanatory variables included (a & c) i.e. including the effect of biotope, and with latent variables only (b & d), i.e. excluding the effect of biotope.

5.4.4 Fourth-corner analysis

For spiders, the strongest trait association with a biotope was a strong positive association of plant-dwellers with fynbos. In addition, active hunters, ground dwellers, and larger-bodied species were positively associated with fynbos, whereas common spider species were negatively associated with fynbos (Figure 5.3a). Predatory and apterous beetles were positively associated with vineyards, and small beetles were positively associated with fynbos, whereas predatory, apterous, and large beetles were negatively associated with fynbos (Figure 5.3b).

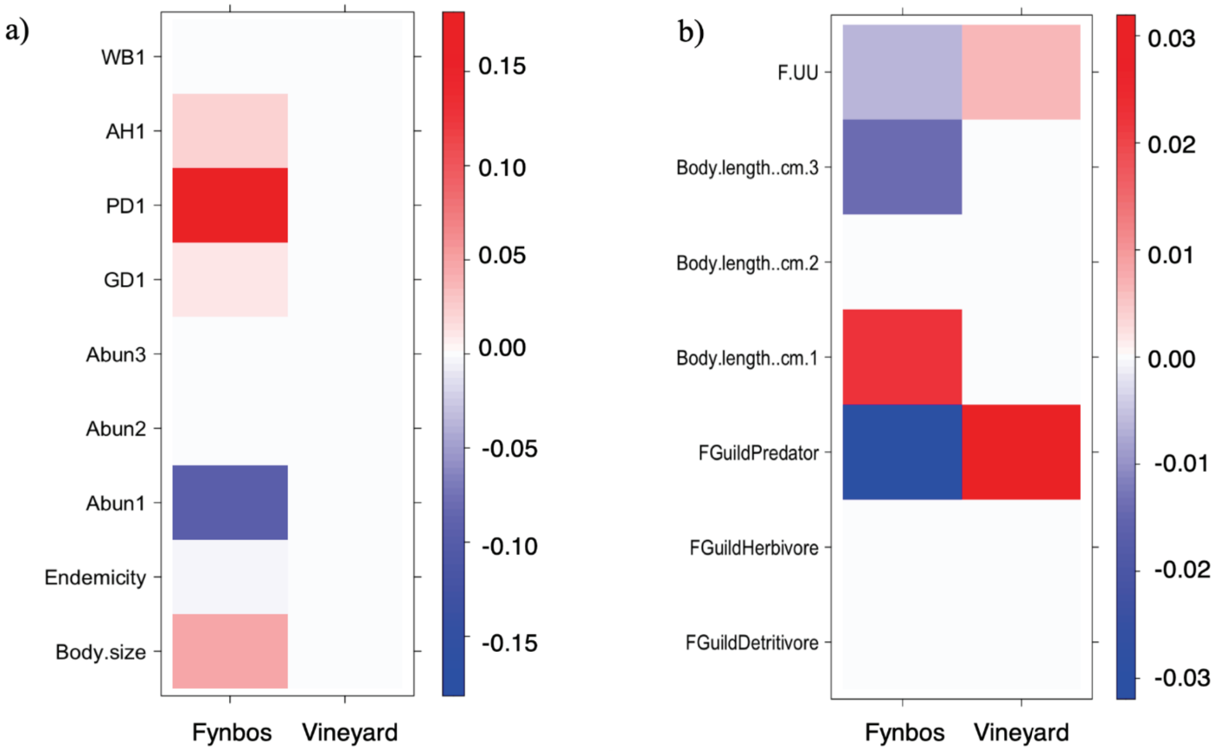

Figure 5.3: Fourth-corner results showing standardised coefficients from linear regression models for species-specific traits of spiders (a) and beetles (b) in fynbos and vineyards. Brighter squares show stronger associations, positive associations are red, and negative associations are blue. Abbreviations: Web builder (WB1), active hunter (AH1), plant dweller (PD1), ground dweller (GD1), apterous (F.UU), feeding guild (FGuild), and Abun1 (common) to Abun3 (rare).

5.5 Discussion

Due to the high diversity of plants and arthropods associated with fynbos, and the lower levels of disturbance compared to cultivated areas, it was expected that the alpha diversity for both spiders and beetles would be much higher in fynbos than in vineyards (Kemp et al., 2017; Kehinde & Samways, 2014c). Although spider alpha diversity was lower in vineyards, generally vineyards were not poor in terms of spider and beetle alpha diversity, and still supported relatively high species numbers. The high alpha diversity within vineyards could be a result of most farmers employing a diverse cover crop in vineyard inter-rows while also following low-intensity pesticide spray programmes, both approaches which increase local-scale spider and beetle species richness in vineyards (Chapter 2 & 3). This result could point to the adaptation of species which led to different habitat preferences and requirements here, i.e. species previously associated with fynbos evolved and are now adapted to vineyard conditions. Species deterministically follow biotic and abiotic conditions to which they are adapted and which lead to the spatial structuring of communities/assemblages within heterogeneous landscapes (Püttker et al., 2015). The pattern of spatial structuring of communities, especially in human-dominated landscapes, may also be the result of maladaptation, i.e. species' preference for a habitat prior to being transformed, led to the species being trapped and becoming adapted to the suboptimal conditions in the now transformed habitat (Mortier & Bonte, 2020). The diverse but different assemblages within vineyards show that vineyards in the CFR are not depauperate in ground living arthropods, as is also the case for pollinators (Kehinde & Samways, 2014b), and can be viewed as novel agricultural ecosystems (Perfecto & Vandermeer, 2015), with high levels of arthropod diversity.

The total beta diversity of spiders was similar within vineyards compared to within fynbos. However, total beta diversity for beetles were lower within vineyards compared to within fynbos. Nonetheless, the difference in total beetle beta diversity between biotopes were not large. In agricultural systems where uniformity is high among farms, homogenisation of species turnover is common (Socolar et al., 2016). However, here the similar turnover of spiders and beetles between the two biotopes may be attributed to the high environmental heterogeneity and diversity of management styles present in the vineyard matrix of the CFR (Chapter 2). This includes factors such as varied crop protection measures, variation in cultivars and vineyard ages, and differences in farmland composition. In addition, it is possible that arthropods in the vineyards respond to the high level of variation in the underlying edaphic and topographical factors that characterises the CFR despite its transformation. The relative contribution of species replacement and species richness differences to total species turnover were broadly similar between vineyards and fynbos. The β_{Ric} of spiders were marginally higher among vineyard assemblages. β_{Ric}, or species richness difference, refers to the absolute number of species that each site hosts irrespective of potential nestedness (Carvalho et al., 2012; Marini et al., 2013). This result indicates that vineyards are maintaining a diverse spider assemblage, as the rate of species loss (or gain) was not significantly different compared to fynbos, and the vineyard assemblage not being so much a subset of the fynbos species but rather a unique assemblage in its own right. The β_{Tot} of beetles, being significantly lower among vineyards, was driven by the β_{Ric} component that was significantly lower for beetles among vineyards. The β_{Rep} component, for both spiders and beetles, not being significantly different between fynbos and vineyards indicates that the level of species turnover of spider and beetle assemblages were as high in vineyards as in fynbos, although the assemblage composition differed between the biotopes. This is a very positive result for vineyard farmers in the CFR, as turnover of species is known to be a primary determinant of the total diversity present in the landscape (Flohre et al., 2011). This pattern may have been influenced by the inclusion of juvenile spiders, however, the same approach was used consistently across all farms, and the proportion of these juvenile morphospecies were similar in vineyards and fynbos, making it unlikely that this would have had a notable effect.

The lower F_{Ric} of spiders among vineyards shows that spider traits occupied significantly less of the multidimensional functional trait space available in vineyards compared to the spiders among fynbos. Lower F_{Ric} indicates that fewer of the resources, or alpha niches, potentially available are being used by the community/assemblage (Mason et al., 2005), or that there were fewer alpha niches and resources available to begin with. Habitat filtering has been shown to increase with increasing disturbance, and which decreases F_{Ric} (Pakeman, 2011). Flynn et al. (2009) and Laliberté et al. (2010) have also shown that functional diversity and redundancy, across multiple taxa, decreased with increasing disturbances. Spiders took up less of the functional trait space among vineyards, but the spider assemblages among vineyards was still relatively high in terms of F_{Ric} (Appendix L). The higher F_{Ric} of spiders in fynbos is a positive result to fynbos conservation, and may hold benefits for viticulturists within the CFR as well, although increased F_{Ric} within vineyards itself would have been greatly beneficial to vineyards in terms of functioning, stability, and resilience of the agroecosystem in the long-term. Functional diversity is directly related to ecosystem functioning (Hooper et al., 2005; Mouillot et al., 2011; Tilman et al., 1997), and the functional trait space of spiders being significantly more occupied in fynbos could indicate that spiders in fynbos are effectively contributing to ecosystem functioning in terms of predation and nutrient cycling (Barnes, 2018). Farmers may unknowingly benefit from consequent services fynbos spiders provide, for example, as a first line of defence in reducing pest pressures within the natural area surrounding vineyards, and multi-trophic level nutrient cycling via depositional effects (Barnes, 2018) surrounding vineyards.

The F_{Div} of beetles was significantly lower in vineyards compared to fynbos, meaning beetles had a low degree of niche differentiation among species within the vineyard assemblages i.e. the most abundant species were functionally very similar and competition for the same resources was high (Mouchet et al., 2010). Lower F_{Div} may indicate decreased ecosystem functioning in vineyards as a result of the less efficient use of available resources (Mason et al., 2005), or that there were fewer resources available due to relatively lower structural and compositional diversity compared to fynbos. The F_{Div} of beetles was significantly higher in fynbos, meaning that there was decreased competition for the same resources and increased ecosystem functioning within fynbos. Schuldt et al. (2014) showed an increase in F_{Div} in more species-rich and older stands of woody plants, as is also the case for fynbos which is hyper-diverse and ancient with little historical, and more recent, disturbances (Linder, 2005).

Species traits are known to influence the environmental tolerances and habitat requirements of species (Cadotte et al., 2011). Common spider species were negatively associated with fynbos, which could point out the relationships or adaptations that more rare or specialist spiders developed to fynbos, and as a result more common spiders are being outcompeted by fynbos specialists. Spiders are significant generalist predators (Halaj & Wise, 2002) of many vineyard pests (Nyffeler & Sunderland, 2003), and farmers could equally benefit from more common spiders, as they might prefer the vineyard habitat to fynbos habitat, possibly due to more abundant prey. Larger spider body size were positively associated with fynbos and could indicate the availability of higher nutritional quality prey items in fynbos which can lead to increased growth, survival, development rates (Toft & Wise, 1999), and increased reproductive success (Bowden et al., 2015). Larger spiders have been associated with more complex landscapes (Gallé et al., 2018) and larger spiders may possibly contribute to a higher rate of removal of potential pest species in fynbos surrounding vineyards, as larger spiders typically have to ingest more prey to sustain their energy requirements (Miyashita, 1992). The positive association of plant- and ground-dwelling spiders to fynbos could be attributed to increased rockiness, topographic complexity, and amount of natural vegetation (Theron et al., 2020) compared to within vineyards.

Predatory beetles were positively associated with vineyards, so it could be expected that there would be increased interspecific competition among vineyard beetles as they are competing for the same prey items which themselves vary in availability, due to temporal changes and pest control programmes in vineyards. The positive association of predatory beetles with vineyards may also be due to enriched conditions within vineyards i.e. the presence of more palatable and herbaceous vegetation and irrigation which in turn may support higher numbers of herbivore prey than relatively unpalatable sclerophyllous fynbos. The positive association of predatory beetles with vineyards maybe a positive result for vineyard management in terms of herbivore reduction, as predatory beetles are known to be major generalist predators in terrestrial habitats (Halaj & Wise, 2002). Small beetles, being positively associated with fynbos, are known to be pollinators of many fynbos plants (Hemborg & Bond, 2005), or that the high quality, undisturbed habitat can better support species that have lower dispersal abilities. Also, configurational heterogeneity promotes species with smaller body sizes (Gámez-Virués et al., 2015).

5.6 Conclusion

Throughout the study region, spider and beetle assemblages were relatively well-supported in vineyards, compared to assemblages in fynbos in terms of both alpha and functional diversity, and species turnover in vineyards at the landscape scale was also similar to that seen in fynbos. However, there were subtle differences in the different diversity measures, and large differences in assemblage composition between biotopes, the latter possibly being influenced by differences in species traits associated with the different biotopes. The lower functional diversity of spider and beetle assemblages in vineyards may point to a homogenising effect that vineyards had on the functional richness and divergence of spiders and beetles, respectively, which in turn, possibly indicates decreased ecosystem services and resilience in vineyards. Consequently, there is room for improvement in terms of spider functional richness and beetle functional divergence in vineyards within the CFR. Although the level and frequency of disturbances in vineyards is already low in this region, this may be achieved by increased ecological intensification.

According to Tscharntke et al. (2005) redundant species, as formulated by the hypothesis of spatiotemporal insurance by biodiversity, may become important in human-dominated landscapes in the future as species in diverse communities could replace others as soon as they disappear. The same may be true in terms of the functional diversity of arthropod assemblages, where a functionally divergent assemblage, such as the fynbos beetles here, ensures that ecosystem functioning remains intact and contributes to the resilience of the agroecosystem.

Common spiders and predatory beetles, being positively associated with vineyards, is a positive outcome for farmers in the CFR, as spiders and beetles generally prey on a wide range of arthropod species including many vineyard pests. This should encourage farm managers and viticulturists in the area to continue farming in an environmentally-friendly manner or according to the IPW guidelines, as vineyards hold potential for biodiversity conservation and consequent ecosystem services (Paiola et al., 2020), which provide benefits for wine production through pest control (Viers et al., 2013).

This assessment of multiple facets of arthropod diversity shows that although vineyard assemblage composition is greatly altered compared to that in fynbos, vineyards are by no means impoverished. These results support the idea that certain agroecosystems, especially sensitively managed perennial systems, can support rich arthropod assemblages at different spatial scales, which suggests that they are also likely to be resilient in the long-term.

5.7 References

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Chapter 6: General discussion

The overarching goal of this thesis was to provide a robust assessment of the role of viticulture as a dominant component of human-transformed landscape mosaics, in terms of its impact on and potential for supporting biodiversity. A main aim was to identify viticultural management practices and environmental variables that enhance arthropod biodiversity, and that influence assemblage structure and patterns of dispersion in vineyard-dominated landscape mosaics. Furthermore, a major focus area was the interaction between vineyards and the surrounding biodiversity-rich landscape. Additionally, I aimed to provide an in-depth assessment of the impact of viticulture on native arthropod biodiversity at a large spatial scale. Different measures of diversity and assemblage composition were assessed at different spatial scales throughout the various chapters, starting at a local scale [on-farm diversity (Chapter 2) and spillover from adjacent fynbos (Chapter 3)] and progressing to a landscape (surrounding landscape complexity; Chapter 4) and regional scale (patterns of beta and functional diversity among farms; Chapter 5).

6.1 Synthesis of findings, with recommendations for management and future research

A major emergent finding from the different chapters was the identification of individual low-cost viticultural management practices that enhanced the diversity and abundance of the three focal arthropod taxa (Araneae, Coleoptera, and Hemiptera), regardless of whether these practices were applied within an integrated or organic vineyard system (Chapter 2), and irrespective of the surrounding landscape complexity (Chapter 4). Throughout the chapters, the most consistent and robust result for enhancing on-farm arthropod diversity was an increased amount of herbaceous vegetation in the vineyard inter-rows. These results are in line with previous investigations in Europe by Fiera et al. (2020), Kratschmer et al. (2019), and Winter et al. (2018) that have demonstrated the significant biodiversity benefits of plant diversification in vineyards. These comparable results suggest that despite great geographical distances this principle is the same in both regions. An increased amount of plant litter on the vineyard floor, and other vegetation-related variables, also came out as important factors for enhancing arthropod diversity in vineyards. These practices most likely enhance arthropod diversity through increasing the number of available niches and providing alternate resources, i.e. food or shelter (Sáenz-Romo et al., 2019).

Greater vegetation diversity has been linked with increased ecosystem services in agroecosystems, i.e. biological pest control, nutrient cycling, pollination, regulation of microclimate and hydrological processes, detoxifying agrochemicals, and reducing soil erosion (Altieri, 1999; Altieri & Rogé, 2010; Anderson, 2012; Daane et al., 2018; Košulič et al., 2014; Sunderland & Samu, 2000; Wilson et al., 2017). In-crop plant diversification may therefore have broad positive outcomes. Additionally, a more extensive management approach in vineyard inter-rows will automatically lead to a reduction in the frequency and intensity of other inter-row associated management practices i.e. tillage and the application of herbicides. The implementation of these biodiversity-friendly measures may thus further promote other positive activities. Furthermore, interviews with visitors to wine farms in other regions showed that they were well aware of, and appreciated the landscape complexity and soil management practices associated with wine farms (Hervé et al., 2018). Viticulturists need to be aware of the cultural ecosystem services that complexity-targeted management practices, i.e. vegetation cover and soil management, may provide (Hervé et al., 2018), as it enhances diversity but may also improve the heritage and recreational value of the landscape itself (Assandri et al., 2018). This is particularly important in the context of the CWBR, with its rich biodiversity and cultural heritage.

A key recommendation from this thesis is therefore to increase the proportion of herbaceous content in vineyard inter-rows and leaving plant litter on the vineyard floor as this will increase arthropod richness and abundance within vineyards. Although this did not promote stenotopic fynbos species presence in vineyards, this approach nonetheless consistently enhanced crop-associated and generalist arthropods (Chapter 3). Maintenance of this in-crop biodiversity is critical to ensure long-term agroecosystem functioning (Loreau et al., 2003). An important consideration is that cover crops interact with the crop itself through competition for water and nutrients. Although in some cases, increased water consumption by diverse cover crops can reduce the vegetative growth of vines and, in turn, improve grape and wine quality (Lopes et al., 2008), competition with vines may be problematic in certain climatic zones (Ruiz-Colmenero et al., 2011). Further in-depth assessment of different types of cover crops in different regions will help inform optimal implementation of this practice to the benefit of biodiversity and production.

Another key finding was the positive effect of low management intensity (Chapter 2). The lack of effect of pesticides and the fact that integrated farms here supported as much arthropod diversity as organic farms, were unexpected results (Chapter 2). Detailed assessment of the management practices revealed that management intensity on integrated farms in the region is already low. This is a positive finding for the Integrated Production of Wine Scheme of South Africa (IPW), highlighting that adherence to the guidelines is indeed limiting agricultural impacts on biodiversity. These findings support the idea that agrochemicals should be applied only when absolutely necessary, and it is recommended to do so in an integrated manner. There are benefits to an integrated farming approach in vineyards in terms of restored ecosystem services (Manzano et al., 2003; Thomson & Hoffmann, 2006), farming less intensively (Bruggisser et al., 2010; Gaigher & Samways, 2010), and maintaining intermediate levels of disturbance (Bruggisser et al., 2010). The fact that the use of synthetic pesticides did not negatively affect any of the arthropod diversity measures here, may be due to sampling being conducted too long after spray applications. This result needs further investigation, especially considering the insidious effects of pesticides that have been demonstrated globally (Desneux et al., 2007). In future studies, fieldwork should be synchronised with spray programmes so that sampling can occur before, during, and after applications in order to assess more specifically the effects of agrochemicals on arthropod population dynamics.

My study area provided an opportunity to assess whether certain agroecological trends also apply in a region where agricultural transformation is relatively recent and significant amounts of natural habitat remain. Interestingly, several key findings in the thesis differed from the main trends in the literature. This supports the idea that there is no universal answer for effective farmland conservation management (Tscharntke et al., 2012). Farms taking part in farmland conservation programmes should move away from a ‘one-size-fits-all’ approach, and management should be adapted to farm-specific conditions e.g. different landscape structures, different crops, and different regions (Batáry et al., 2011). One example of this is that here in the CFR, edges between vineyards and fynbos seem to be a point of abrupt change in arthropod assemblage structures (Chapter 3). This was contrary to my hypotheses, as many studies in other regions have demonstrated significant species exchange among natural and cultivated fields (Rand et al., 2006). Furthermore, no direct drivers for the spillover of stenotopic arthropods from adjacent fynbos into vineyards were identified. This highlights the irreplaceability of fynbos in farmland, as it supports sensitive species that may be restricted to remnant vegetation. Furthermore, due to the limited permeability of the vineyard-fynbos edges for stenotopic arthropods, farmland conservation planning may need to focus on the retention of remnant stepping-stone habitats or conservation corridors, and maintain remnant patches close to each other, in order to enhance landscape connectivity for more spatially restricted species throughout the CWBR landscape. This will be important to maintain metapopulation dynamics and prevent ecological relaxation in these fragmented natural areas in the long-term (Kuussaari et al., 2009). Additionally, there is evidence for the unique contribution of preserving remnant patches of natural vegetation for the conservation of natural species in the landscape (Theron et al., 2020). It is critically important to maintain this component of biodiversity in agricultural landscapes as certain species, i.e. beneficial arthropods, may reduce pest pressures or provide pollination services on farms. Although this would require planning at a spatial scale larger than an individual farm, it would be feasible to consider, since there is existing cooperation among neighbouring wine farms in the form of conservancies throughout the CWBR, in addition to the overall biosphere reserve cooperative platform.

As the arthropod sampling represented a snapshot in time, the lack of spillover detected may be an artefact of sampling during times that are associated with limited immigration of arthropods into vineyards. Future fieldwork should account for temporal variation by sampling across a longer time-period. This should give a clearer picture on how arthropod migration patterns respond to vine phenology and seasonal variation in fynbos ecosystems. The spillover of arthropods between farmlands and fynbos in the CFR is under-studied and requires more research, as arthropod spillover from natural to cultivated areas may hold major economic benefits to agricultural production, as has been demonstrated in other regions (Schellhorn et al., 2014). Spillover of cultural arthropods in the vineyard-fynbos direction was detected (Chapter 3), which corresponded to my expectations. Native arthropod populations and their associated function in fynbos may be altered by cultural species (Rand & Louda, 2006). Therefore, spillover in this direction requires some careful attention as it may have deleterious effects on native arthropod assemblages which, in turn, may decrease ecosystem function and services (Blitzer et al., 2012; Kaiser et al., 2008; Rand et al., 2006). This may be especially important in smaller fynbos remnants that have high edge to interior ratios, which can make them vulnerable to adjacent agricultural practices.

Previous studies have found mediating effects of the surrounding landscape on local management practices, i.e. the surrounding landscape complexity affects the effectiveness of certain local management practices for enhancing on-farm species richness or abundance, and related ecosystem services (Batáry et al., 2011; Tscharntke et al., 2005; Tscharntke et al., 2012). Here, there was a lack of interaction between landscape complexity and local management practices (proportion herbaceous vegetation in the inter-rows and farming approach) on arthropod richness and abundance. As discussed in Chapter 4, this may be related to the true remnant nature of the fynbos vegetation and the generally higher overall landscape complexity compared to more intensively studied regions. This further emphasises that agroecological trends may vary greatly between regions. Although organic farming per se did not improve arthropod species richness or abundance, there were strong interactions between this farming approach and the surrounding landscape complexity on assemblage composition. Arthropod assemblages on organic farms diverged over a large spatial scale, whereas arthropod assemblages converged more on integrated farms (Chapter 4), suggesting that the organic farms better represented the local natural species pool. More research on the interaction between local management practices, environmental variables, and the surrounding landscape complexity within the different complementary zones of a biosphere reserve is required. This will help identify site-specific management practices that could be tailored to the surrounding landscape complexity in order to maximise on-farm diversity and benefit production. A good understanding of the local and landscape contexts and associated processes for a specific area will ensure that future agricultural lands are optimally located in order to achieve maximum arthropod biodiversity and ecosystem services (Isaacs et al., 2009; Landis & Werling, 2010).

Due to the high plant and arthropod diversity associated with fynbos, and the link between agricultural transformation and biotic homogenisation (Flohre et al., 2011; Olden & Rooney, 2006), I expected to find reduced alpha, beta, and functional diversity of arthropods within vineyards. However, vineyards performed relatively well compared to fynbos in terms of spider and beetle alpha and beta diversity. In the same region, Kehinde & Samways (2014) did not find a homogenising effect of vineyards on pollinator interaction networks and flower-visitor assemblages. This suggests that the local vineyards, with relatively low levels of disturbance and high environmental heterogeneity, can support high arthropod diversity at different spatial scales. There were, however, subtle differences between fynbos and vineyard assemblages in terms of their functional diversity and trait composition. For example, vineyards had lower functional diversity which could indicate decreased ecosystem function and services, and less resilience in vineyard systems. There were also shifts in arthropod trait composition between fynbos and vineyards, e.g. predatory beetles were more strongly associated with vineyards, whereas plant-dwelling spiders and small-bodied beetles were more strongly associated with fynbos. The effect of these shifts in assemblage trait composition on ecosystem functioning is currently unknown and would be important to investigate in future research.

The close proximity of the two biotopes may have contributed to vineyards performing similar to fynbos in terms of certain diversity measures. It may be that viticulture in the CFR did not negatively affect the surrounding fynbos, as all farms are compliant with the Integrated Production of Wine scheme’s standards for integrated farming. However, it may be that fynbos in close proximity to vineyards had already been compromised, which may have contributed to the similar patterns among the two biotopes. I recommend that sampling should occur at greater distances away from the edges between farmland and adjacent natural vegetation in order to exclude possible influences of agricultural practices, i.e. spray drift. Future studies aimed at determining landscape and regional scale effects on specific arthropod assemblages in the CFR will benefit from assessing beta and functional diversity along environmental, land-use, and/or temporal gradients over geographical distance, and partitioning arthropods into finer-scale taxonomic groups i.e. species level. Additionally, I recommend that future studies omit juvenile spiders from their data in order to avoid the possibility of artificially inflating species richness. Furthermore, it would be interesting to test whether organic farming has less of a homogenising effect compared to integrated farming, which may become feasible with an increase in the number of organic farms in the region.

6.2 Concluding remarks

Overall, my study demonstrated that sensitively managed vineyards have the potential to maintain resilient arthropod assemblages at different spatial scales, which supports the idea of vineyards being novel ecosystems that are able to support abundant and diverse assemblages of arthropods (Paiola et al., 2020; Viers et al., 2013). Extensively managing vineyards within the buffer and transition zones of the CWBR hold benefits for both wine production and biodiversity conservation, and supports the concept of a biosphere reserve. Here, I expanded on previous work and demonstrated how farm managers or viticulturists across different systems may enhance arthropod diversity through adopting low-cost management practices (i.e. increasing herbaceous vegetation in vineyard inter-rows) without abandoning their current management approach. These results are vital for ensuring the sustainability of viticulture in a global biodiversity hotspot, and for gaining continued support and approval from the general public, as there is a growing demand for sustainably produced products in South Africa (Kelly & Metelerkamp, 2015). Furthermore, I highlight the importance of increasing functional connectivity in the landscape. In the CWBR many wine farms are neighbouring or adjacent to one another and effective conservation management requires a coordinated effort from farmers within the region to ensure the persistence of e.g., a vagile generalist predator with a dispersal range that spans over more than a single farm. It would make little sense, from a biodiversity conservation perspective, for one farm to promote ecological intensification while, on the other hand, the neighbouring farm is doing little to promote diversity and adheres to a more conventional approach. This would go against the goal of ensuring connectivity (in terms of stepping-stone habitats and conservation corridors) and heterogeneity in the landscape in order to enhance and share the benefits of increased ecosystem services in such an area (Inclán et al., 2015). Stronger evidence for shared benefits of ecological intensification could persuade more farm managers to adopt environmentally sound practices (Kleijn et al., 2019). Further work on these dynamics will help inform local viticultural guidelines, such as the IPW programme, and may feed into land-use policy for promoting biodiversity in the Cape Winelands.

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Appendix A: Taxonomic list of species used in chapter 2.

Morpho-species code	Order/sub-order	Superfamily/family/sub-family	Genus	Species	Feeding guild	Abundance
Ara54	Araneae	Amaurobiidae	*Chresiona*	sp.1	Predator	64
Ara46	Araneae	Amaurobiidae	*Obatala*	sp.1	Predator	1
Ara22	Araneae	Amaurobiidae	*Pseudauximus*	*reticulatus* (Simon, 1902)	Predator	16
Ara98	Araneae	Ammoxenidae	*Ammoxenus*	*kalaharicus* (Benoit, 1972)	Predator	9
Ara256	Araneae	Anapidae	*Crozetulus*	*rhodesiensis* (Brignoli, 1981)	Predator	42
Ara24	Araneae	Anapidae	*Metanapis*	*bimaculata* (Simon, 1895)	Predator	1
Ara362	Araneae	Araneidae	*Araneus*	*apricus* (Karsch, 1884)	Predator	10
Ara363	Araneae	Araneidae	*Argiope*	sp.1	Predator	1
Ara304	Araneae	Araneidae	*Cyrtophora*	*citricola* (Forsskål, 1775)	Predator	1
Ara336	Araneae	Araneidae	*Hypsosinga*	*pygmaea* (Sundevall, 1831)	Predator	2
Ara399	Araneae	Araneidae	*Kilima*	*decens* (Blackwall, 1866)	Predator	8
Ara353	Araneae	Araneidae	*Larinia*	*natalensis* (Grasshoff, 1971)	Predator	3
Ara276	Araneae	Araneidae	*Neoscona*	*blondeli* (Simon, 1886)	Predator	68
Ara398	Araneae	Araneidae	*Neoscona*	*subfusca* (Koch, 1837)	Predator	1
Ara30	Araneae	Clubionidae	*Clubiona*	sp.5	Predator	212
Ara103	Araneae	Corinnidae	*Castianeira*	sp.1	Predator	13
Ara155	Araneae	Dysderidae	*Dysdera*	*crocata* (Kock, 1838)	Predator	2
Ara220	Araneae	Eutichuridae	*Cheiracanthium*	*furculatum* (Karsch, 1879)	Predator	16
Ara222	Araneae	Eutichuridae	*Cheiramiona*	*ansiae* (Lotz, 2002)	Predator	1
Ara154	Araneae	Gnaphosdae	*Megamyrmaekion*	*schreineri* (Tucker, 1923)	Predator	2
Ara111	Araneae	Gnaphosidae	*Asemesthes*	*reflexus* (Tucker, 1923)	Predator	11
Ara17	Araneae	Gnaphosidae	*Camillina*	sp.1	Predator	94
Ara20	Araneae	Gnaphosidae	*Nomisia*	*australis* (Dalmas, 1921)	Predator	33
Ara63	Araneae	Gnaphosidae	*Setaphis*	*subtilis* (Simon, 1897)	Predator	51
Ara208	Araneae	Gnaphosidae	*Urozelotes*	*rusticus* (Koch, 1872)	Predator	42
Ara138	Araneae	Gnaphosidae	*Xerophaeus*	*aurariarum* (Purcell, 1907)	Predator	6
Ara61	Araneae	Gnaphosidae	*Zelotes*	*capsula* (Tucker, 1923)	Predator	41

Ara47	Araneae	Gnaphosidae	*Zelotes*	*flavitarsis* (Purcell, 1908)	Predator	5
Ara71	Araneae	Gnaphosidae	*Zelotes*	*fuligineus* (Purcell, 1907)	Predator	7
Ara225	Araneae	Gnaphosidae	*Zelotes*	*gooldi* (Purcell, 1907)	Predator	1
Ara11	Araneae	Gnaphosidae	*Zelotes*	*reduncus* (Purcell, 1907)	Predator	37
Ara39	Araneae	Hahniidae	*Hahnia*	*laticeps* (Simon, 1898)	Predator	2
Ara44	Araneae	Linyphiidae	*Agyneta*	*habra* (Locket, 1968)	Predator	436
Ara356	Araneae	Linyphiidae	*Limoneta*	*sirimoni* (Bosmans, 1979)	Predator	4
Ara114	Araneae	Linyphiidae	*Mermessus*	*fradeorum* (Berland, 1932)	Predator	11
Ara70	Araneae	Linyphiidae	*Microlinyphia*	*sterilis* (Pavesi, 1883)	Predator	2
Ara69	Araneae	Linyphiidae	*Ostearius*	*melanopygius* (Cambridge, 1879)	Predator	4
Ara1	Araneae	Linyphiidae	*Pelecopsis*	*janus* (Jocqué, 1984)	Predator	219
Ara13	Araneae	Lycosidae	*Allocosa*	sp.1	Predator	73
Ara113	Araneae	Lycosidae	*Arctosa*	*promontorii* (Pocock, 1900)	Predator	2
Ara55	Araneae	Lycosidae	*Lycosa*	*rimicola* (Purcell, 1903)	Predator	7
Ara21	Araneae	Lycosidae	*Pardosa*	*crassipalpis* (Purcell, 1903)	Predator	112
Ara179	Araneae	Lycosidae	*Pterartoria*	*confusa* (Russell-Smith & Roberts, 2017)	Predator	18
Ara107	Araneae	Lycosidae	*Trabea*	*purcelli* (Roewer, 1951)	Predator	213
Ara49	Araneae	Lycosidae	*Trabea*	*rubriceps* (Lawrence, 1952)	Predator	10
Ara40	Araneae	Nemesiidae	*Spiroctenus*	*cambierae* (Purcell, 1902)	Predator	3
Ara147	Araneae	Oxyopidae	*Oxyopes*	*hoggi* (Lessert, 1915)	Predator	18
Ara239	Araneae	Oxyopidae	*Oxyopes*	*pallidecoloratus* (Strand, 1906)	Predator	2
Ara273	Araneae	Philodromidae	*Philodromus*	*guineensis* (Millot, 1941)	Predator	5
Ara104	Araneae	Philodromidae	*Thanatus*	*vulgaris* (Simon, 1870)	Predator	75
Ara196	Araneae	Philodromidae	*Tibellus*	*minor* (Lessert, 1919)	Predator	45
Ara29	Araneae	Phyxelididae	*Vidole*	*sothoana* (Griswold, 1990)	Predator	3
Ara277	Araneae	Pisauridae	*Afropisaura*	*rothiformis* (Strand, 1908)	Predator	14
Ara112	Araneae	Pisauridae	*Rothus*	*aethiopicus* (Pavesi, 1883)	Predator	9
Ara18	Araneae	Prodidomidae	*Theuma*	*fusca* (Purcell, 1907)	Predator	1
Ara408	Araneae	Salticidae	*Baryphas*	*ahenus* (Simon, 1902)	Predator	4
Ara293	Araneae	Salticidae	*Evarcha*	*striolata* (Wesolowska & Haddad, 2009)	Predator	18

Ara270	Araneae	Salticidae	*Heliophanus*	*capricola* (Simon, 1901)	Predator	11
Ara267	Araneae	Salticidae	*Heliophanus*	*debilis* (Simon, 1901)	Predator	77
Ara204	Araneae	Salticidae	*Heliophanus*	*horrifer* (Wesolowska, 1986)	Predator	1
Ara125	Araneae	Salticidae	*Langelurillus*	sp.1	Predator	3
Ara14	Araneae	Salticidae	*Langona*	*hirsuta* (Haddad & Wesolowska, 2011)	Predator	13
Ara148	Araneae	Salticidae	*Menemerus*	*pilosus* (Wesolowska, 1999)	Predator	3
Ara215	Araneae	Salticidae	*Pellenes*	*beani* (Peckham & Peckham, 1903)	Predator	1
Ara92	Araneae	Salticidae	*Phlegra*	sp.1	Predator	1
Ara319	Araneae	Salticidae	*Rhene*	*machadoi* (Berland & Millot, 1941)	Predator	2
Ara36	Araneae	Salticidae	*Tanzania*	*striatus* (Wesolowska, Azarkina & Russell-Smith, 2014)	Predator	26
Ara384	Araneae	Salticidae	*Thyene*	*thyenioides* (Lessert, 1925)	Predator	2
Ara234	Araneae	Salticidae	*Thyenula*	*natalica* (Simon, 1902)	Predator	2
Ara248	Araneae	Scytodidae	*Scytodes*	*caffra* (Purcell, 1904)	Predator	1
Ara166	Araneae	Scytodidae	*Scytodes*	*elizabethae* (Purcell, 1904)	Predator	17
Ara83	Araneae	Scytodidae	*Scytodes*	*testudo* (Purcell, 1904)	Predator	59
Ara134	Araneae	Segestriidae	*Ariadna*	*bilineata* (Purcell, 1904)	Predator	1
Ara244	Araneae	Selenopidae	*Anyphops*	sp.1	Predator	2
Ara332	Araneae	Tetragnathidae	*Leucauge*	*levanderi* (Kulczynski, 1901)	Predator	3
Ara377	Araneae	Theridiidae	*Anelosimus*	*nelsoni* (Agnarsson, 2006)	Predator	6
Ara416	Araneae	Theridiidae	*Argyrodes*	*convivans* (Lawrence, 1937)	Predator	4
Ara321	Araneae	Theridiidae	*Coleosoma*	sp.1	Predator	1
Ara2	Araneae	Theridiidae	*Dipoena*	sp.1	Predator	145
Ara188	Araneae	Theridiidae	*Enoplognatha*	*molesta* (Cambridge, 1904)	Predator	9
Ara357	Araneae	Theridiidae	*Episinus*	sp.1	Predator	2
Ara77	Araneae	Theridiidae	*Euryopis*	*episinoides* (Walckenaer, 1847)	Predator	8
Ara290	Araneae	Theridiidae	*Latrodectus*	*geometricus* (Koch, 1841)	Predator	5
Ara317	Araneae	Theridiidae	*Phoroncidia*	*capensis* (Simon, 1895)	Predator	4
Ara53	Araneae	Theridiidae	*Phycosoma*	sp.1	Predator	1
Ara9	Araneae	Theridiidae	*Steatoda*	*capensis* (Hann, 1990)	Predator	4
Ara255	Araneae	Theridiidae	*Theridion*	sp.	Predator	28

Ara328	Araneae	Theridiidae	*Theridion*	sp.1	Predator	1
Ara269	Araneae	Theridiidae	*Theridion*	sp.2	Predator	23
Ara123	Araneae	Theridiidae	*Theridion*	sp.3	Predator	5
Ara375	Araneae	Theridiidae	*Theridion*	sp.4	Predator	6
Ara307	Araneae	Theridiidae	*Theridion*	sp.5	Predator	6
Ara59	Araneae	Theridiidae	*Theridion*	sp.6	Predator	1
Ara186	Araneae	Thomisidae	*Misumenops*	*rubrodecoratus* (Millot, 1942)	Predator	6
Ara386	Araneae	Thomisidae	*Runcinia*	*insecta* (Koch, 1875)	Predator	31
Ara338	Araneae	Thomisidae	*Synema*	*imitator* (Pavesi, 1883)	Predator	3
Ara172	Araneae	Thomisidae	*Thomisops*	*sulcatus* (Simon, 1895)	Predator	1
Ara253	Araneae	Thomisidae	*Thomisus*	*australis* (Comellini, 1957)	Predator	24
Ara115	Araneae	Thomisidae	*Xysticus*	*havilandi* (Lawrence, 1942)	Predator	9
Ara164	Araneae	Thomisidae	*Xysticus*	*sagittifer* (Lawrence, 1927)	Predator	20
Ara145	Araneae	Trachelidae	*Afroceto*	*arca* (Lyle & Haddad, 2010)	Predator	1
Ara351	Araneae	Trachelidae	*Fuchiba*	*capensis* (Haddad & Lyle, 2008)	Predator	5
Ara6	Araneae	Trachelidae	*Thysanina*	*scopulifer* (Simon, 1896)	Predator	1
Ara306	Araneae	Uloboridae	*Philoponella*	sp.1	Predator	1
Ara84	Araneae	Zodariidae	*Caesetius*	*schultzei* (Simon, 1910)	Predator	1
Ara342	Araneae	Zodariidae	*Chariobas*	*lineatus* (Pocock, 1900)	Predator	1
Ara25	Araneae	Zodariidae	*Cydrela*	*spinimana* (Pocock, 1898)	Predator	3
Ara237	Araneae	Zodariidae	*Diores*	*leleupi* (Jocqué, 1990)	Predator	2
Ara15	Araneae	Zodariidae	*Diores*	sp.2	Predator	137
Ara28	Araneae	Zodariidae	*Heraldida*	sp.2	Predator	7
Ara279	Araneae	Zodariidae	*Systenoplacis*	*fagei* (Lawrence, 1936)	Predator	4
Ara81	Araneae	Zoropsidae	*Phanotea*	*orestria* (Griswold, 1994)	Predator	9
Col123	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	1
Col160	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	3
Col198	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	1
Col21	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	101
Col210	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	6
Col305	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	1

Col312	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	1
Col313	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	2
Col323	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	2
Col342	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	49
Col375	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	6
Col38	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	83
Col389	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	2
Col390	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	4
Col44	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	1
Col5	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	684
Col64	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	8
Col76	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	5
Col8	Coleoptera	Anthicidae	Undetermined	Undetermined	Predator	236
Col365	Coleoptera	Bostrichidae	Undetermined	Undetermined	Herbivore	2
Col370	Coleoptera	Bruchidae	Undetermined	Undetermined	Herbivore	1
Col350	Coleoptera	Buprestidae	Undetermined	Undetermined	Herbivore	1
Col27	Coleoptera	Cantharidae	Undetermined	Undetermined	Predator	126
Col341	Coleoptera	Cantharidae	Undetermined	Undetermined	Predator	3
Col10	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	4
Col106	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	15
Col116	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	1
Col119	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	36
Col141	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	2
Col145	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	4
Col148	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	9
Col149	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	1
Col168	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	2
Col211	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	104
Col212	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	1
Col227	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	1
Col231	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	2

Col235	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	1
Col244	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	1
Col39	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	77
Col49	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	3
Col66	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	25
Col67	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	7
Col69	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	64
Col70	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	12
Col9	Coleoptera	Carabidae	Undetermined	Undetermined	Predator	15
Col108	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	9
Col121	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	3
Col158	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	2
Col180	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	13
Col187	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	3
Col189	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	1
Col226	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	1
Col260	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	1
Col29	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	18
Col328	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	10
Col337	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	2
Col345	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	23
Col347	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	2
Col374	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	2
Col378	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	1
Col380	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	8
Col393	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	1
Col4	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Herbivore	183
Col293	Coleoptera	Clambidae	Undetermined	Undetermined	Detritivore	1
Col52	Coleoptera	Clambidae	Undetermined	Undetermined	Detritivore	1
Col65	Coleoptera	Clambidae	Undetermined	Undetermined	Detritivore	1
Col83	Coleoptera	Clambidae	Undetermined	Undetermined	Detritivore	1

Col336	Coleoptera	Cleridae	Undetermined	Undetermined	Predator	42
Col354	Coleoptera	Cleridae	Undetermined	Undetermined	Predator	5
Col118	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	11
Col13	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	117
Col252	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col277	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col281	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	4
Col287	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col288	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	9
Col291	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	38
Col296	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	4
Col31	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	2
Col316	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col329	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col333	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col343	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	9
Col51	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	2
Col60	Coleoptera	Coccinellidae	Undetermined	Undetermined	Predator	1
Col103	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	2
Col124	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	3
Col179	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	2
Col182	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	16
Col310	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	1
Col311	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	5
Col332	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	18
Col334	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	22
Col37	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	3
Col42	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	1
Col43	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	1
Col62	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	22
Col72	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	273

Col91	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Detritivore	78
Col101	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	9
Col111	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	5
Col12	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	37
Col126	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	43
Col135	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col143	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	63
Col16	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	2
Col166	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	45
Col170	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	2
Col174	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	5
Col175	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col185	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col195	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col215	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	2
Col217	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	8
Col218	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	5
Col228	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col229	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col236	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col243	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col25	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	6
Col26	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	31
Col267	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col273	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	4
Col30	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	18
Col330	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col340	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col360	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	2
Col361	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col369	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	4

Col381	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	4
Col54	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	10
Col56	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	3
Col68	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	10
Col75	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	3
Col80	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	5
Col86	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	5
Col88	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	2
Col89	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	1
Col98	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	11
Col99	Coleoptera	Curculionidae	Undetermined	Undetermined	Herbivore	49
Col142	Coleoptera	Dermestidae	Undetermined	Undetermined	Herbivore	32
Col331	Coleoptera	Dermestidae	Undetermined	Undetermined	Herbivore	1
Col11	Coleoptera	Elateridae	Undetermined	Undetermined	Herbivore	21
Col125	Coleoptera	Elateridae	Undetermined	Undetermined	Herbivore	5
Col139	Coleoptera	Elateridae	Undetermined	Undetermined	Herbivore	3
Col147	Coleoptera	Elateridae	Undetermined	Undetermined	Herbivore	1
Col232	Coleoptera	Elateridae	Undetermined	Undetermined	Herbivore	7
Col144	Coleoptera	Histeridae	Undetermined	Undetermined	Predator	2
Col167	Coleoptera	Histeridae	Undetermined	Undetermined	Predator	15
Col2	Coleoptera	Histeridae	Undetermined	Undetermined	Predator	140
Col35	Coleoptera	Histeridae	Undetermined	Undetermined	Predator	32
Col36	Coleoptera	Histeridae	Undetermined	Undetermined	Predator	10
Col130	Coleoptera	Hydrochidae	Undetermined	Undetermined	Detritivore	6
Col22	Coleoptera	Lathrididae	Undetermined	Undetermined	Detritivore	2
Col292	Coleoptera	Melyridae	Undetermined	Undetermined	Predator	3
Col356	Coleoptera	Melyridae	Undetermined	Undetermined	Predator	1
Col358	Coleoptera	Melyridae	Undetermined	Undetermined	Predator	2
Col377	Coleoptera	Melyridae	Undetermined	Undetermined	Predator	5
Col95	Coleoptera	Melyridae	Undetermined	Undetermined	Predator	5
Col271	Coleoptera	Mycetophogidae	Undetermined	Undetermined	Detritivore	2

Col14	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	6
Col159	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	2
Col184	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	18
Col188	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	2
Col216	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	2
Col306	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	6
Col324	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	1
Col326	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	2
Col339	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	4
Col364	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	5
Col50	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	2
Col53	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	2
Col63	Coleoptera	Nitidulidae	Undetermined	Undetermined	Detritivore	3
Col32	Coleoptera	Pausiidae	Undetermined	Undetermined	Predator	2
Col6	Coleoptera	Rhizophagidae	Undetermined	Undetermined	Detritivore	918
Col107	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Detritivore	2
Col221	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Detritivore	1
Col253	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Detritivore	1
Col7	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Detritivore	185
Col104	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Herbivore	1
Col138	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Herbivore	1
Col366	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Herbivore	1
Col55	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Herbivore	2
Col114	Coleoptera	Silphidae	Undetermined	Undetermined	Detritivore	5
Col117	Coleoptera	Silphidae	Undetermined	Undetermined	Detritivore	1
Col230	Coleoptera	Staphylinidae	Undetermined	Undetermined	Detritivore	2
Col100	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	46
Col105	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col109	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	27
Col146	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	5
Col150	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1

Col161	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col162	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	17
Col165	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col176	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	2
Col213	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col214	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	11
Col23	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	5
Col234	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	3
Col246	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	7
Col3	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	208
Col40	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	149
Col41	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col45	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	4
Col71	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col73	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	1
Col90	Coleoptera	Staphylinidae	Undetermined	Undetermined	Predator	396
Col33	Coleoptera	Sylpidae	Undetermined	Undetermined	Detritivore	419
Col34	Coleoptera	Sylpidae	Undetermined	Undetermined	Detritivore	6
Col1	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Detritivore	344
Col164	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Detritivore	1
Col247	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Detritivore	1
Col28	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Detritivore	121
Col59	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Detritivore	37
Col61	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Detritivore	2
Col15	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Herbivore	10
Col355	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Herbivore	1
Hem123	Hemiptera	Nabidae	Undetermined	Undetermined	Predator	1
Hem46	Hemiptera	Nabidae	Undetermined	Undetermined	Predator	62
Hem11	Hemiptera	Reduviidae	Undetermined	Undetermined	Predator	5
Hem161	Hemiptera	Reduviidae	Undetermined	Undetermined	Predator	2
Hem82	Hemiptera	Reduviidae	Undetermined	Undetermined	Predator	14

Hem1	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2238
Hem10	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	11
Hem100	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	230
Hem101	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem102	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem103	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem104	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	4
Hem105	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	49
Hem106	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	10
Hem107	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem108	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem109	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	124
Hem110	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem114	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	23
Hem116	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	80
Hem117	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1294
Hem119	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem12	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	88
Hem121	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem125	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem126	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem129	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem13	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	43
Hem138	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	35
Hem139	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	4
Hem14	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	130
Hem140	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem141	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	10
Hem142	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	30
Hem143	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem144	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2

Hem145	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem146	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem147	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem148	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem149	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem152	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem153	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	4
Hem154	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	6
Hem155	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem156	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem157	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	81
Hem158	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem159	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	16
Hem16	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	6
Hem160	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem162	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem164	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	10
Hem168	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem169	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem17	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	339
Hem170	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	27
Hem171	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	24
Hem172	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	125
Hem173	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem174	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem175	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	24
Hem177	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem178	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem179	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	9
Hem18	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem180	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	6

Hem182	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem183	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	6
Hem184	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem186	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem187	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	12
Hem189	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem19	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	27
Hem194	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem198	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem199	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	4
Hem2	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	116
Hem20	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	187
Hem200	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	18
Hem201	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	11
Hem205	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	30
Hem206	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem207	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	17
Hem208	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem21	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	10
Hem215	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem216	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem219	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem25	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	138
Hem26	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	104
Hem27	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	5
Hem28	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	24
Hem29	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	58
Hem3	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2387
Hem30	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem31	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	181
Hem32	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	29

Hem35	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem37	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem39	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	100
Hem4	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	275
Hem40	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem43	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	8
Hem45	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	82
Hem47	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	238
Hem48	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	259
Hem49	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	100
Hem5	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem50	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	190
Hem51	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	20
Hem52	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	21
Hem53	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	20
Hem54	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	33
Hem57	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	127
Hem58	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	7
Hem59	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	19
Hem6	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem60	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	19
Hem61	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	22
Hem63	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	87
Hem64	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	25
Hem65	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	104
Hem66	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	6
Hem67	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	30
Hem68	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	45
Hem69	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	11
Hem7	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	393
Hem70	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1

Hem71	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem72	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	7
Hem73	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	12
Hem74	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem75	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	68
Hem76	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	18
Hem77	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	51
Hem78	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem79	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	14
Hem8	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	58
Hem80	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	3
Hem81	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	8
Hem83	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	28
Hem84	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem85	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	31
Hem87	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	9
Hem9	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	603
Hem90	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	17
Hem91	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem92	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	34
Hem93	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	2
Hem94	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	7
Hem95	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	18
Hem96	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	1
Hem97	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	6
Hem98	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	11
Hem99	Hemiptera	Undetermined	Undetermined	Undetermined	Herbivore	8

Appendix B: Taxonomic list of species used in chapter 3.

Morpho-species code	Order/sub-order	Superfamily/family/sub-family	Genus	Species	Biotope association	Abundance
Ara54	Araneae	Amaurobiidae	*Chresiona*	sp.1	Fynbos-associated	107
Ara22	Araneae	Amaurobiidae	*Pseudauximus*	*reticulatus* (Simon, 1902)	Fynbos-associated	51
Ara98	Araneae	Ammoxenidae	*Ammoxenus*	*kalaharicus* (Benoit, 1972)	Fynbos-associated	131
Ara256	Araneae	Anapidae	*Crozetulus*	*rhodesiensis* (Brignoli, 1981)	Ubiquitous	66
Ara24	Araneae	Anapidae	*Metanapis*	*bimaculata* (Simon, 1895)	Fynbos-associated	25
Ara362	Araneae	Araneidae	*Araneus*	*apricus* (Karsch, 1884)	Ubiquitous	2
Ara275	Araneae	Araneidae	*Hypsosinga*	sp.1	Fynbos-associated	11
Ara276	Araneae	Araneidae	*Neoscona*	*blondeli* (Simon, 1886)	Ubiquitous	133
Ara398	Araneae	Araneidae	*Neoscona*	*subfusca* (Koch, 1837)	Ubiquitous	3
Ara389	Araneae	Clubionidae	*Clubiona*	sp.1	Ubiquitous	7
Ara292	Araneae	Clubionidae	*Clubiona*	sp.3	Ubiquitous	157
Ara30	Araneae	Clubionidae	*Clubiona*	sp.5	Ubiquitous	2
Ara343	Araneae	Clubionidae	*Clubiona*	sp.7	Ubiquitous	13
Ara103	Araneae	Corinnidae	*Castianeira*	sp.1	Ubiquitous	20
Ara73	Araneae	Eutichuridae	*Cheiracanthium*	sp.2	Ubiquitous	10
Ara222	Araneae	Eutichuridae	*Cheiramiona*	*ansiae* (Lotz, 2002)	Ubiquitous	6
Ara7	Araneae	Gallieniellidae	*Drassodella*	*septemmaculata* (Strand, 1909)	Ubiquitous	8
Ara48	Araneae	Gnaphosidae	*Asemesthes*	sp.2	Ubiquitous	10
Ara127	Araneae	Gnaphosidae	*Camillina*	sp.1	Ubiquitous	6
Ara133	Araneae	Gnaphosidae	*Camillina*	sp.2	Ubiquitous	40
Ara168	Araneae	Gnaphosidae	*Camillina*	sp.3	Ubiquitous	2
Ara17	Araneae	Gnaphosidae	*Camillina*	sp.4	Ubiquitous	12
Ara66	Araneae	Gnaphosidae	*Camillina*	sp.6	Ubiquitous	71
Ara90	Araneae	Gnaphosidae	*Camillina*	sp.8	Ubiquitous	21
Ara154	Araneae	Gnaphosidae	*Megamyrmaekion*	*schreineri* (Tucker, 1923)	Ubiquitous	2
Ara20	Araneae	Gnaphosidae	*Nomisia*	*australis* (Dalmas, 1921)	Crop-associated	20
Ara63	Araneae	Gnaphosidae	*Setaphis*	*subtilis* (Simon, 1897)	Ubiquitous	67

Ara208	Araneae	Gnaphosidae	*Urozelotes*	*rusticus* (Koch, 1872)	Crop-associated	27
Ara138	Araneae	Gnaphosidae	*Xerophaeus*	*aurariarum* (Purcell, 1907)	Ubiquitous	12
Ara61	Araneae	Gnaphosidae	*Zelotes*	*capsula* (Tucker, 1923)	Crop-associated	41
Ara47	Araneae	Gnaphosidae	*Zelotes*	*flavitarsis* (Purcell, 1908)	Ubiquitous	10
Ara11	Araneae	Gnaphosidae	*Zelotes*	*reduncus* (Purcell, 1907)	Ubiquitous	64
Ara10	Araneae	Gnaphosidae	*Zelotes*	sp.1	Ubiquitous	6
Ara26	Araneae	Gnaphosidae	*Zelotes*	sp.10	Ubiquitous	154
Ara60	Araneae	Gnaphosidae	*Zelotes*	sp.11	Ubiquitous	22
Ara101	Araneae	Gnaphosidae	*Zelotes*	sp.2	Ubiquitous	15
Ara105	Araneae	Gnaphosidae	*Zelotes*	sp.3	Crop-associated	27
Ara12	Araneae	Gnaphosidae	*Zelotes*	sp.4	Ubiquitous	142
Ara124	Araneae	Gnaphosidae	*Zelotes*	sp.5	Crop-associated	21
Ara132	Araneae	Gnaphosidae	*Zelotes*	sp.7	Ubiquitous	3
Ara207	Araneae	Gnaphosidae	*Zelotes*	sp.9	Ubiquitous	5
Ara44	Araneae	Linyphiidae	*Agyneta*	*habra* (Locket, 1968)	Ubiquitous	368
Ara173	Araneae	Linyphiidae	*Agyneta*	sp.4	Ubiquitous	2
Ara289	Araneae	Linyphiidae	*Agyneta*	sp.6	Ubiquitous	48
Ara330	Araneae	Linyphiidae	*Agyneta*	sp.7	Ubiquitous	6
Ara5	Araneae	Linyphiidae	*Agyneta*	sp.8	Ubiquitous	102
Ara114	Araneae	Linyphiidae	*Mermessus*	*fradeorum* (Berland, 1932)	Ubiquitous	4
Ara69	Araneae	Linyphiidae	*Ostearius*	*melanopygius* (Cambridge, 1879)	Ubiquitous	3
Ara1	Araneae	Linyphiidae	*Pelecopsis*	*janus* (Jocqué, 1984)	Ubiquitous	279
Ara13	Araneae	Lycosidae	*Allocosa*	sp.1	Ubiquitous	23
Ara263	Araneae	Lycosidae	*Allocosa*	sp.3	Ubiquitous	53
Ara94	Araneae	Lycosidae	*Allocosa*	sp.8	Ubiquitous	5
Ara113	Araneae	Lycosidae	*Arctosa*	*promontorii* (Pocock, 1900)	Ubiquitous	7
Ara55	Araneae	Lycosidae	*Lycosa*	*rimicola* (Purcell, 1903)	Crop-associated	20
Ara21	Araneae	Lycosidae	*Pardosa*	*crassipalpis* (Purcell, 1903)	Ubiquitous	47
Ara195	Araneae	Lycosidae	*Pardosa*	sp.2	Ubiquitous	2
Ara203	Araneae	Lycosidae	*Pardosa*	sp.3	Ubiquitous	32

Ara179	Araneae	Lycosidae	*Pterartoria*	*confusa* (Russell-Smith & Roberts, 2017)	Ubiquitous	41
Ara107	Araneae	Lycosidae	*Trabea*	*purcelli* (Roewer, 1951)	Ubiquitous	617
Ara121	Araneae	Lycosidae	*Trabea*	sp.1	Ubiquitous	3
Ara27	Araneae	Lycosidae	*Trabea*	sp.3	Ubiquitous	172
Ara8	Araneae	Lycosidae	*Trabea*	sp.6	Ubiquitous	22
Ara99	Araneae	Migidae	*Moggridgea*	*loistata* (Griswold, 1987)	Ubiquitous	3
Ara342	Araneae	Miturgidae	*Voraptus*	sp.2	Ubiquitous	5
Ara40	Araneae	Nemesiidae	*Spiroctenus*	*cambierae* (Purcell, 1902)	Ubiquitous	18
Ara223	Araneae	Oonopidae	*Australoonops*	sp.1	Ubiquitous	9
Ara147	Araneae	Oxyopidae	*Oxyopes*	*hoggi* (Lessert, 1915)	Fynbos-associated	85
Ara364	Araneae	Oxyopidae	*Oxyopes*	sp.1	Ubiquitous	7
Ara383	Araneae	Oxyopidae	*Oxyopes*	sp.3	Fynbos-associated	121
Ara260	Araneae	Philodromidae	*Gephyrota*	*glauca* (Jézéquel, 1966)	Ubiquitous	3
Ara273	Araneae	Philodromidae	*Philodromus*	*guineensis* (Millot, 1941)	Fynbos-associated	65
Ara104	Araneae	Philodromidae	*Thanatus*	*vulgaris* (Simon, 1870)	Ubiquitous	84
Ara196	Araneae	Philodromidae	*Tibellus*	*minor* (Lessert, 1919)	Ubiquitous	67
Ara29	Araneae	Phyxelididae	*Vidole*	*sothoana* (Griswold, 1990)	Ubiquitous	5
Ara277	Araneae	Pisauridae	*Afropisaura*	*rothiformis* (Strand, 1908)	Fynbos-associated	51
Ara112	Araneae	Pisauridae	*Rothus*	*aethiopicus* (Pavesi, 1883)	Ubiquitous	31
Ara408	Araneae	Salticidae	*Baryphas*	*ahenus* (Simon, 1902)	Ubiquitous	7
Ara355	Araneae	Salticidae	*Evarcha*	sp.4	Ubiquitous	10
Ara293	Araneae	Salticidae	*Evarcha*	*striolata* (Wesolowska & Haddad, 2009)	Ubiquitous	3
Ara270	Araneae	Salticidae	*Heliophanus*	*capricola* (Simon, 1901)	Ubiquitous	16
Ara148	Araneae	Salticidae	*Heliophanus*	*debilis* (Simon, 1901)	Ubiquitous	102
Ara204	Araneae	Salticidae	*Heliophanus*	*horrifer* (Wesolowska, 1986)	Ubiquitous	3
Ara189	Araneae	Salticidae	*Heliophanus*	sp.1	Ubiquitous	9
Ara320	Araneae	Salticidae	*Heliophanus*	sp.4	Ubiquitous	5
Ara413	Araneae	Salticidae	*Heliophanus*	sp.6	Ubiquitous	2
Ara125	Araneae	Salticidae	*Langelurillus*	sp.1	Ubiquitous	4
Ara131	Araneae	Salticidae	*Langelurillus*	sp.3	Ubiquitous	3

Ara14	Araneae	Salticidae	*Langona*	*hirsuta* (Haddad & Wesolowska, 2011)	Ubiquitous	16
Ara36	Araneae	Salticidae	*Tanzania*	*striatus* (Wesolowska, Azarkina & Russell-Smith, 2014)	Ubiquitous	48
Ara406	Araneae	Salticidae	*Thyenula*	sp.2	Ubiquitous	2
Ara248	Araneae	Scytodidae	*Scytodes*	*caffra* (Purcell, 1904)	Ubiquitous	2
Ara166	Araneae	Scytodidae	*Scytodes*	*elizabethae* (Purcell, 1904)	Ubiquitous	13
Ara83	Araneae	Scytodidae	*Scytodes*	*testudo* (Purcell, 1904)	Ubiquitous	59
Ara317	Araneae	Theridiidae	*Anelosimus*	sp.2	Fynbos-associated	53
Ara346	Araneae	Theridiidae	*Argyrodes*	sp.1	Ubiquitous	7
Ara2	Araneae	Theridiidae	*Dipoena*	sp.1	Crop-associated	184
Ara341	Araneae	Theridiidae	*Enoplognatha*	sp.2	Fynbos-associated	18
Ara290	Araneae	Theridiidae	*Latrodectus*	*geometricus* (Koch, 1841)	Ubiquitous	16
Ara388	Araneae	Theridiidae	*Theridiidae*	sp.1	Ubiquitous	7
Ara269	Araneae	Theridiidae	*Theridion*	sp.2	Fynbos-associated	79
Ara123	Araneae	Theridiidae	*Theridion*	sp.3	Ubiquitous	6
Ara375	Araneae	Theridiidae	*Theridion*	sp.4	Ubiquitous	28
Ara59	Araneae	Theridiidae	*Theridion*	sp.6	Ubiquitous	86
Ara186	Araneae	Thomisidae	*Misumenops*	*rubrodecoratus* (Millot, 1942)	Crop-associated	15
Ara287	Araneae	Thomisidae	*Runcinia*	sp.1	Fynbos-associated	52
Ara172	Araneae	Thomisidae	*Thomisops*	*sulcatus* (Simon, 1895)	Ubiquitous	6
Ara253	Araneae	Thomisidae	*Thomisus*	*australis* (Comellini, 1957)	Ubiquitous	63
Ara259	Araneae	Thomisidae	*Thomisus*	sp.1	Ubiquitous	8
Ara115	Araneae	Thomisidae	*Xysticus*	*havilandi* (Lawrence, 1942)	Ubiquitous	3
Ara164	Araneae	Thomisidae	*Xysticus*	*sagittifer* (Lawrence, 1927)	Ubiquitous	29
Ara6	Araneae	Trachelidae	*Thysanina*	*scopulifer* (Simon, 1896)	Ubiquitous	3
Ara25	Araneae	Zodariidae	*Cydrela*	*spinimana* (Pocock, 1898)	Ubiquitous	9
Ara45	Araneae	Zodariidae	*Diores*	sp.1	Ubiquitous	4
Ara15	Araneae	Zodariidae	*Diores*	sp.2	Ubiquitous	68
Ara19	Araneae	Zodariidae	*Diores*	*simoni* (Cambridge, 1904)	Ubiquitous	4
Ara137	Araneae	Zodariidae	*Heraldida*	sp.1	Fynbos-associated	9
Ara279	Araneae	Zodariidae	*Systenoplacis*	*fagei* (Lawrence, 1936)	Ubiquitous	5

Ara76	Araneae	Zoropsidae	*Phanotea*	*margarita* (Griswold, 1994)	Ubiquitous	5
Ara81	Araneae	Zoropsidae	*Phanotea*	*orestria* (Griswold, 1994)	Ubiquitous	9
Col18	Coleoptera	Anthicidae	Undetermined	Undetermined	Fynbos-associated	81
Col198	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	4
Col21	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	535
Col313	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	3
Col323	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	3
Col325	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	4
Col342	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	76
Col38	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	157
Col5	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	499
Col8	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	1175
Col274	Coleoptera	Apionidae	Undetermined	Undetermined	Fynbos-associated	39
Col10	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	4
Col106	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	12
Col119	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	64
Col136	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	55
Col211	Coleoptera	Carabidae	Undetermined	Undetermined	Crop-associated	43
Col39	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	15
Col49	Coleoptera	Carabidae	Undetermined	Undetermined	Fynbos-associated	17
Col66	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	16
Col69	Coleoptera	Carabidae	Undetermined	Undetermined	Crop-associated	29
Col70	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	19
Col9	Coleoptera	Carabidae	Undetermined	Undetermined	Crop-associated	30
Col108	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	7
Col121	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	17
Col158	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	3
Col187	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	2
Col261	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Fynbos-associated	28
Col285	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	6
Col29	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Crop-associated	11

Col328	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	13
Col337	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	6
Col345	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Crop-associated	21
Col374	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	14
Col4	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	231
Col84	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Fynbos-associated	10
Col93	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	141
Col293	Coleoptera	Clambidae	Undetermined	Undetermined	Ubiquitous	3
Col65	Coleoptera	Clambidae	Undetermined	Undetermined	Ubiquitous	3
Col336	Coleoptera	Cleridae	Undetermined	Undetermined	Ubiquitous	37
Col13	Coleoptera	Coccinellidae	Undetermined	Undetermined	Crop-associated	147
Col296	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	10
Col316	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	2
Col333	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	3
Col343	Coleoptera	Coccinellidae	Undetermined	Undetermined	Crop-associated	7
Col367	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	2
Col51	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	5
Col179	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Fynbos-associated	7
Col182	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	19
Col310	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	3
Col311	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	7
Col334	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	17
Col349	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	3
Col62	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	68
Col72	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	275
Col91	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Crop-associated	154
Col101	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	2
Col111	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	7
Col12	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	73
Col126	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	64
Col143	Coleoptera	Curculionidae	Undetermined	Undetermined	Crop-associated	62

Col172	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	3
Col195	Coleoptera	Curculionidae	Undetermined	Undetermined	Fynbos-associated	58
Col217	Coleoptera	Curculionidae	Undetermined	Undetermined	Crop-associated	22
Col237	Coleoptera	Curculionidae	Undetermined	Undetermined	Fynbos-associated	27
Col243	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	3
Col245	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	3
Col25	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	12
Col26	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	18
Col273	Coleoptera	Curculionidae	Undetermined	Undetermined	Fynbos-associated	53
Col290	Coleoptera	Curculionidae	Undetermined	Undetermined	Fynbos-associated	12
Col30	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	21
Col395	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	3
Col396	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	7
Col54	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	10
Col56	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	6
Col68	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	11
Col86	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	6
Col89	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	5
Col98	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	12
Col99	Coleoptera	Curculionidae	Undetermined	Undetermined	Crop-associated	81
Col142	Coleoptera	Dermestidae	Undetermined	Undetermined	Ubiquitous	63
Col11	Coleoptera	Elateridae	Undetermined	Undetermined	Ubiquitous	7
Col139	Coleoptera	Elateridae	Undetermined	Undetermined	Ubiquitous	4
Col373	Coleoptera	Elateridae	Undetermined	Undetermined	Ubiquitous	3
Col2	Coleoptera	Histeridae	Undetermined	Undetermined	Crop-associated	229
Col36	Coleoptera	Histeridae	Undetermined	Undetermined	Ubiquitous	15
Col95	Coleoptera	Melyridae	Undetermined	Undetermined	Ubiquitous	10
Col110	Coleoptera	Mordeliidae	Undetermined	Undetermined	Ubiquitous	8
Col271	Coleoptera	Mycetophogidae	Undetermined	Undetermined	Fynbos-associated	65
Col14	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	9
Col184	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	70

Col216	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	2
Col306	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	20
Col324	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	4
Col326	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	3
Col50	Coleoptera	Nitidulidae	Undetermined	Undetermined	Fynbos-associated	22
Col53	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	7
Col63	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	15
Col6	Coleoptera	Rhizophagidae	Undetermined	Undetermined	Ubiquitous	949
Col17	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Fynbos-associated	97
Col357	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Ubiquitous	3
Col7	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Crop-associated	164
Col100	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	223
Col105	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	10
Col109	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	11
Col146	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	11
Col162	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	30
Col214	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	25
Col23	Coleoptera	Staphylinidae	Undetermined	Undetermined	Fynbos-associated	597
Col24	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	2
Col3	Coleoptera	Staphylinidae	Undetermined	Undetermined	Crop-associated	168
Col40	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	145
Col41	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	2
Col45	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	10
Col73	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	3
Col90	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	202
Col33	Coleoptera	Sylpidae	Undetermined	Undetermined	Ubiquitous	356
Col34	Coleoptera	Sylpidae	Undetermined	Undetermined	Ubiquitous	7
Col1	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Crop-associated	290
Col163	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	6
Col254	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	2
Col28	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	184

Col59	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	31
Col61	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	14
Col74	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	2
Hem46	Hemiptera	Nabidae	Undetermined	Undetermined	Crop-associated	50
Hem11	Hemiptera	Reduviidae	Undetermined	Undetermined	Ubiquitous	7
Hem82	Hemiptera	Reduviidae	Undetermined	Undetermined	Ubiquitous	26
Hem1	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	1504
Hem10	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	12
Hem100	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	934
Hem102	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	4
Hem103	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem105	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	31
Hem106	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	256
Hem114	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	123
Hem116	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	94
Hem117	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	1059
Hem118	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	14
Hem119	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	34
Hem12	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	64
Hem126	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	13
Hem13	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	31
Hem138	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	18
Hem14	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	155
Hem140	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	71
Hem141	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	42
Hem142	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	117
Hem148	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem149	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	35
Hem151	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	35
Hem154	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	44
Hem157	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	97

Hem158	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	52
Hem16	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	9
Hem166	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem169	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	8
Hem17	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	186
Hem171	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	7
Hem175	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	26
Hem184	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem186	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem19	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	147
Hem190	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	46
Hem198	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	6
Hem199	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	17
Hem2	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	182
Hem20	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	572
Hem200	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	29
Hem201	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	12
Hem202	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem209	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem21	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	1019
Hem211	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem215	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem25	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	71
Hem26	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	230
Hem27	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	11
Hem28	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	20
Hem29	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	29
Hem3	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	2175
Hem31	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	300
Hem32	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	53
Hem33	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	4

Hem34	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	33
Hem37	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	13
Hem39	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	125
Hem4	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	340
Hem41	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	7
Hem43	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	243
Hem45	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	125
Hem47	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	295
Hem48	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	189
Hem49	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	153
Hem5	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem50	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	214
Hem51	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	26
Hem53	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	16
Hem56	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	11
Hem57	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	224
Hem59	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	195
Hem60	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	28
Hem61	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	18
Hem63	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	126
Hem64	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	147
Hem65	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	152
Hem66	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	81
Hem67	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	114
Hem68	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	53
Hem69	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem7	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	329
Hem70	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem72	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	16
Hem74	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	8
Hem75	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	130

Hem76	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	13
Hem77	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	76
Hem79	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	440
Hem8	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	42
Hem81	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	68
Hem83	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	15
Hem85	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	5
Hem87	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	530
Hem88	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	40
Hem9	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	159
Hem92	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	30
Hem93	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	10
Hem94	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	676
Hem95	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	162
Hem96	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	27
Hem98	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	14
Hem99	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	6

Appendix C: Taxonomic list of species used in chapter 4.

Morpho-species code	Order/sub-order	Superfamily/family/sub-family	Genus	Species	Biotope association	Abundance
Ara54	Araneae	Amaurobiidae	*Chresiona*	sp.1	Fynbos-associated	64
Ara46	Araneae	Amaurobiidae	*Obatala*	sp.1		1
Ara22	Araneae	Amaurobiidae	*Pseudauximus*	*reticulatus* (Simon, 1902)	Fynbos-associated	16
Ara98	Araneae	Ammoxenidae	*Ammoxenus*	*kalaharicus* (Benoit, 1972)	Fynbos-associated	9
Ara256	Araneae	Anapidae	*Crozetulus*	*rhodesiensis* (Brignoli, 1981)	Ubiquitous	42
Ara24	Araneae	Anapidae	*Metanapis*	*bimaculata* (Simon, 1895)	Fynbos-associated	1
Ara363	Araneae	Araneidae	*Argiope*	sp.1		1
Ara304	Araneae	Araneidae	*Cyrtophora*	*citricola* (Forsskål, 1775)		1
Ara275	Araneae	Araneidae	*Hypsosinga*	sp.1	Fynbos-associated	2
Ara399	Araneae	Araneidae	*Kilima*	*decens* (Blackwall, 1866)		8
Ara353	Araneae	Araneidae	*Larinia*	*natalensis* (Grasshoff, 1971)		3
Ara276	Araneae	Araneidae	*Neoscona*	*blondeli* (Simon, 1886)	Ubiquitous	68
Ara274	Araneae	Araneidae	*Neoscona*	sp.1		16
Ara315	Araneae	Araneidae	*Neoscona*	sp.2		1
Ara398	Araneae	Araneidae	*Neoscona*	*subfusca* (Koch, 1837)	Ubiquitous	1
Ara389	Araneae	Clubionidae	*Clubiona*	sp.1	Ubiquitous	6
Ara286	Araneae	Clubionidae	*Clubiona*	sp.2		9
Ara292	Araneae	Clubionidae	*Clubiona*	sp.3	Ubiquitous	194
Ara34	Araneae	Clubionidae	*Clubiona*	sp.6		1
Ara343	Araneae	Clubionidae	*Clubiona*	sp.7	Ubiquitous	7
Ara103	Araneae	Corinnidae	*Castianeira*	sp.1	Ubiquitous	12
Ara182	Araneae	Corinnidae	*Castianeira*	sp.2		1
Ara155	Araneae	Dysderidae	*Dysdera*	*crocata* (Kock, 1838)		2
Ara220	Araneae	Eutichuridae	*Cheiracanthium*	*furculatum* (Karsch, 1879)		1
Ara316	Araneae	Eutichuridae	*Cheiracanthium*	sp.1		8
Ara73	Araneae	Eutichuridae	*Cheiracanthium*	sp.2	Ubiquitous	7
Ara222	Araneae	Eutichuridae	*Cheiramiona*	*ansiae* (Lotz, 2002)	Ubiquitous	1

Ara4	Araneae	Gnaphosidae	*Asemesthes*	sp.1		4
Ara48	Araneae	Gnaphosidae	*Asemesthes*	sp.2	Ubiquitous	9
Ara127	Araneae	Gnaphosidae	*Camillina*	sp.1	Ubiquitous	11
Ara133	Araneae	Gnaphosidae	*Camillina*	sp.2	Ubiquitous	25
Ara168	Araneae	Gnaphosidae	*Camillina*	sp.3	Ubiquitous	1
Ara17	Araneae	Gnaphosidae	*Camillina*	sp.4	Ubiquitous	1
Ara33	Araneae	Gnaphosidae	*Camillina*	sp.5		1
Ara66	Araneae	Gnaphosidae	*Camillina*	sp.6	Ubiquitous	36
Ara87	Araneae	Gnaphosidae	*Camillina*	sp.7		10
Ara90	Araneae	Gnaphosidae	*Camillina*	sp.8	Ubiquitous	12
Ara154	Araneae	Gnaphosidae	*Megamyrmaekion*	*schreineri* (Tucker, 1923)	Ubiquitous	2
Ara20	Araneae	Gnaphosidae	*Nomisia*	*australis* (Dalmas, 1921)	Crop-associated	33
Ara63	Araneae	Gnaphosidae	*Setaphis*	*subtilis* (Simon, 1897)	Ubiquitous	51
Ara208	Araneae	Gnaphosidae	*Urozelotes*	*rusticus* (Koch, 1872)	Crop-associated	42
Ara138	Araneae	Gnaphosidae	*Xerophaeus*	*aurariarum* (Purcell, 1907)	Ubiquitous	6
Ara61	Araneae	Gnaphosidae	*Zelotes*	*capsula* (Tucker, 1923)	Crop-associated	41
Ara47	Araneae	Gnaphosidae	*Zelotes*	*flavitarsis* (Purcell, 1908)	Ubiquitous	6
Ara71	Araneae	Gnaphosidae	*Zelotes*	*fuligineus* (Purcell, 1907)		7
Ara225	Araneae	Gnaphosidae	*Zelotes*	*gooldi* (Purcell, 1907)		1
Ara11	Araneae	Gnaphosidae	*Zelotes*	*reduncus* (Purcell, 1907)	Ubiquitous	37
Ara26	Araneae	Gnaphosidae	*Zelotes*	sp.10	Ubiquitous	100
Ara60	Araneae	Gnaphosidae	*Zelotes*	sp.11	Ubiquitous	14
Ara101	Araneae	Gnaphosidae	*Zelotes*	sp.2	Ubiquitous	2
Ara105	Araneae	Gnaphosidae	*Zelotes*	sp.3	Crop-associated	2
Ara12	Araneae	Gnaphosidae	*Zelotes*	sp.4	Ubiquitous	90
Ara124	Araneae	Gnaphosidae	*Zelotes*	sp.5	Crop-associated	19
Ara129	Araneae	Gnaphosidae	*Zelotes*	sp.6		1
Ara132	Araneae	Gnaphosidae	*Zelotes*	sp.7	Ubiquitous	1
Ara177	Araneae	Gnaphosidae	*Zelotes*	sp.8		1
Ara207	Araneae	Gnaphosidae	*Zelotes*	sp.9	Ubiquitous	4
Ara39	Araneae	Hahniidae	*Hahnia*	*laticeps* (Simon, 1898)		2

Ara44	Araneae	Linyphiidae	*Agyneta*	*habra* (Locket, 1968)	Ubiquitous	293
Ara100	Araneae	Linyphiidae	*Agyneta*	sp.1		5
Ara159	Araneae	Linyphiidae	*Agyneta*	sp.2		1
Ara16	Araneae	Linyphiidae	*Agyneta*	sp.3		1
Ara226	Araneae	Linyphiidae	*Agyneta*	sp.5		1
Ara289	Araneae	Linyphiidae	*Agyneta*	sp.6	Ubiquitous	56
Ara330	Araneae	Linyphiidae	*Agyneta*	sp.7	Ubiquitous	1
Ara5	Araneae	Linyphiidae	*Agyneta*	sp.8	Ubiquitous	79
Ara356	Araneae	Linyphiidae	*Limoneta*	*sirimoni* (Bosmans, 1979)		4
Ara114	Araneae	Linyphiidae	*Mermessus*	*fradeorum* (Berland, 1932)	Ubiquitous	11
Ara70	Araneae	Linyphiidae	*Microlinyphia*	*sterilis* (Pavesi, 1883)		2
Ara69	Araneae	Linyphiidae	*Ostearius*	*melanopygius* (Cambridge, 1879)	Ubiquitous	4
Ara1	Araneae	Linyphiidae	*Pelecopsis*	*janus* (Jocqué, 1984)	Ubiquitous	219
Ara13	Araneae	Lycosidae	*Allocosa*	sp.1	Ubiquitous	7
Ara263	Araneae	Lycosidae	*Allocosa*	sp.3	Ubiquitous	56
Ara43	Araneae	Lycosidae	*Allocosa*	sp.6		2
Ara56	Araneae	Lycosidae	*Allocosa*	sp.7		6
Ara113	Araneae	Lycosidae	*Arctosa*	*promontorii* (Pocock, 1900)	Ubiquitous	2
Ara55	Araneae	Lycosidae	*Lycosa*	*rimicola* (Purcell, 1903)	Crop-associated	7
Ara21	Araneae	Lycosidae	*Pardosa*	*crassipalpis* (Purcell, 1903)	Ubiquitous	59
Ara117	Araneae	Lycosidae	*Pardosa*	sp.1		2
Ara195	Araneae	Lycosidae	*Pardosa*	sp.2	Ubiquitous	1
Ara203	Araneae	Lycosidae	*Pardosa*	sp.3	Ubiquitous	41
Ara64	Araneae	Lycosidae	*Pardosa*	sp.4		6
Ara72	Araneae	Lycosidae	*Pardosa*	sp.5		3
Ara179	Araneae	Lycosidae	*Pterartoria*	*confusa* (Russell-Smith & Roberts, 2017)	Ubiquitous	18
Ara107	Araneae	Lycosidae	*Trabea*	*purcelli* (Roewer, 1951)	Ubiquitous	213
Ara49	Araneae	Lycosidae	*Trabea*	*rubriceps* (Lawrence, 1952)		10
Ara27	Araneae	Lycosidae	*Trabea*	sp.3	Ubiquitous	74
Ara3	Araneae	Lycosidae	*Trabea*	sp.4		1

Ara8	Araneae	Lycosidae	*Trabea*	sp.6	Ubiquitous	14
Ara80	Araneae	Lycosidae	*Trabea*	sp.7		2
Ara342	Araneae	Miturgidae	*Voraptus*	sp.2	Ubiquitous	1
Ara40	Araneae	Nemesiidae	*Spiroctenus*	*cambierae* (Purcell, 1902)	Ubiquitous	3
Ara147	Araneae	Oxyopidae	*Oxyopes*	*hoggi* (Lessert, 1915)	Fynbos-associated	18
Ara239	Araneae	Oxyopidae	*Oxyopes*	*pallidecoloratus* (Strand, 1906)		2
Ara364	Araneae	Oxyopidae	*Oxyopes*	sp.1	Ubiquitous	4
Ara383	Araneae	Oxyopidae	*Oxyopes*	sp.3	Fynbos-associated	12
Ara273	Araneae	Philodromidae	*Philodromus*	*guineensis* (Millot, 1941)	Fynbos-associated	6
Ara104	Araneae	Philodromidae	*Thanatus*	*vulgaris* (Simon, 1870)	Ubiquitous	75
Ara196	Araneae	Philodromidae	*Tibellus*	*minor* (Lessert, 1919)	Ubiquitous	45
Ara29	Araneae	Phyxelididae	*Vidole*	*sothoana* (Griswold, 1990)	Ubiquitous	3
Ara277	Araneae	Pisauridae	*Afropisaura*	*rothiformis* (Strand, 1908)	Fynbos-associated	14
Ara112	Araneae	Pisauridae	*Rothus*	*aethiopicus* (Pavesi, 1883)	Ubiquitous	9
Ara18	Araneae	Prodidomidae	*Theuma*	*fusca* (Purcell, 1907)		1
Ara282	Araneae	Salticidae	*Baryphas*	sp.1		4
Ara303	Araneae	Salticidae	*Evarcha*	sp.2		3
Ara354	Araneae	Salticidae	*Evarcha*	sp.3		10
Ara355	Araneae	Salticidae	*Evarcha*	sp.4	Ubiquitous	3
Ara396	Araneae	Salticidae	*Evarcha*	sp.5		1
Ara293	Araneae	Salticidae	*Evarcha*	*striolata* (Wesolowska & Haddad, 2009)	Ubiquitous	1
Ara270	Araneae	Salticidae	*Heliophanus*	*capricola* (Simon, 1901)	Ubiquitous	11
Ara148	Araneae	Salticidae	*Heliophanus*	*debilis* (Simon, 1901)	Ubiquitous	81
Ara204	Araneae	Salticidae	*Heliophanus*	*horrifer* (Wesolowska, 1986)	Ubiquitous	1
Ara189	Araneae	Salticidae	*Heliophanus*	sp.1	Ubiquitous	8
Ara320	Araneae	Salticidae	*Heliophanus*	sp.4	Ubiquitous	4
Ara413	Araneae	Salticidae	*Heliophanus*	sp.6	Ubiquitous	1
Ara125	Araneae	Salticidae	*Langelurillus*	sp.1	Ubiquitous	2
Ara128	Araneae	Salticidae	*Langelurillus*	sp.2		1
Ara131	Araneae	Salticidae	*Langelurillus*	sp.3	Ubiquitous	1

Ara14	Araneae	Salticidae	*Langona*	*hirsuta* (Haddad & Wesolowska, 2011)	Ubiquitous	13
Ara215	Araneae	Salticidae	*Pellenes*	*beani* (Peckham & Peckham, 1903)		1
Ara314	Araneae	Salticidae	*Pellenes*	sp.1		2
Ara324	Araneae	Salticidae	*Pellenes*	sp.2		2
Ara92	Araneae	Salticidae	*Phlegra*	sp.1		1
Ara319	Araneae	Salticidae	*Rhene*	*machadoi* (Berland & Millot, 1941)		2
Ara36	Araneae	Salticidae	*Tanzania*	*striatus* (Wesolowska, Azarkina & Russell-Smith, 2014)	Ubiquitous	27
Ara384	Araneae	Salticidae	*Thyene*	*thyenioides* (Lessert, 1925)		2
Ara326	Araneae	Salticidae	*Thyenula*	sp.1		1
Ara406	Araneae	Salticidae	*Thyenula*	sp.2	Ubiquitous	1
Ara248	Araneae	Scytodidae	*Scytodes*	*caffra* (Purcell, 1904)	Ubiquitous	1
Ara166	Araneae	Scytodidae	*Scytodes*	*elizabethae* (Purcell, 1904)	Ubiquitous	17
Ara83	Araneae	Scytodidae	*Scytodes*	*testudo* (Purcell, 1904)	Ubiquitous	59
Ara134	Araneae	Segestriidae	*Ariadna*	*bilineata* (Purcell, 1904)		1
Ara425	Araneae	Selenopidae	*Anyphops*	sp.2		1
Ara426	Araneae	Selenopidae	*Anyphops*	sp.3		1
Ara284	Araneae	Tetragnathidae	*Leucauge*	sp.1		3
Ara377	Araneae	Theridiidae	*Anelosimus*	*nelsoni* (Agnarsson, 2006)		1
Ara285	Araneae	Theridiidae	*Anelosimus*	sp.1		5
Ara317	Araneae	Theridiidae	*Anelosimus*	sp.2	Fynbos-associated	4
Ara346	Araneae	Theridiidae	*Argyrodes*	sp.1	Ubiquitous	4
Ara321	Araneae	Theridiidae	*Coleosoma*	sp.1		1
Ara2	Araneae	Theridiidae	*Dipoena*	sp.1	Crop-associated	145
Ara188	Araneae	Theridiidae	*Enoplognatha*	*molesta* (Cambridge, 1904)		1
Ara341	Araneae	Theridiidae	*Enoplognatha*	sp.2	Fynbos-associated	8
Ara357	Araneae	Theridiidae	*Episinus*	sp.1		2
Ara77	Araneae	Theridiidae	*Euryopis*	*episinoides* (Walckenaer, 1847)		8
Ara290	Araneae	Theridiidae	*Latrodectus*	*geometricus* (Koch, 1841)	Ubiquitous	5

Ara53	Araneae	Theridiidae	*Phycosoma*	sp.1		1
Ara9	Araneae	Theridiidae	*Steatoda*	*capensis* (Simon, 1895)		4
Ara328	Araneae	Theridiidae	*Theridion*	sp.1		1
Ara269	Araneae	Theridiidae	*Theridion*	sp.2	Fynbos-associated	23
Ara123	Araneae	Theridiidae	*Theridion*	sp.3	Ubiquitous	5
Ara375	Araneae	Theridiidae	*Theridion*	sp.4	Ubiquitous	6
Ara307	Araneae	Theridiidae	*Theridion*	sp.5		6
Ara59	Araneae	Theridiidae	*Theridion*	sp.6	Ubiquitous	29
Ara288	Araneae	Theridiidae	*Theridion*	sp.7		10
Ara186	Araneae	Thomisidae	*Misumenops*	*rubrodecoratus* (Millot, 1942)	Crop-associated	6
Ara287	Araneae	Thomisidae	*Runcinia*	sp.1	Fynbos-associated	31
Ara338	Araneae	Thomisidae	*Synema*	*imitator* (Pavesi, 1883)		3
Ara172	Araneae	Thomisidae	*Thomisops*	*sulcatus* (Simon, 1895)	Ubiquitous	1
Ara253	Araneae	Thomisidae	*Thomisus*	*australis* (Comellini, 1957)	Ubiquitous	22
Ara259	Araneae	Thomisidae	*Thomisus*	sp.1	Ubiquitous	2
Ara115	Araneae	Thomisidae	*Xysticus*	*havilandi* (Lawrence, 1942)	Ubiquitous	9
Ara164	Araneae	Thomisidae	*Xysticus*	*sagittifer* (Lawrence, 1927)	Ubiquitous	20
Ara106	Araneae	Thomisidae	*Xysticus*	sp.1		1
Ara141	Araneae	Thomisidae	*Xysticus*	sp.2		1
Ara312	Araneae	Thomisidae	*Xysticus*	sp.3		1
Ara313	Araneae	Thomisidae	*Xysticus*	sp.4		1
Ara345	Araneae	Trachelidae	*Afroceto*	sp.1		1
Ara351	Araneae	Trachelidae	*Fuchiba*	*capensis* (Haddad & Lyle, 2008)		5
Ara6	Araneae	Trachelidae	*Thysanina*	*scopulifer* (Simon, 1896)	Ubiquitous	1
Ara306	Araneae	Uloboridae	*Philoponella*	sp.1		1
Ara84	Araneae	Zodariidae	*Caesetius*	*schultzei* (Simon, 1910)		1
Ara25	Araneae	Zodariidae	*Cydrela*	*spinimana* (Pocock, 1898)	Ubiquitous	3
Ara45	Araneae	Zodariidae	*Diores*	sp.1	Ubiquitous	6
Ara15	Araneae	Zodariidae	*Diores*	sp.2	Ubiquitous	136
Ara237	Araneae	Zodariidae	*Diores*	*leleupi* (Jocqué, 1990)		2
Ara19	Araneae	Zodariidae	*Diores*	*simoni* (Cambridge, 1904)	Ubiquitous	1

Ara28	Araneae	Zodariidae	*Heraldida*	sp.2		7
Ara279	Araneae	Zodariidae	*Systenoplacis*	*fagei* (Lawrence, 1936)	Ubiquitous	4
Ara81	Araneae	Zoropsidae	*Phanotea*	*orestria* (Griswold, 1994)	Ubiquitous	9
Col123	Coleoptera	Anthicidae	Undetermined	Undetermined		1
Col160	Coleoptera	Anthicidae	Undetermined	Undetermined		3
Col198	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	1
Col21	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	101
Col210	Coleoptera	Anthicidae	Undetermined	Undetermined		6
Col305	Coleoptera	Anthicidae	Undetermined	Undetermined		1
Col312	Coleoptera	Anthicidae	Undetermined	Undetermined		1
Col313	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	2
Col323	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	2
Col342	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	49
Col375	Coleoptera	Anthicidae	Undetermined	Undetermined		6
Col38	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	83
Col389	Coleoptera	Anthicidae	Undetermined	Undetermined		2
Col390	Coleoptera	Anthicidae	Undetermined	Undetermined		4
Col44	Coleoptera	Anthicidae	Undetermined	Undetermined		1
Col5	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	684
Col64	Coleoptera	Anthicidae	Undetermined	Undetermined		8
Col76	Coleoptera	Anthicidae	Undetermined	Undetermined		5
Col8	Coleoptera	Anthicidae	Undetermined	Undetermined	Ubiquitous	236
Col365	Coleoptera	Bostrichidae	Undetermined	Undetermined		2
Col370	Coleoptera	Bruchidae	Undetermined	Undetermined		1
Col350	Coleoptera	Buprestidae	Undetermined	Undetermined		1
Col27	Coleoptera	Cantharidae	Undetermined	Undetermined		126
Col341	Coleoptera	Cantharidae	Undetermined	Undetermined		3
Col10	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	4
Col106	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	15
Col116	Coleoptera	Carabidae	Undetermined	Undetermined		1
Col119	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	36

Col141	Coleoptera	Carabidae	Undetermined	Undetermined		2
Col145	Coleoptera	Carabidae	Undetermined	Undetermined		4
Col148	Coleoptera	Carabidae	Undetermined	Undetermined		9
Col149	Coleoptera	Carabidae	Undetermined	Undetermined		1
Col168	Coleoptera	Carabidae	Undetermined	Undetermined		2
Col211	Coleoptera	Carabidae	Undetermined	Undetermined	Crop-associated	104
Col212	Coleoptera	Carabidae	Undetermined	Undetermined		1
Col227	Coleoptera	Carabidae	Undetermined	Undetermined		1
Col231	Coleoptera	Carabidae	Undetermined	Undetermined		2
Col235	Coleoptera	Carabidae	Undetermined	Undetermined		1
Col244	Coleoptera	Carabidae	Undetermined	Undetermined		1
Col39	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	77
Col49	Coleoptera	Carabidae	Undetermined	Undetermined	Fynbos-associated	3
Col66	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	25
Col67	Coleoptera	Carabidae	Undetermined	Undetermined		7
Col69	Coleoptera	Carabidae	Undetermined	Undetermined	Crop-associated	64
Col70	Coleoptera	Carabidae	Undetermined	Undetermined	Ubiquitous	12
Col9	Coleoptera	Carabidae	Undetermined	Undetermined	Crop-associated	15
Col108	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	9
Col121	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	3
Col158	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	2
Col180	Coleoptera	Chrysomelidae	Undetermined	Undetermined		13
Col187	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	3
Col189	Coleoptera	Chrysomelidae	Undetermined	Undetermined		1
Col226	Coleoptera	Chrysomelidae	Undetermined	Undetermined		1
Col260	Coleoptera	Chrysomelidae	Undetermined	Undetermined		1
Col29	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Crop-associated	18
Col328	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	10
Col337	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	2
Col345	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Crop-associated	23
Col347	Coleoptera	Chrysomelidae	Undetermined	Undetermined		2

Col374	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	2
Col378	Coleoptera	Chrysomelidae	Undetermined	Undetermined		1
Col380	Coleoptera	Chrysomelidae	Undetermined	Undetermined		8
Col393	Coleoptera	Chrysomelidae	Undetermined	Undetermined		1
Col4	Coleoptera	Chrysomelidae	Undetermined	Undetermined	Ubiquitous	183
Col293	Coleoptera	Clambidae	Undetermined	Undetermined	Ubiquitous	1
Col52	Coleoptera	Clambidae	Undetermined	Undetermined		1
Col65	Coleoptera	Clambidae	Undetermined	Undetermined	Ubiquitous	1
Col83	Coleoptera	Clambidae	Undetermined	Undetermined		1
Col336	Coleoptera	Cleridae	Undetermined	Undetermined	Ubiquitous	42
Col354	Coleoptera	Cleridae	Undetermined	Undetermined		5
Col118	Coleoptera	Coccinellidae	Undetermined	Undetermined		11
Col13	Coleoptera	Coccinellidae	Undetermined	Undetermined	Crop-associated	117
Col252	Coleoptera	Coccinellidae	Undetermined	Undetermined		1
Col277	Coleoptera	Coccinellidae	Undetermined	Undetermined		1
Col281	Coleoptera	Coccinellidae	Undetermined	Undetermined		4
Col287	Coleoptera	Coccinellidae	Undetermined	Undetermined		1
Col288	Coleoptera	Coccinellidae	Undetermined	Undetermined		9
Col291	Coleoptera	Coccinellidae	Undetermined	Undetermined		38
Col296	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	4
Col31	Coleoptera	Coccinellidae	Undetermined	Undetermined		2
Col316	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	1
Col329	Coleoptera	Coccinellidae	Undetermined	Undetermined		1
Col333	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	1
Col343	Coleoptera	Coccinellidae	Undetermined	Undetermined	Crop-associated	9
Col51	Coleoptera	Coccinellidae	Undetermined	Undetermined	Ubiquitous	2
Col60	Coleoptera	Coccinellidae	Undetermined	Undetermined		1
Col103	Coleoptera	Cryptophagidae	Undetermined	Undetermined		2
Col124	Coleoptera	Cryptophagidae	Undetermined	Undetermined		3
Col179	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Fynbos-associated	2
Col182	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	16

Col310	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	1
Col311	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	5
Col332	Coleoptera	Cryptophagidae	Undetermined	Undetermined		18
Col334	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	22
Col37	Coleoptera	Cryptophagidae	Undetermined	Undetermined		3
Col42	Coleoptera	Cryptophagidae	Undetermined	Undetermined		1
Col43	Coleoptera	Cryptophagidae	Undetermined	Undetermined		1
Col62	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	22
Col72	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Ubiquitous	273
Col91	Coleoptera	Cryptophagidae	Undetermined	Undetermined	Crop-associated	78
Col101	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	9
Col111	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	5
Col12	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	37
Col126	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	43
Col135	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col143	Coleoptera	Curculionidae	Undetermined	Undetermined	Crop-associated	63
Col16	Coleoptera	Curculionidae	Undetermined	Undetermined		2
Col166	Coleoptera	Curculionidae	Undetermined	Undetermined		45
Col170	Coleoptera	Curculionidae	Undetermined	Undetermined		2
Col174	Coleoptera	Curculionidae	Undetermined	Undetermined		5
Col175	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col185	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col195	Coleoptera	Curculionidae	Undetermined	Undetermined	Fynbos-associated	1
Col215	Coleoptera	Curculionidae	Undetermined	Undetermined		2
Col217	Coleoptera	Curculionidae	Undetermined	Undetermined	Crop-associated	8
Col218	Coleoptera	Curculionidae	Undetermined	Undetermined		5
Col228	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col229	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col236	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col243	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	1
Col25	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	6

Col26	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	31
Col267	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col273	Coleoptera	Curculionidae	Undetermined	Undetermined	Fynbos-associated	4
Col30	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	18
Col330	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col340	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col360	Coleoptera	Curculionidae	Undetermined	Undetermined		2
Col361	Coleoptera	Curculionidae	Undetermined	Undetermined		1
Col369	Coleoptera	Curculionidae	Undetermined	Undetermined		4
Col381	Coleoptera	Curculionidae	Undetermined	Undetermined		4
Col54	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	10
Col56	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	3
Col68	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	10
Col75	Coleoptera	Curculionidae	Undetermined	Undetermined		3
Col80	Coleoptera	Curculionidae	Undetermined	Undetermined		5
Col86	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	5
Col88	Coleoptera	Curculionidae	Undetermined	Undetermined		2
Col89	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	1
Col98	Coleoptera	Curculionidae	Undetermined	Undetermined	Ubiquitous	11
Col99	Coleoptera	Curculionidae	Undetermined	Undetermined	Crop-associated	49
Col142	Coleoptera	Dermestidae	Undetermined	Undetermined	Ubiquitous	32
Col331	Coleoptera	Dermestidae	Undetermined	Undetermined		1
Col11	Coleoptera	Elateridae	Undetermined	Undetermined	Ubiquitous	21
Col125	Coleoptera	Elateridae	Undetermined	Undetermined		5
Col139	Coleoptera	Elateridae	Undetermined	Undetermined	Ubiquitous	3
Col147	Coleoptera	Elateridae	Undetermined	Undetermined		1
Col232	Coleoptera	Elateridae	Undetermined	Undetermined		7
Col144	Coleoptera	Histeridae	Undetermined	Undetermined		2
Col167	Coleoptera	Histeridae	Undetermined	Undetermined		15
Col2	Coleoptera	Histeridae	Undetermined	Undetermined	Crop-associated	140
Col35	Coleoptera	Histeridae	Undetermined	Undetermined		32

Col36	Coleoptera	Histeridae	Undetermined	Undetermined	Ubiquitous	10
Col130	Coleoptera	Hydrochidae	Undetermined	Undetermined		6
Col22	Coleoptera	Lathrididae	Undetermined	Undetermined		2
Col292	Coleoptera	Melyridae	Undetermined	Undetermined		3
Col356	Coleoptera	Melyridae	Undetermined	Undetermined		1
Col358	Coleoptera	Melyridae	Undetermined	Undetermined		2
Col377	Coleoptera	Melyridae	Undetermined	Undetermined		5
Col95	Coleoptera	Melyridae	Undetermined	Undetermined	Ubiquitous	5
Col271	Coleoptera	Mycetophogidae	Undetermined	Undetermined	Fynbos-associated	2
Col14	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	6
Col159	Coleoptera	Nitidulidae	Undetermined	Undetermined		2
Col184	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	18
Col188	Coleoptera	Nitidulidae	Undetermined	Undetermined		2
Col216	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	2
Col306	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	6
Col324	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	1
Col326	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	2
Col339	Coleoptera	Nitidulidae	Undetermined	Undetermined		4
Col364	Coleoptera	Nitidulidae	Undetermined	Undetermined		5
Col50	Coleoptera	Nitidulidae	Undetermined	Undetermined	Fynbos-associated	2
Col53	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	2
Col63	Coleoptera	Nitidulidae	Undetermined	Undetermined	Ubiquitous	3
Col32	Coleoptera	Pausiidae	Undetermined	Undetermined		2
Col6	Coleoptera	Rhizophagidae	Undetermined	Undetermined	Ubiquitous	918
Col104	Coleoptera	Scarabaeidae	Undetermined	Undetermined		1
Col107	Coleoptera	Scarabaeidae	Undetermined	Undetermined		2
Col138	Coleoptera	Scarabaeidae	Undetermined	Undetermined		1
Col221	Coleoptera	Scarabaeidae	Undetermined	Undetermined		1
Col253	Coleoptera	Scarabaeidae	Undetermined	Undetermined		1
Col366	Coleoptera	Scarabaeidae	Undetermined	Undetermined		1
Col55	Coleoptera	Scarabaeidae	Undetermined	Undetermined		2

Col7	Coleoptera	Scarabaeidae	Undetermined	Undetermined	Crop-associated	185
Col114	Coleoptera	Silphidae	Undetermined	Undetermined		5
Col117	Coleoptera	Silphidae	Undetermined	Undetermined		1
Col100	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	46
Col105	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	1
Col109	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	27
Col146	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	5
Col150	Coleoptera	Staphylinidae	Undetermined	Undetermined		1
Col161	Coleoptera	Staphylinidae	Undetermined	Undetermined		1
Col162	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	17
Col165	Coleoptera	Staphylinidae	Undetermined	Undetermined		1
Col176	Coleoptera	Staphylinidae	Undetermined	Undetermined		2
Col213	Coleoptera	Staphylinidae	Undetermined	Undetermined		1
Col214	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	11
Col23	Coleoptera	Staphylinidae	Undetermined	Undetermined	Fynbos-associated	5
Col230	Coleoptera	Staphylinidae	Undetermined	Undetermined		2
Col234	Coleoptera	Staphylinidae	Undetermined	Undetermined		3
Col246	Coleoptera	Staphylinidae	Undetermined	Undetermined		7
Col3	Coleoptera	Staphylinidae	Undetermined	Undetermined	Crop-associated	208
Col40	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	149
Col41	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	1
Col45	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	4
Col71	Coleoptera	Staphylinidae	Undetermined	Undetermined		1
Col73	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	1
Col90	Coleoptera	Staphylinidae	Undetermined	Undetermined	Ubiquitous	396
Col33	Coleoptera	Sylpidae	Undetermined	Undetermined	Ubiquitous	419
Col34	Coleoptera	Sylpidae	Undetermined	Undetermined	Ubiquitous	6
Col1	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Crop-associated	344
Col15	Coleoptera	Tenebrionidae	Undetermined	Undetermined		10
Col164	Coleoptera	Tenebrionidae	Undetermined	Undetermined		1
Col247	Coleoptera	Tenebrionidae	Undetermined	Undetermined		1

Col28	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	121
Col355	Coleoptera	Tenebrionidae	Undetermined	Undetermined		1
Col59	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	37
Col61	Coleoptera	Tenebrionidae	Undetermined	Undetermined	Ubiquitous	2
Hem123	Hemiptera	Nabidae	Undetermined	Undetermined		1
Hem46	Hemiptera	Nabidae	Undetermined	Undetermined	Crop-associated	62
Hem11	Hemiptera	Reduviidae	Undetermined	Undetermined	Ubiquitous	5
Hem161	Hemiptera	Reduviidae	Undetermined	Undetermined		2
Hem82	Hemiptera	Reduviidae	Undetermined	Undetermined	Ubiquitous	14
Hem1	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	2238
Hem10	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	11
Hem100	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	230
Hem101	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem102	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem103	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem104	Hemiptera	Undetermined	Undetermined	Undetermined		4
Hem105	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	49
Hem106	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	10
Hem107	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem108	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem109	Hemiptera	Undetermined	Undetermined	Undetermined		124
Hem110	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem114	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	23
Hem116	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	80
Hem117	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	1294
Hem119	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem12	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	88
Hem121	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem125	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem126	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem129	Hemiptera	Undetermined	Undetermined	Undetermined		2

Hem13	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	43
Hem138	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	35
Hem139	Hemiptera	Undetermined	Undetermined	Undetermined		4
Hem14	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	130
Hem140	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem141	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	10
Hem142	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	30
Hem143	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem144	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem145	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem146	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem147	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem148	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	1
Hem149	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	3
Hem152	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem153	Hemiptera	Undetermined	Undetermined	Undetermined		4
Hem154	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	6
Hem155	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem156	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem157	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	81
Hem158	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	3
Hem159	Hemiptera	Undetermined	Undetermined	Undetermined		16
Hem16	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	6
Hem160	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem162	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem164	Hemiptera	Undetermined	Undetermined	Undetermined		10
Hem168	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem169	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem17	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	339
Hem170	Hemiptera	Undetermined	Undetermined	Undetermined		27
Hem171	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	24

Hem172	Hemiptera	Undetermined	Undetermined	Undetermined		125
Hem173	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem174	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem175	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	24
Hem177	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem178	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem179	Hemiptera	Undetermined	Undetermined	Undetermined		9
Hem18	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem180	Hemiptera	Undetermined	Undetermined	Undetermined		6
Hem182	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem183	Hemiptera	Undetermined	Undetermined	Undetermined		6
Hem184	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	1
Hem186	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem187	Hemiptera	Undetermined	Undetermined	Undetermined		12
Hem189	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem19	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	27
Hem194	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem198	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem199	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	4
Hem2	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	116
Hem20	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	187
Hem200	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	18
Hem201	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	11
Hem205	Hemiptera	Undetermined	Undetermined	Undetermined		30
Hem206	Hemiptera	Undetermined	Undetermined	Undetermined		2
Hem207	Hemiptera	Undetermined	Undetermined	Undetermined		17
Hem208	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem21	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	10
Hem215	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	1
Hem216	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem219	Hemiptera	Undetermined	Undetermined	Undetermined		1

Hem25	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	138
Hem26	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	104
Hem27	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	5
Hem28	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	24
Hem29	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	58
Hem3	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	2387
Hem30	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem31	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	181
Hem32	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	29
Hem35	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem37	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	3
Hem39	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	100
Hem4	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	275
Hem40	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem43	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	8
Hem45	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	82
Hem47	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	238
Hem48	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	259
Hem49	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	100
Hem5	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	1
Hem50	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	190
Hem51	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	20
Hem52	Hemiptera	Undetermined	Undetermined	Undetermined		21
Hem53	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	20
Hem54	Hemiptera	Undetermined	Undetermined	Undetermined		33
Hem57	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	127
Hem58	Hemiptera	Undetermined	Undetermined	Undetermined		7
Hem59	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	19
Hem6	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem60	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	19
Hem61	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	22

Hem63	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	87
Hem64	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	25
Hem65	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	104
Hem66	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	6
Hem67	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	30
Hem68	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	45
Hem69	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	11
Hem7	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	393
Hem70	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	1
Hem71	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem72	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	7
Hem73	Hemiptera	Undetermined	Undetermined	Undetermined		12
Hem74	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	1
Hem75	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	68
Hem76	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	18
Hem77	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	51
Hem78	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem79	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	14
Hem8	Hemiptera	Undetermined	Undetermined	Undetermined	Crop-associated	58
Hem80	Hemiptera	Undetermined	Undetermined	Undetermined		3
Hem81	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	8
Hem83	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	28
Hem84	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem85	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	31
Hem87	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	9
Hem9	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	603
Hem90	Hemiptera	Undetermined	Undetermined	Undetermined		17
Hem91	Hemiptera	Undetermined	Undetermined	Undetermined		1
Hem92	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	34
Hem93	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	2
Hem94	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	7

Hem95	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	18
Hem96	Hemiptera	Undetermined	Undetermined	Undetermined	Fynbos-associated	1
Hem97	Hemiptera	Undetermined	Undetermined	Undetermined		6
Hem98	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	11
Hem99	Hemiptera	Undetermined	Undetermined	Undetermined	Ubiquitous	8

Appendix D: Taxonomic list of species used in chapter 5. Abbreviations for spider traits are active hunters (AH), web builders (WB), ground dweller (GD), and plant dweller (PD). Local abundance: 1 is common (known from > 10 localities) and 3 is rare (known from 1 - 3 localities). Endemicity: Extent of distribution of a recorded species, where 0 is cosmopolitan/introduced and 6 is endemic i.e. known from one locality only. Beetle body lengths were categorised as small = 1 (0-0.33 cm), medium = 2 (0.34-0.66 cm), and large = 3 (> 0.66 cm).

Morpho-species code	Superfamily/family /sub-family	Genus	Species	Abundance	Mean body size (mm)	Hunting mode	Preferred substrate	Local abundance	Endemicity
Ara54	Amaurobiidae	*Chresiona*	sp.1	107	9.5	WB	GD	NA	NA
Ara22	Amaurobiidae	*Pseudauximus*	*reticulatus* (Simon, 1902)	51	9.5	WB	GD	3	5
Ara98	Ammoxenidae	*Ammoxenus*	*kalaharicus* (Benoit, 1972)	131	6	AH	GD	2	2
Ara256	Anapidae	*Crozetulus*	*rhodesiensis* (Brignoli, 1981)	65	2	WB	NA	2	2
Ara24	Anapidae	*Metanapis*	*bimaculata* (Simon, 1895)	25	2	WB	NA	3	3
Ara362	Araneidae	*Araneus*	*apricus* (Karsch, 1884)	2	6.5	WB	NA	1	1
Ara363	Araneidae	*Argiope*	sp.1	1	16.5	WB	NA	NA	NA
Ara421	Araneidae	*Cyclosa*	*insulana* (Costa, 1834)	1	5.5	WB	NA	1	1
Ara393	Araneidae	*Cyclosa*	sp.1	1	16.5	WB	NA	NA	NA
Ara271	Araneidae	*Gasteracantha*	sp.1	2	16.5	WB	NA	NA	NA
Ara336	Araneidae	*Hypsosinga*	*pygmaea* (Sundevall, 1831)	3	16.5	WB	NA	NA	NA
Ara275	Araneidae	*Hypsosinga*	sp.1	11	16.5	WB	NA	NA	NA
Ara399	Araneidae	*Kilima*	*decens* (Blackwall, 1866)	6	8	WB	NA	1	1
Ara353	Araneidae	*Larinia*	*natalensis* (Grasshoff, 1971)	12	9	WB	NA	3	4
Ara276	Araneidae	*Neoscona*	*blondeli* (Simon, 1886)	120	6.5	WB	NA	1	1
Ara352	Araneidae	*Neoscona*	*quincasea* (Roberts, 1983)	1	5.5	WB	NA	1	1
Ara274	Araneidae	*Neoscona*	sp.1	118	16.5	WB	NA	NA	NA
Ara398	Araneidae	*Neoscona*	*subfusca* (Koch, 1837)	3	6.5	WB	NA	1	1
Ara163	Caponiidae	*Caponia*	*capensis* (Purcell, 1904)	8	7.5	AH	NA	2	2
Ara389	Clubionidae	*Clubiona*	sp.1	6	8.5	AH	PD	NA	NA
Ara286	Clubionidae	*Clubiona*	sp.2	116	8.5	AH	PD	NA	NA
Ara292	Clubionidae	*Clubiona*	sp.3	129	8.5	AH	PD	NA	NA
Ara296	Clubionidae	*Clubiona*	sp.4	1	8.5	AH	PD	NA	NA
Ara30	Clubionidae	*Clubiona*	sp.5	2	8.5	AH	PD	NA	NA

Ara343	Clubionidae	*Clubiona*	sp.7	9	8.5	AH	PD	NA	NA
Ara103	Corinnidae	*Castianeira*	sp.1	20	6.5	AH	GD	NA	NA
Ara182	Corinnidae	*Castianeira*	sp.2	7	6.5	AH	GD	NA	NA
Ara261	Cyatholipidae	*Cyatholipus*	*quadrimaculatus* (Simon, 1894)	2	2.5	WB	PD	2	4
Ara210	Cyrtaucheniidae	*Ancylotrypha*	sp.1	3	20.5	NA	GD	NA	NA
Ara38	Cyrtaucheniidae	*Ancylotrypha*	sp.2	4	20.5	NA	GD	NA	NA
Ara412	Deinopidae	*Menneus*	*camelus* (Pocock, 1902)	1	12	WB	PD	1	3
Ara371	Deinopidae	*Menneus*	*capensis* (Purcell, 1904)	2	9.5	WB	PD	1	5
Ara155	Dysderidae	*Dysdera*	*crocata* (Kock, 1838)	1	9.5	AH	GD	2	0
Ara316	Eutichuridae	*Cheiracanthium*	sp.1	2	9	AH	GD	NA	NA
Ara73	Eutichuridae	*Cheiracanthium*	sp.2	10	9	AH	GD	NA	NA
Ara222	Eutichuridae	*Cheiramiona*	*ansiae* (Lotz, 2002)	3	9	AH	GD	1	4
Ara205	Eutichuridae	*Cheiramiona*	*ferrumfontis* (Lotz, 2002)	2	9	AH	GD	2	4
Ara7	Gallieniellidae	*Drassodella*	*septemmaculata* (Strand, 1909)	8	5	AH	GD	2	5
Ara111	Gnaphosidae	*Asemesthes*	*reflexus* (Tucker, 1923)	11	5.5	AH	GD	1	3
Ara48	Gnaphosidae	*Asemesthes*	sp.2	10	6	AH	GD	NA	NA
Ara127	Gnaphosidae	*Camillina*	sp.1	6	5	AH	GD	NA	NA
Ara133	Gnaphosidae	*Camillina*	sp.2	40	5	AH	GD	NA	NA
Ara168	Gnaphosidae	*Camillina*	sp.3	2	5	AH	GD	NA	NA
Ara17	Gnaphosidae	*Camillina*	sp.4	12	5	AH	GD	NA	NA
Ara33	Gnaphosidae	*Camillina*	sp.5	1	5	AH	GD	NA	NA
Ara66	Gnaphosidae	*Camillina*	sp.6	71	5	AH	GD	NA	NA
Ara87	Gnaphosidae	*Camillina*	sp.7	18	5	AH	GD	NA	NA
Ara90	Gnaphosidae	*Camillina*	sp.8	21	5	AH	GD	NA	NA
Ara154	Gnaphosidae	*Megamyrmaekion*	*schreineri* (Tucker, 1923)	2	6.5	AH	GD	2	3
Ara20	Gnaphosidae	*Nomisia*	*australis* (Dalmas, 1921)	20	7	AH	GD	3	6
Ara63	Gnaphosidae	*Setaphis*	*subtilis* (Simon, 1897)	67	4	AH	GD	1	1
Ara208	Gnaphosidae	*Urozelotes*	*rusticus* (Koch, 1872)	27	10	AH	GD	2	0
Ara138	Gnaphosidae	*Xerophaeus*	*aurariarum* (Purcell, 1907)	12	4.5	AH	GD	1	3
Ara209	Gnaphosidae	*Xerophaeus*	sp.1	1	5	AH	GD	NA	NA

Ara61	Gnaphosidae	*Zelotes*	*capsula* (Tucker, 1923)	41	5	AH	GD	2	3
Ara47	Gnaphosidae	*Zelotes*	*flavitarsis* (Purcell, 1908)	10	5.5	AH	GD	3	6
Ara71	Gnaphosidae	*Zelotes*	*fuligineus* (Purcell, 1907)	11	5.5	AH	GD	1	1
Ara11	Gnaphosidae	*Zelotes*	*reduncus* (Purcell, 1907)	64	5.5	AH	GD	1	3
Ara10	Gnaphosidae	*Zelotes*	sp.1	6	5.5	AH	GD	NA	NA
Ara26	Gnaphosidae	*Zelotes*	sp.10	153	5.5	AH	GD	NA	NA
Ara60	Gnaphosidae	*Zelotes*	sp.11	22	5.5	AH	GD	NA	NA
Ara101	Gnaphosidae	*Zelotes*	sp.2	15	5.5	AH	GD	NA	NA
Ara105	Gnaphosidae	*Zelotes*	sp.3	27	5.5	AH	GD	NA	NA
Ara12	Gnaphosidae	*Zelotes*	sp.4	142	5.5	AH	GD	NA	NA
Ara124	Gnaphosidae	*Zelotes*	sp.5	21	5.5	AH	GD	NA	NA
Ara132	Gnaphosidae	*Zelotes*	sp.7	3	5.5	AH	GD	NA	NA
Ara177	Gnaphosidae	*Zelotes*	sp.8	1	5.5	AH	GD	NA	NA
Ara207	Gnaphosidae	*Zelotes*	sp.9	5	5.5	AH	GD	NA	NA
Ara39	Hahniidae	*Hahnia*	*laticeps* (Simon, 1898)	3	3	WB	NA	2	5
Ara79	Idiopidae	*Ctenolophus*	*kolbei* (Purcell, 1902)	1	18.5	NA	GD	3	4
Ara44	Linyphiidae	*Agyneta*	*habra* (Locket, 1968)	365	2.5	WB	NA	NA	NA
Ara100	Linyphiidae	*Agyneta*	sp.1	3	2.5	WB	NA	NA	NA
Ara173	Linyphiidae	*Agyneta*	sp.4	2	2.5	WB	NA	NA	NA
Ara226	Linyphiidae	*Agyneta*	sp.5	1	2.5	WB	NA	NA	NA
Ara289	Linyphiidae	*Agyneta*	sp.6	44	2.5	WB	NA	NA	NA
Ara330	Linyphiidae	*Agyneta*	sp.7	6	2.5	WB	NA	NA	NA
Ara5	Linyphiidae	*Agyneta*	sp.8	102	2.5	WB	NA	NA	NA
Ara356	Linyphiidae	*Limoneta*	*sirimoni* (Bosmans, 1979)	1	2	WB	NA	2	1
Ara114	Linyphiidae	*Mermessus*	*fradeorum* (Berland, 1932)	4	3.5	WB	NA	2	0
Ara70	Linyphiidae	*Microlinyphia*	*sterilis* (Pavesi, 1883)	5	4	WB	NA	1	1
Ara69	Linyphiidae	*Ostearius*	*melanopygius* (Cambridge, 1879)	3	3.5	WB	NA	1	0
Ara1	Linyphiidae	*Pelecopsis*	*janus* (Jocqué, 1984)	279	2	WB	NA	1	2
Ara41	Liocranidae	*Rhaeboctesis*	*matroosbergensis* (Tucker, 1920)	8	9	AH	GD	3	6
Ara13	Lycosidae	*Allocosa*	sp.1	23	10	AH	GD	NA	NA

Ara246	Lycosidae	*Allocosa*	sp.2	1		AH	GD	NA	NA
Ara263	Lycosidae	*Allocosa*	sp.3	51		AH	GD	NA	NA
Ara32	Lycosidae	*Allocosa*	sp.4	2		AH	GD	NA	NA
Ara414	Lycosidae	*Allocosa*	sp.5	6		AH	GD	NA	NA
Ara43	Lycosidae	*Allocosa*	sp.6	1		AH	GD	NA	NA
Ara56	Lycosidae	*Allocosa*	sp.7	7		AH	GD	NA	NA
Ara94	Lycosidae	*Allocosa*	sp.8	5		AH	GD	NA	NA
Ara113	Lycosidae	*Arctosa*	*promontorii* (Pocock, 1900)	7	16.5	AH	GD	NA	NA
Ara191	Lycosidae	*Evippomma*	*squamulatum* (Simon, 1898)	2	6.5	AH	GD	1	2
Ara55	Lycosidae	*Lycosa*	*rimicola* (Purcell, 1903)	19	16.5	NA	GD	3	5
Ara21	Lycosidae	*Pardosa*	*crassipalpis* (Purcell, 1903)	47	4.5	AH	GD	1	2
Ara117	Lycosidae	*Pardosa*	sp.1	3	16.5	AH	GD	NA	NA
Ara195	Lycosidae	*Pardosa*	sp.2	2	16.5	AH	GD	NA	NA
Ara203	Lycosidae	*Pardosa*	sp.3	32	16.5	AH	GD	NA	NA
Ara64	Lycosidae	*Pardosa*	sp.4	7	16.5	AH	GD	NA	NA
Ara72	Lycosidae	*Pardosa*	sp.5	1	16.5	AH	GD	NA	NA
Ara179	Lycosidae	*Pterartoria*	*confusa* (Russell-Smith & Roberts, 2017)	41	16.5	AH	GD	NA	NA
Ara107	Lycosidae	*Trabea*	*purcelli* (Roewer, 1951)	616	6	AH	GD	1	3
Ara49	Lycosidae	*Trabea*	*rubriceps* (Lawrence, 1952)	15	16.5	AH	GD	2	3
Ara121	Lycosidae	*Trabea*	sp.1	3	16.5	AH	GD	NA	NA
Ara198	Lycosidae	*Trabea*	sp.2	1	16.5	AH	GD	NA	NA
Ara27	Lycosidae	*Trabea*	sp.3	172	16.5	AH	GD	NA	NA
Ara51	Lycosidae	*Trabea*	sp.5	1	16.5	AH	GD	NA	NA
Ara8	Lycosidae	*Trabea*	sp.6	22	16.5	AH	GD	NA	NA
Ara80	Lycosidae	*Trabea*	sp.7	4	16.5	AH	GD	NA	NA
Ara99	Migidae	*Moggridgea*	*loistata* (Griswold, 1987)	3	17.5	NA	GD	3	6
Ara335	Miturgidae	*Voraptus*	sp.1	2	9	AH	GD	NA	NA
Ara342	Miturgidae	*Voraptus*	sp.2	5	9	AH	GD	NA	NA
Ara68	Nemesiidae	*Hermacha*	*curvipes* (Purcell, 1902)	2	15	NA	GD	2	5
Ara108	Nemesiidae	*Leptercus*	sp.1	1	21.5	NA	GD	NA	NA

Ara40	Nemesiidae	*Spiroctenus*	*cambierae* (Purcell, 1902)	18	21.5	NA	GD	3	6
Ara74	Nemesiidae	*Spiroctenus*	sp.1	3	21.5	NA	GD	NA	NA
Ara223	Oonopidae	*Australoonops*	sp.1	9	3	AH	GD	NA	NA
Ara240	Oonopidae	*Australoonops*	sp.2	1	3	AH	GD	NA	NA
Ara334	Oxyopidae	*Hamataliwa*	sp.1	14	6.5	AH	PD	NA	NA
Ara194	Oxyopidae	*Oxyopes*	*affinis* (Lessert, 1915)	2	5.5	AH	PD	1	1
Ara147	Oxyopidae	*Oxyopes*	*hoggi* (Lessert, 1915)	83	5.5	AH	PD	1	1
Ara239	Oxyopidae	*Oxyopes*	*pallidecoloratus* (Strand, 1906)	3	5.5	AH	PD	1	1
Ara364	Oxyopidae	*Oxyopes*	sp.1	5	35.5	AH	PD	NA	NA
Ara374	Oxyopidae	*Oxyopes*	sp.2	1	35.5	AH	PD	NA	NA
Ara383	Oxyopidae	*Oxyopes*	sp.3	121	35.5	AH	PD	NA	NA
Ara110	Palpimanidae	*Palpimanus*	*capensis* (Simon, 1893)	2	10	AH	GD	2	3
Ara201	Palpimanidae	*Palpimanus*	sp.1	4	10	AH	GD	NA	NA
Ara260	Philodromidae	*Gephyrota*	*glauca* (Jézéquel, 1966)	3	5	AH	PD	NA	NA
Ara273	Philodromidae	*Philodromus*	*guineensis* (Millot, 1941)	62	6.5	AH	PD	1	1
Ara104	Philodromidae	*Thanatus*	*vulgaris* (Simon, 1870)	77	6	AH	GD	1	0
Ara196	Philodromidae	*Tibellus*	*minor* (Lessert, 1919)	67	9	AH	PD	1	1
Ara88	Pholcidae	*Smeringopus*	*natalensis* (Lawrence, 1947)	1	6.5	WB	NA	1	3
Ara78	Pholcidae	*Spermophora*	*peninsulae* (Lawrence, 1964)	10	4	WB	NA	2	3
Ara29	Phyxelididae	*Vidole*	*sothoana* (Griswold, 1990)	5	9	AH	GD	1	2
Ara277	Pisauridae	*Afropisaura*	*rothiformis* (Strand, 1908)	51	9	AH	PD	2	1
Ara252	Pisauridae	*Euprosthenopsis*	*pulchella* (Pocock, 1902)	2	13.5	WB	PD	1	2
Ara112	Pisauridae	*Rothus*	*aethiopicus* (Pavesi, 1883)	30	19	AH	PD	NA	NA
Ara408	Salticidae	*Baryphas*	*ahenus* (Simon, 1902)	4	8	AH	PD	1	1
Ara282	Salticidae	*Baryphas*	sp.1	4	10	AH	PD	NA	NA
Ara139	Salticidae	*Evarcha*	sp.1	1	5	AH	PD	NA	NA
Ara303	Salticidae	*Evarcha*	sp.2	2	5	AH	PD	NA	NA
Ara354	Salticidae	*Evarcha*	sp.3	1	5	AH	PD	NA	NA
Ara355	Salticidae	*Evarcha*	sp.4	10	5	AH	PD	NA	NA
Ara405	Salticidae	*Evarcha*	sp.6	1	5	AH	PD	NA	NA

Ara293	Salticidae	*Evarcha*	*striolata* (Wesolowska & Haddad, 2009)	3	5	AH	PD	3	6
Ara270	Salticidae	*Heliophanus*	*capricola* (Simon, 1901)	15	4	AH	PD	2	3
Ara148	Salticidae	*Heliophanus*	*debilis* (Simon, 1901)	98	3	AH	PD	1	1
Ara204	Salticidae	*Heliophanus*	*horrifer* (Wesolowska, 1986)	3	4	AH	PD	3	6
Ara189	Salticidae	*Heliophanus*	sp.1	9	4	AH	PD	NA	NA
Ara190	Salticidae	*Heliophanus*	sp.2	1	4	AH	PD	NA	NA
Ara266	Salticidae	*Heliophanus*	sp.3	10	4	AH	PD	NA	NA
Ara320	Salticidae	*Heliophanus*	sp.4	5	4	AH	PD	NA	NA
Ara365	Salticidae	*Heliophanus*	sp.5	1	4	AH	PD	NA	NA
Ara413	Salticidae	*Heliophanus*	sp.6	2	4	AH	PD	NA	NA
Ara125	Salticidae	*Langelurillus*	sp.1	4	10	AH	PD	NA	NA
Ara131	Salticidae	*Langelurillus*	sp.3	3	10	AH	PD	NA	NA
Ara14	Salticidae	*Langona*	*hirsuta* (Haddad & Wesolowska, 2011)	16	6.5	AH	GD	2	4
Ara165	Salticidae	*Menemerus*	*pilosus* (Wesolowska, 1999)	1	6	AH	GD	3	2
Ara370	Salticidae	*Myrmarachne*	sp.1	3	5.5	AH	PD	NA	NA
Ara314	Salticidae	*Pellenes*	sp.1	1	5	AH	GD	NA	NA
Ara324	Salticidae	*Pellenes*	sp.2	5	5	AH	GD	NA	NA
Ara97	Salticidae	*Pellenes*	*tharinae* (Wesolowska, 2006)	6	4.5	AH	GD	2	2
Ara92	Salticidae	*Phlegra*	sp.1	2	5	AH	GD	NA	NA
Ara294	Salticidae	*Rhene*	*banksi* (Peckham & Peckham, 1902)	1	4.5	AH	PD	3	6
Ara319	Salticidae	*Rhene*	*machadoi* (Berland & Millot, 1941)	9	4.5	AH	PD	3	1
Ara36	Salticidae	*Tanzania*	*striatus* (Wesolowska, Azarkina & Russell-Smith, 2014)	48	1.5	AH	NA	NA	NA
Ara391	Salticidae	*Thyene*	*leighi* (Peckham & Peckham, 1903)	1	6.5	AH	PD	NA	NA
Ara384	Salticidae	*Thyene*	*thyenioides* (Lessert, 1925)	3	6	AH	PD	2	1
Ara234	Salticidae	*Thyenula*	*natalica* (Simon, 1902)	1	7	AH	PD	NA	NA

Ara326	Salticidae	*Thyenula*	sp.1	5	7	AH	PD	NA	NA
Ara406	Salticidae	*Thyenula*	sp.2	2	7	AH	PD	NA	NA
Ara248	Scytodidae	*Scytodes*	*caffra* (Purcell, 1904)	2	5	AH	PD	1	1
Ara166	Scytodidae	*Scytodes*	*elizabethae* (Purcell, 1904)	13	4	AH	PD	3	3
Ara83	Scytodidae	*Scytodes*	*testudo* (Purcell, 1904)	59	6	AH	PD	1	4
Ara134	Segestriidae	*Ariadna*	*bilineata* (Purcell, 1904)	2	10.5	WB	NA	2	3
Ara244	Selenopidae	*Anyphops*	sp.1	1	14.5	NA	GD	NA	NA
Ara425	Selenopidae	*Anyphops*	sp.2	1	14.5	NA	GD	NA	NA
Ara153	Sparassidae	*Parapalystes*	*megacephalus* (Koch, 1845)	4	23	AH	PD	3	5
Ara332	Tetragnathidae	*Leucauge*	*levanderi* (Kulczynski, 1901)	1	9.5	WB	NA	1	1
Ara284	Tetragnathidae	*Leucauge*	sp.1	1	8	WB	NA	NA	NA
Ara295	Tetragnathidae	*Leucauge*	sp.2	1	8	WB	NA	NA	NA
Ara377	Theridiidae	*Anelosimus*	*nelsoni* (Agnarsson, 2006)	3	6	WB	PD	1	3
Ara285	Theridiidae	*Anelosimus*	sp.1	6	6	WB	PD	NA	NA
Ara317	Theridiidae	*Anelosimus*	sp.2	52	6	WB	PD	NA	NA
Ara416	Theridiidae	*Argyrodes*	*convivans* (Lawrence, 1937)	1	3.5	NA	NA	1	3
Ara346	Theridiidae	*Argyrodes*	sp.1	7	3.5	NA	NA	NA	NA
Ara2	Theridiidae	*Dipoena*	sp.1	184	4	WB	NA	1	1
Ara188	Theridiidae	*Enoplognatha*	*molesta* (Cambridge, 1904)	1	7.5	WB	NA	1	3
Ara262	Theridiidae	*Enoplognatha*	sp.1	1	7.5	WB	NA	NA	NA
Ara341	Theridiidae	*Enoplognatha*	sp.2	18	7.5	WB	NA	NA	NA
Ara357	Theridiidae	*Episinus*	sp.1	2	4	WB	NA	NA	NA
Ara77	Theridiidae	*Euryopis*	*episinoides* (Walckenaer, 1847)	23	3	AH	GD	3	0
Ara290	Theridiidae	*Latrodectus*	*geometricus* (Koch, 1841)	16	7.5	WB	NA	1	1
Ara53	Theridiidae	*Phycosoma*	sp.1	6	3	WB	NA	NA	NA
Ara9	Theridiidae	*Steatoda*	*capensis* (Simon, 1895)	4	7	WB	NA	1	1
Ara388	Theridiidae	*Theridiidae*	sp.1	5	3.5	WB	PD	NA	NA
Ara328	Theridiidae	*Theridion*	sp.1	2	3.5	WB	PD	NA	NA
Ara269	Theridiidae	*Theridion*	sp.2	78	3.5	WB	PD	NA	NA
Ara123	Theridiidae	*Theridion*	sp.3	6	3.5	WB	PD	NA	NA

Ara375	Theridiidae	*Theridion*	sp.4	28	3.5	WB	PD	NA	NA
Ara307	Theridiidae	*Theridion*	sp.5	27	3.5	WB	PD	NA	NA
Ara59	Theridiidae	*Theridion*	sp.6	84	3.5	WB	PD	NA	NA
Ara288	Theridiidae	*Theridion*	sp.7	22	3.5	WB	PD	NA	NA
Ara325	Thomisidae	*Diaea*	*puncta* (Karsch, 1884)	7	4.5	AH	PD	1	1
Ara300	Thomisidae	*Heriaeus*	*zanii* (van Niekerk & Dippenaar-Schoeman, 2013)	3	5	AH	PD	NA	NA
Ara329	Thomisidae	*Hewittia*	*gracilis* (Lessert, 1928)	3	4.5	AH	PD	1	1
Ara186	Thomisidae	*Misumenops*	*rubrodecoratus* (Millot, 1942)	11	2.5	AH	PD	1	1
Ara423	Thomisidae	*Monaeses*	*pustulosus* (Pavesi, 1895)	1	8	AH	PD	1	1
Ara331	Thomisidae	*Pherecydes*	*tuberculatus* (Cambridge, 1883)	6	4	AH	PD	1	2
Ara272	Thomisidae	*Phrynarachne*	*melloleitaoi* (Lessert, 1933)	2	5.5	AH	PD	1	2
Ara386	Thomisidae	*Runcinia*	*insecta* (Koch, 1875)	3	8	AH	PD	NA	NA
Ara287	Thomisidae	*Runcinia*	sp.1	51	8	AH	PD	NA	NA
Ara338	Thomisidae	*Synema*	*imitator* (Pavesi, 1883)	14	5.5	AH	PD	1	1
Ara172	Thomisidae	*Thomisops*	*sulcatus* (Simon, 1895)	6	3.5	AH	PD	1	1
Ara253	Thomisidae	*Thomisus*	*australis* (Comellini, 1957)	61	5	AH	PD	1	1
Ara259	Thomisidae	*Thomisus*	sp.1	8	6.5	AH	PD	NA	NA
Ara368	Thomisidae	*Trichopagis*	sp.1	2	5.5	AH	PD	NA	NA
Ara115	Thomisidae	*Xysticus*	*havilandi* (Lawrence, 1942)	3	4	AH	NA	3	3
Ara164	Thomisidae	*Xysticus*	*sagittifer* (Lawrence, 1927)	29	5	AH	NA	NA	NA
Ara141	Thomisidae	*Xysticus*	sp.2	1	5	AH	NA	NA	NA
Ara313	Thomisidae	*Xysticus*	sp.4	1	5	AH	NA	NA	NA
Ara145	Trachelidae	*Afroceto*	*arca* (Lyle & Haddad, 2010)	1	6	AH	GD	1	2
Ara345	Trachelidae	*Afroceto*	sp.1	5	6	AH	GD	NA	NA
Ara351	Trachelidae	*Fuchiba*	*capensis* (Haddad & Lyle, 2008)	12	4	AH	GD	1	4
Ara6	Trachelidae	*Thysanina*	*scopulifer* (Simon, 1896)	3	5	AH	GD	3	5
Ara422	Trachelidae	*Trachelas*	*schenkeli* (Lessert, 1923)	1	5	AH	GD	1	2

Ara387	Uloboridae	*Miagrammopes*	*brevicaudus* (Cambridge, 1882)	2	7	WB	PD	1	3
Ara306	Uloboridae	*Philoponella*	sp.1	1	4	WB	NA	NA	NA
Ara424	Uloboridae	*Philoponella*	sp.2	2	4	WB	NA	NA	NA
Ara119	Zodariidae	*Akyttara*	sp.1	1	2.5	AH	GD	NA	NA
Ara84	Zodariidae	*Caesetius*	*schultzei* (Simon, 1910)	8	9	AH	GD	2	4
Ara37	Zodariidae	*Cydrela*	sp.1	1	10	NA	GD	NA	NA
Ara25	Zodariidae	*Cydrela*	*spinimana* (Pocock, 1898)	9	7	AH	GD	2	5
Ara217	Zodariidae	*Cyrioctea*	*griswoldorum* (Platnick & Jocqué, 1992)	4	7.5	AH	GD	NA	NA
Ara45	Zodariidae	*Diores*	sp.1	4	3.5	AH	GD	NA	NA
Ara15	Zodariidae	*Diores*	sp.2	68	3.5	AH	GD	2	5
Ara237	Zodariidae	*Diores*	*leleupi* (Jocqué, 1990)	2	3.5	AH	GD	2	5
Ara19	Zodariidae	*Diores*	*simoni* (Cambridge, 1904)	4	3.5	AH	GD	NA	NA
Ara137	Zodariidae	*Heraldida*	sp.1	9	2	AH	GD	NA	NA
Ara28	Zodariidae	*Heraldida*	sp.2	8	2	AH	GD	NA	NA
Ara213	Zodariidae	*Rotundrela*	*rotunda* (Jocqué, 1999)	2	7.5	NA	GD	3	6
Ara279	Zodariidae	*Systenoplacis*	*fagei* (Lawrence, 1936)	4	8	NA	GD	2	3
Ara76	Zoropsidae	*Phanotea*	*margarita* (Griswold, 1994)	5	10	AH	GD	3	6
Ara81	Zoropsidae	*Phanotea*	*orestria* (Griswold, 1994)	9	10	AH	GD	3	6

Morpho-species code	Superfamily/family /sub-family	Genus	Species	Abundance	Body length (cm)	Winged/ Apterous
Col18	Anthicidae	Undetermined	Undetermined	81	0.3	W
Col198	Anthicidae	Undetermined	Undetermined	4	0.2	W
Col205	Anthicidae	Undetermined	Undetermined	2	0.37	W
Col21	Anthicidae	Undetermined	Undetermined	535	0.31	W
Col210	Anthicidae	Undetermined	Undetermined	3	0.27	W
Col313	Anthicidae	Undetermined	Undetermined	2	0.32	A
Col323	Anthicidae	Undetermined	Undetermined	2	0.25	W
Col325	Anthicidae	Undetermined	Undetermined	3	0.15	W
Col342	Anthicidae	Undetermined	Undetermined	69	0.42	W

Col375	Anthicidae	Undetermined	Undetermined	2	0.17	W
Col38	Anthicidae	Undetermined	Undetermined	157	0.33	A
Col390	Anthicidae	Undetermined	Undetermined	2	0.25	W
Col391	Anthicidae	Undetermined	Undetermined	1	0.92	A
Col5	Anthicidae	Undetermined	Undetermined	499	0.12	W
Col76	Anthicidae	Undetermined	Undetermined	10	0.33	W
Col79	Anthicidae	Undetermined	Undetermined	11	0.21	W
Col8	Anthicidae	Undetermined	Undetermined	1003	0.46	A
Col220	Apionidae	Undetermined	Undetermined	1	0.25	W
Col274	Apionidae	Undetermined	Undetermined	39	0.21	W
Col365	Bostrichidae	Undetermined	Undetermined	1	0.35	W
Col307	Brentidae	Undetermined	Undetermined	1	0.28	W
Col299	Buprestidae	Undetermined	Undetermined	1	NA	W
Col327	Buprestidae	Undetermined	Undetermined	3	1.14	W
Col350	Buprestidae	Undetermined	Undetermined	3	NA	W
Col27	Cantharidae	Undetermined	Undetermined	5	1.15	W
Col341	Cantharidae	Undetermined	Undetermined	61	0.35	W
Col10	Carabidae	Undetermined	Undetermined	4	0.74	NA
Col106	Carabidae	Undetermined	Undetermined	12	1.06	W
Col113	Carabidae	Undetermined	Undetermined	2	0.99	W
Col116	Carabidae	Undetermined	Undetermined	4	0.4	NA
Col119	Carabidae	Undetermined	Undetermined	64	1.13	NA
Col136	Carabidae	Undetermined	Undetermined	55	0.74	NA
Col140	Carabidae	Undetermined	Undetermined	3	1.97	A
Col145	Carabidae	Undetermined	Undetermined	2	0.33	W
Col149	Carabidae	Undetermined	Undetermined	2	1.03	NA
Col151	Carabidae	Undetermined	Undetermined	1	3.3	A
Col152	Carabidae	Undetermined	Undetermined	1	2.15	A
Col168	Carabidae	Undetermined	Undetermined	1	NA	NA
Col169	Carabidae	Undetermined	Undetermined	2	0.27	NA
Col211	Carabidae	Undetermined	Undetermined	43	1.2	A

Col212	Carabidae	Undetermined	Undetermined	1	1.2	A
Col223	Carabidae	Undetermined	Undetermined	1	1.91	W
Col227	Carabidae	Undetermined	Undetermined	2	0.78	W
Col233	Carabidae	Undetermined	Undetermined	1	1.44	A
Col242	Carabidae	Undetermined	Undetermined	3	0.21	NA
Col251	Carabidae	Undetermined	Undetermined	2	0.27	NA
Col269	Carabidae	Undetermined	Undetermined	2	1.12	NA
Col302	Carabidae	Undetermined	Undetermined	7	0.23	NA
Col39	Carabidae	Undetermined	Undetermined	15	0.28	NA
Col49	Carabidae	Undetermined	Undetermined	17	0.61	W
Col66	Carabidae	Undetermined	Undetermined	16	2.49	W
Col67	Carabidae	Undetermined	Undetermined	14	1.76	A
Col69	Carabidae	Undetermined	Undetermined	29	0.61	W
Col70	Carabidae	Undetermined	Undetermined	19	0.42	NA
Col9	Carabidae	Undetermined	Undetermined	30	1.03	NA
Col108	Chrysomelidae	Undetermined	Undetermined	7	0.23	W
Col120	Chrysomelidae	Undetermined	Undetermined	2	0.54	W
Col121	Chrysomelidae	Undetermined	Undetermined	11	0.86	A
Col134	Chrysomelidae	Undetermined	Undetermined	30	0.54	W
Col154	Chrysomelidae	Undetermined	Undetermined	2	0.45	W
Col155	Chrysomelidae	Undetermined	Undetermined	1	0.69	W
Col158	Chrysomelidae	Undetermined	Undetermined	3	0.34	A
Col177	Chrysomelidae	Undetermined	Undetermined	1	0.57	W
Col180	Chrysomelidae	Undetermined	Undetermined	1	0.51	W
Col183	Chrysomelidae	Undetermined	Undetermined	1	0.36	W
Col187	Chrysomelidae	Undetermined	Undetermined	2	0.38	W
Col189	Chrysomelidae	Undetermined	Undetermined	1	0.51	W
Col219	Chrysomelidae	Undetermined	Undetermined	4	0.26	W
Col225	Chrysomelidae	Undetermined	Undetermined	1	0.3	W
Col226	Chrysomelidae	Undetermined	Undetermined	5	0.14	W
Col239	Chrysomelidae	Undetermined	Undetermined	2	0.25	W

Col240	Chrysomelidae	Undetermined	Undetermined	2	0.31	A
Col248	Chrysomelidae	Undetermined	Undetermined	2	0.34	W
Col250	Chrysomelidae	Undetermined	Undetermined	4	0.54	W
Col255	Chrysomelidae	Undetermined	Undetermined	3	0.41	W
Col258	Chrysomelidae	Undetermined	Undetermined	9	0.21	W
Col260	Chrysomelidae	Undetermined	Undetermined	1	0.44	W
Col261	Chrysomelidae	Undetermined	Undetermined	28	0.27	W
Col264	Chrysomelidae	Undetermined	Undetermined	1	0.25	W
Col279	Chrysomelidae	Undetermined	Undetermined	1	0.32	W
Col283	Chrysomelidae	Undetermined	Undetermined	39	0.25	W
Col284	Chrysomelidae	Undetermined	Undetermined	10	0.23	W
Col285	Chrysomelidae	Undetermined	Undetermined	6	0.3	W
Col286	Chrysomelidae	Undetermined	Undetermined	4	0.25	W
Col29	Chrysomelidae	Undetermined	Undetermined	11	0.2	W
Col298	Chrysomelidae	Undetermined	Undetermined	1	0.25	W
Col303	Chrysomelidae	Undetermined	Undetermined	3	0.22	W
Col314	Chrysomelidae	Undetermined	Undetermined	1	0.55	W
Col320	Chrysomelidae	Undetermined	Undetermined	1	0.57	W
Col328	Chrysomelidae	Undetermined	Undetermined	13	0.43	W
Col335	Chrysomelidae	Undetermined	Undetermined	4	0.55	W
Col337	Chrysomelidae	Undetermined	Undetermined	5	0.59	W
Col338	Chrysomelidae	Undetermined	Undetermined	14	NA	W
Col344	Chrysomelidae	Undetermined	Undetermined	6	NA	W
Col345	Chrysomelidae	Undetermined	Undetermined	19	0.17	W
Col346	Chrysomelidae	Undetermined	Undetermined	8	0.25	W
Col347	Chrysomelidae	Undetermined	Undetermined	2	0.7	W
Col374	Chrysomelidae	Undetermined	Undetermined	14	0.78	W
Col379	Chrysomelidae	Undetermined	Undetermined	2	0.13	W
Col380	Chrysomelidae	Undetermined	Undetermined	1	0.46	W
Col385	Chrysomelidae	Undetermined	Undetermined	1	0.64	W
Col393	Chrysomelidae	Undetermined	Undetermined	1	0.21	W

Col394	Chrysomelidae	Undetermined	Undetermined	2	0.27	W
Col4	Chrysomelidae	Undetermined	Undetermined	230	0.18	W
Col46	Chrysomelidae	Undetermined	Undetermined	8	0.58	W
Col57	Chrysomelidae	Undetermined	Undetermined	15	0.27	W
Col84	Chrysomelidae	Undetermined	Undetermined	10	0.51	W
Col93	Chrysomelidae	Undetermined	Undetermined	141	0.38	W
Col77	Ciidae	Undetermined	Undetermined	2	0.11	W
Col272	Clambidae	Undetermined	Undetermined	3	0.16	W
Col293	Clambidae	Undetermined	Undetermined	3	0.19	W
Col65	Clambidae	Undetermined	Undetermined	3	0.1	W
Col83	Clambidae	Undetermined	Undetermined	1	0.13	W
Col276	Cleridae	Undetermined	Undetermined	2	0.22	W
Col280	Cleridae	Undetermined	Undetermined	2	0.97	W
Col297	Cleridae	Undetermined	Undetermined	3	0.41	W
Col336	Cleridae	Undetermined	Undetermined	37	0.27	W
Col354	Cleridae	Undetermined	Undetermined	13	0.32	W
Col362	Cleridae	Undetermined	Undetermined	1	0.94	W
Col118	Coccinellidae	Undetermined	Undetermined	2	0.82	W
Col13	Coccinellidae	Undetermined	Undetermined	100	0.71	W
Col252	Coccinellidae	Undetermined	Undetermined	1	0.22	A
Col277	Coccinellidae	Undetermined	Undetermined	4	0.19	W
Col281	Coccinellidae	Undetermined	Undetermined	13	0.2	W
Col288	Coccinellidae	Undetermined	Undetermined	4	0.82	W
Col291	Coccinellidae	Undetermined	Undetermined	4	0.41	W
Col294	Coccinellidae	Undetermined	Undetermined	17	0.2	W
Col296	Coccinellidae	Undetermined	Undetermined	7	0.46	W
Col304	Coccinellidae	Undetermined	Undetermined	2	0.13	W
Col31	Coccinellidae	Undetermined	Undetermined	1	1.57	W
Col316	Coccinellidae	Undetermined	Undetermined	1	0.18	W
Col329	Coccinellidae	Undetermined	Undetermined	1	0.16	W
Col333	Coccinellidae	Undetermined	Undetermined	2	0.58	W

Col367	Coccinellidae	Undetermined	Undetermined	2	0.27	W
Col368	Coccinellidae	Undetermined	Undetermined	7	0.15	W
Col51	Coccinellidae	Undetermined	Undetermined	5	0.25	W
Col60	Coccinellidae	Undetermined	Undetermined	2	0.22	W
Col103	Cryptophagidae	Undetermined	Undetermined	7	0.13	W
Col124	Cryptophagidae	Undetermined	Undetermined	1	0.12	W
Col179	Cryptophagidae	Undetermined	Undetermined	7	0.12	W
Col182	Cryptophagidae	Undetermined	Undetermined	17	0.11	W
Col192	Cryptophagidae	Undetermined	Undetermined	1	0.38	W
Col193	Cryptophagidae	Undetermined	Undetermined	1	0.34	W
Col199	Cryptophagidae	Undetermined	Undetermined	2	0.15	W
Col20	Cryptophagidae	Undetermined	Undetermined	1	0.27	W
Col203	Cryptophagidae	Undetermined	Undetermined	10	0.27	W
Col301	Cryptophagidae	Undetermined	Undetermined	1	0.22	W
Col310	Cryptophagidae	Undetermined	Undetermined	2	0.25	W
Col311	Cryptophagidae	Undetermined	Undetermined	5	0.15	W
Col332	Cryptophagidae	Undetermined	Undetermined	12	0.15	W
Col334	Cryptophagidae	Undetermined	Undetermined	15	0.27	W
Col349	Cryptophagidae	Undetermined	Undetermined	3	0.22	W
Col37	Cryptophagidae	Undetermined	Undetermined	1	0.3	W
Col43	Cryptophagidae	Undetermined	Undetermined	10	0.21	W
Col62	Cryptophagidae	Undetermined	Undetermined	62	0.24	W
Col72	Cryptophagidae	Undetermined	Undetermined	266	0.27	W
Col91	Cryptophagidae	Undetermined	Undetermined	151	0.12	W
Col101	Curculionidae	Undetermined	Undetermined	2	0.7	A
Col102	Curculionidae	Undetermined	Undetermined	1	0.78	A
Col111	Curculionidae	Undetermined	Undetermined	6	0.73	A
Col112	Curculionidae	Undetermined	Undetermined	1	0.46	A
Col12	Curculionidae	Undetermined	Undetermined	62	0.97	A
Col122	Curculionidae	Undetermined	Undetermined	1	0.35	A
Col126	Curculionidae	Undetermined	Undetermined	60	0.64	A

Col127	Curculionidae	Undetermined	Undetermined	1	0.16	NA
Col135	Curculionidae	Undetermined	Undetermined	7	0.93	A
Col137	Curculionidae	Undetermined	Undetermined	1	0.19	NA
Col143	Curculionidae	Undetermined	Undetermined	59	0.34	NA
Col16	Curculionidae	Undetermined	Undetermined	30	0.53	A
Col170	Curculionidae	Undetermined	Undetermined	4	0.49	A
Col172	Curculionidae	Undetermined	Undetermined	3	0.3	A
Col173	Curculionidae	Undetermined	Undetermined	2	NA	NA
Col181	Curculionidae	Undetermined	Undetermined	1	0.2	NA
Col185	Curculionidae	Undetermined	Undetermined	10	0.16	NA
Col186	Curculionidae	Undetermined	Undetermined	1	1.79	A
Col191	Curculionidae	Undetermined	Undetermined	1	1.6	A
Col194	Curculionidae	Undetermined	Undetermined	3	0.3	NA
Col195	Curculionidae	Undetermined	Undetermined	57	0.24	NA
Col197	Curculionidae	Undetermined	Undetermined	19	0.4	A
Col215	Curculionidae	Undetermined	Undetermined	2	0.86	A
Col217	Curculionidae	Undetermined	Undetermined	22	1.26	A
Col218	Curculionidae	Undetermined	Undetermined	2	0.85	A
Col222	Curculionidae	Undetermined	Undetermined	1	0.74	A
Col224	Curculionidae	Undetermined	Undetermined	5	0.62	A
Col229	Curculionidae	Undetermined	Undetermined	1	0.32	A
Col236	Curculionidae	Undetermined	Undetermined	93	0.22	NA
Col237	Curculionidae	Undetermined	Undetermined	27	0.26	NA
Col241	Curculionidae	Undetermined	Undetermined	1	0.82	A
Col243	Curculionidae	Undetermined	Undetermined	3	0.32	A
Col245	Curculionidae	Undetermined	Undetermined	3	0.15	NA
Col25	Curculionidae	Undetermined	Undetermined	12	0.13	NA
Col257	Curculionidae	Undetermined	Undetermined	2	0.7	A
Col259	Curculionidae	Undetermined	Undetermined	1	0.81	A
Col26	Curculionidae	Undetermined	Undetermined	18	0.6	A
Col262	Curculionidae	Undetermined	Undetermined	2	0.76	A

Col265	Curculionidae	Undetermined	Undetermined	1	0.18	NA
Col267	Curculionidae	Undetermined	Undetermined	1	0.61	A
Col273	Curculionidae	Undetermined	Undetermined	49	0.16	NA
Col275	Curculionidae	Undetermined	Undetermined	1	0.24	NA
Col289	Curculionidae	Undetermined	Undetermined	1	0.13	NA
Col290	Curculionidae	Undetermined	Undetermined	12	0.18	NA
Col295	Curculionidae	Undetermined	Undetermined	1	0.27	NA
Col30	Curculionidae	Undetermined	Undetermined	20	0.68	NA
Col308	Curculionidae	Undetermined	Undetermined	3	0.15	NA
Col309	Curculionidae	Undetermined	Undetermined	9	0.16	NA
Col319	Curculionidae	Undetermined	Undetermined	1	1.27	A
Col340	Curculionidae	Undetermined	Undetermined	1	0.44	A
Col351	Curculionidae	Undetermined	Undetermined	19	0.16	NA
Col352	Curculionidae	Undetermined	Undetermined	12	0.34	A
Col359	Curculionidae	Undetermined	Undetermined	2	0.2	NA
Col360	Curculionidae	Undetermined	Undetermined	2	0.36	A
Col369	Curculionidae	Undetermined	Undetermined	1	0.89	A
Col381	Curculionidae	Undetermined	Undetermined	5	0.4	A
Col383	Curculionidae	Undetermined	Undetermined	1	0.44	A
Col388	Curculionidae	Undetermined	Undetermined	3	0.39	A
Col395	Curculionidae	Undetermined	Undetermined	3	0.41	NA
Col396	Curculionidae	Undetermined	Undetermined	7	0.14	NA
Col397	Curculionidae	Undetermined	Undetermined	1	0.16	NA
Col398	Curculionidae	Undetermined	Undetermined	1	0.33	W
Col47	Curculionidae	Undetermined	Undetermined	1	0.39	A
Col48	Curculionidae	Undetermined	Undetermined	1	0.38	A
Col54	Curculionidae	Undetermined	Undetermined	10	0.67	A
Col56	Curculionidae	Undetermined	Undetermined	6	0.35	A
Col58	Curculionidae	Undetermined	Undetermined	1	0.22	A
Col68	Curculionidae	Undetermined	Undetermined	11	0.57	A
Col75	Curculionidae	Undetermined	Undetermined	10	0.88	A

Col80	Curculionidae	Undetermined	Undetermined	89	0.33	A
Col81	Curculionidae	Undetermined	Undetermined	2	0.47	A
Col86	Curculionidae	Undetermined	Undetermined	6	0.71	A
Col87	Curculionidae	Undetermined	Undetermined	1	0.25	NA
Col88	Curculionidae	Undetermined	Undetermined	2	0.93	A
Col89	Curculionidae	Undetermined	Undetermined	5	0.21	NA
Col92	Curculionidae	Undetermined	Undetermined	1	0.34	A
Col96	Curculionidae	Undetermined	Undetermined	2	0.36	W
Col98	Curculionidae	Undetermined	Undetermined	11	0.7	A
Col99	Curculionidae	Undetermined	Undetermined	32	0.7	A
Col142	Dermestidae	Undetermined	Undetermined	59	0.35	W
Col331	Dermestidae	Undetermined	Undetermined	25	0.14	W
Col278	Discolomidae	Undetermined	Undetermined	7	0.39	A
Col11	Elateridae	Undetermined	Undetermined	7	0.98	W
Col125	Elateridae	Undetermined	Undetermined	12	0.65	W
Col132	Elateridae	Undetermined	Undetermined	2	0.55	W
Col139	Elateridae	Undetermined	Undetermined	2	0.8	W
Col147	Elateridae	Undetermined	Undetermined	10	0.64	W
Col156	Elateridae	Undetermined	Undetermined	6	0.37	W
Col232	Elateridae	Undetermined	Undetermined	1	0.93	W
Col268	Elateridae	Undetermined	Undetermined	2	0.99	W
Col373	Elateridae	Undetermined	Undetermined	3	0.77	W
Col167	Histeridae	Undetermined	Undetermined	9	0.6	W
Col171	Histeridae	Undetermined	Undetermined	2	1.18	W
Col2	Histeridae	Undetermined	Undetermined	229	0.26	W
Col207	Histeridae	Undetermined	Undetermined	1	0.99	W
Col35	Histeridae	Undetermined	Undetermined	15	0.4	W
Col36	Histeridae	Undetermined	Undetermined	15	0.7	W
Col130	Hydrochidae	Undetermined	Undetermined	5	0.14	W
Col204	Languriidae	Undetermined	Undetermined	1	0.2	W
Col22	Lathrididae	Undetermined	Undetermined	4	0.1	W

Col282	Melandryidae	Undetermined	Undetermined	3	0.13	W
Col321	Meloidae	Undetermined	Undetermined	1	0.93	W
Col131	Melyridae	Undetermined	Undetermined	5	0.15	W
Col292	Melyridae	Undetermined	Undetermined	4	0.34	W
Col356	Melyridae	Undetermined	Undetermined	15	0.22	W
Col358	Melyridae	Undetermined	Undetermined	2	0.56	W
Col387	Melyridae	Undetermined	Undetermined	8	0.62	W
Col95	Melyridae	Undetermined	Undetermined	10	0.32	W
Col110	Mordeliidae	Undetermined	Undetermined	8	0.27	W
Col271	Mycetophogidae	Undetermined	Undetermined	64	0.32	W
Col14	Nitidulidae	Undetermined	Undetermined	9	0.2	W
Col159	Nitidulidae	Undetermined	Undetermined	3	0.33	W
Col184	Nitidulidae	Undetermined	Undetermined	66	0.24	W
Col188	Nitidulidae	Undetermined	Undetermined	1	0.27	W
Col216	Nitidulidae	Undetermined	Undetermined	2	0.36	W
Col306	Nitidulidae	Undetermined	Undetermined	17	0.15	W
Col315	Nitidulidae	Undetermined	Undetermined	1	0.15	W
Col324	Nitidulidae	Undetermined	Undetermined	4	0.15	W
Col326	Nitidulidae	Undetermined	Undetermined	2	0.18	W
Col363	Nitidulidae	Undetermined	Undetermined	1	1.2	W
Col364	Nitidulidae	Undetermined	Undetermined	2	0.21	W
Col50	Nitidulidae	Undetermined	Undetermined	22	0.15	W
Col53	Nitidulidae	Undetermined	Undetermined	7	0.25	W
Col63	Nitidulidae	Undetermined	Undetermined	15	0.11	W
Col32	Pausiidae	Undetermined	Undetermined	1	NA	W
Col6	Rhizophagidae	Undetermined	Undetermined	867	0.3	W
Col104	Scarabaeidae	Undetermined	Undetermined	2	0.65	W
Col115	Scarabaeidae	Undetermined	Undetermined	3	2.41	W
Col128	Scarabaeidae	Undetermined	Undetermined	1	0.59	W
Col133	Scarabaeidae	Undetermined	Undetermined	1	1.2	W
Col17	Scarabaeidae	Undetermined	Undetermined	97	NA	W

Col19	Scarabaeidae	Undetermined	Undetermined	1	0.9	W
Col200	Scarabaeidae	Undetermined	Undetermined	1	NA	W
Col201	Scarabaeidae	Undetermined	Undetermined	1	NA	W
Col206	Scarabaeidae	Undetermined	Undetermined	11	NA	W
Col221	Scarabaeidae	Undetermined	Undetermined	1	0.51	W
Col238	Scarabaeidae	Undetermined	Undetermined	3	0.61	W
Col249	Scarabaeidae	Undetermined	Undetermined	2	NA	W
Col263	Scarabaeidae	Undetermined	Undetermined	1		W
Col317	Scarabaeidae	Undetermined	Undetermined	3	0.77	W
Col348	Scarabaeidae	Undetermined	Undetermined	1	0.44	W
Col353	Scarabaeidae	Undetermined	Undetermined	1	0.48	W
Col357	Scarabaeidae	Undetermined	Undetermined	3	0.86	W
Col366	Scarabaeidae	Undetermined	Undetermined	1	NA	W
Col386	Scarabaeidae	Undetermined	Undetermined	1	0.53	W
Col392	Scarabaeidae	Undetermined	Undetermined	1	0.57	W
Col55	Scarabaeidae	Undetermined	Undetermined	18	0.27	W
Col7	Scarabaeidae	Undetermined	Undetermined	164	0.44	W
Col114	Silphidae	Undetermined	Undetermined	175	2.12	A
Col117	Silphidae	Undetermined	Undetermined	1	1.44	W
Col209	Silphidae	Undetermined	Undetermined	1	1.44	W
Col266	Silvaniidae	Undetermined	Undetermined	1	0.46	W
Col82	Silvaniidae	Undetermined	Undetermined	16	0.2	W
Col100	Staphylinidae	Undetermined	Undetermined	223	0.17	NA
Col105	Staphylinidae	Undetermined	Undetermined	10	0.29	NA
Col109	Staphylinidae	Undetermined	Undetermined	11	0.42	W
Col146	Staphylinidae	Undetermined	Undetermined	11	0.42	NA
Col161	Staphylinidae	Undetermined	Undetermined	9	0.11	NA
Col162	Staphylinidae	Undetermined	Undetermined	29	0.8	A
Col176	Staphylinidae	Undetermined	Undetermined	1	0.2	NA
Col178	Staphylinidae	Undetermined	Undetermined	13	0.21	NA
Col214	Staphylinidae	Undetermined	Undetermined	25	2.21	A

Col23	Staphylinidae	Undetermined	Undetermined	597	0.26	NA
Col230	Staphylinidae	Undetermined	Undetermined	1	0.3	NA
Col234	Staphylinidae	Undetermined	Undetermined	1	0.33	NA
Col24	Staphylinidae	Undetermined	Undetermined	2	0.15	NA
Col246	Staphylinidae	Undetermined	Undetermined	32	0.44	NA
Col256	Staphylinidae	Undetermined	Undetermined	1	1.03	A
Col270	Staphylinidae	Undetermined	Undetermined	7	0.58	W
Col3	Staphylinidae	Undetermined	Undetermined	168	0.79	A
Col40	Staphylinidae	Undetermined	Undetermined	144	0.2	NA
Col41	Staphylinidae	Undetermined	Undetermined	2	0.42	NA
Col45	Staphylinidae	Undetermined	Undetermined	10	0.63	W
Col71	Staphylinidae	Undetermined	Undetermined	1	0.34	NA
Col73	Staphylinidae	Undetermined	Undetermined	3	0.33	NA
Col78	Staphylinidae	Undetermined	Undetermined	1	0.16	NA
Col85	Staphylinidae	Undetermined	*Undetermined*	1	0.31	W
Col90	Staphylinidae	Undetermined	*Undetermined*	202	0.25	NA
Col33	Sylpidae	Undetermined	*Undetermined*	356	2.21	W
Col34	Sylpidae	Undetermined	*Undetermined*	7	1.22	W
Col1	Tenebrionidae	Undetermined	*Undetermined*	290	1.2	W
Col129	Tenebrionidae	Undetermined	*Undetermined*	10	0.36	W
Col15	Tenebrionidae	Undetermined	*Undetermined*	8	0.85	W
Col153	Tenebrionidae	Undetermined	*Undetermined*	1	0.71	A
Col157	Tenebrionidae	Undetermined	*Undetermined*	2	0.75	W
Col163	Tenebrionidae	Undetermined	*Undetermined*	6	0.64	A
Col164	Tenebrionidae	Undetermined	*Undetermined*	1	1.11	W
Col190	Tenebrionidae	Undetermined	*Undetermined*	1	1.02	NA
Col196	Tenebrionidae	Undetermined	*Undetermined*	1	1.04	A
Col208	Tenebrionidae	Undetermined	*Undetermined*	1	0.11	NA
Col247	Tenebrionidae	Undetermined	*Undetermined*	1	0.22	NA
Col254	Tenebrionidae	Undetermined	*Undetermined*	2	0.39	A
Col28	Tenebrionidae	Undetermined	*Undetermined*	184	0.98	NA

Col322	Tenebrionidae	Undetermined	*Undetermined*	1	0.5	NA
Col355	Tenebrionidae	Undetermined	*Undetermined*	3	0.9	W
Col371	Tenebrionidae	Undetermined	*Undetermined*	1	0.25	W
Col372	Tenebrionidae	Undetermined	*Undetermined*	2	0.82	W
Col382	Tenebrionidae	Undetermined	*Undetermined*	1	0.58	NA
Col384	Tenebrionidae	Undetermined	*Undetermined*	1	0.28	NA
Col59	Tenebrionidae	Undetermined	*Undetermined*	31	0.54	W
Col61	Tenebrionidae	Undetermined	*Undetermined*	14	0.34	NA
Col74	Tenebrionidae	Undetermined	*Undetermined*	2	2.49	A
Col94	Tenebrionidae	Undetermined	*Undetermined*	3	1.77	W
Col97	Tenebrionidae	Undetermined	*Undetermined*	5	0.67	NA
Col202	Trogidae	Undetermined	*Undetermined*	3	1.07	A

Appendix E: Fungicides, herbicides and insecticides used on the sampled integrated and organic vineyards. The mean number of applications were calculated as the number of applications per vineyard block per season across all farms.

Integrated Farms

Class	Trade name	Active Ingredient	IP Coding	# Farms applied	Mean # applications per vineyard block
Fungicide	Bio-Impilo	Metabolites of Trichoderma spp	0	1	7
Fungicide	Brilliant	Phosphorous acid	2	4	5
Fungicide	Collis	Boscalid + kresoxim-methyl	2	2	2
Fungicide	Controller	Cymoxanil + mancozeb	2	1	5
Fungicide	Copstar 120 SC	Copper hydroxide	2	1	9.5
Fungicide	Cuprofix	Copper sulphate & lime	4	1	2
Fungicide	Cymax	Cymoxanil + mancozeb	2	1	2
Fungicide	Cymoxazeb	Cymoxanil + mancozeb	2	1	2
Fungicide	Dimethozeb	Dimethomorph + mancozeb	2	4	1.7
Fungicide	Dithane	Mancozeb	1	2	2.8
Fungicide	Domark	Tetraconazole	1	2	2.8
Fungicide	Excalibur	Penconazole	1	1	1
Fungicide	Fighter	Phosphorous acid	2	1	7
Fungicide	Flint Max	Trifloxystrobin + tebuconazole	1	3	1.63
Fungicide	Folpan	Folpet	1	5	1.4
Fungicide	Funguran-OH	Copper hydroxide	2	1	6
Fungicide	Hygrophos	Pottasium phosphite	2	2	5.2
Fungicide	Hyperphos	Phosphorous acid	2	2	4
Fungicide	Karathane	Dinocap	2	2	2
Fungicide	Kumulus	Sulphur	2	3	6
Fungicide	Luna experience	Fluopyram + tebuconazole	2	3	1.57
Fungicide	Mancozeb	Mancozeb	1	5	4

Fungicide	Mariphos	Pottasium phosphite & phosphorous acid	2	2	3.6
Fungicide	Microthiol	Sulphur	2	2	4.75
Fungicide	Microthiol special	Sulphur	2	1	6
Fungicide	Pencomax	Penconazole	1	1	1
Fungicide	Penconazole	Penconazole	1	3	1.29
Fungicide	Pennfluid	Mancozeb	1	3	4.14
Fungicide	Potential	Spiroxamine	2	1	2
Fungicide	Prosper	Spiroxamine	2	7	2.5
Fungicide	Spiral	Spiroxamine	2	1	2
Fungicide	Striker	Sulphur	2	3	1.67
Fungicide	Sulfostar	Sulphur	2	5	4.67
Fungicide	Talendo	Proquinazid	1	1	2
Fungicide	Teldor	Fenhexamid	1	1	2
Fungicide	Topaz	Penconazole	1	1	2
Fungicide	Topguard	tebuconazole + flutriafol	2	1	1
Fungicide	Tridex	Mancozeb	1	1	1
Fungicide	Vantex	Gamma-cyhalothrin	2	1	1
Fungicide	Vivando	Metrafenone	1	2	2
Fungicide	Zetanil	Cymoxanil + mancozeb	2	2	3
Herbicide	Galigan	Oxyfluorfen	1	2	1
Herbicide	Gramoxone	Paraquat	4	1	1
Herbicide	Kalach	Glyphosate-sodium	1	2	1
Herbicide	MCPA	MCPA	2	2	1.4
Herbicide	Paraquat	Paraquat	4	2	1
Herbicide	Poquer	Clethodim	1	1	2
Herbicide	Roundup	Glyphosate iso-propyl ammonium	2	3	1.33
Herbicide	Roundup Turbo	Glyphosate iso-propyl ammonium	2	3	1.29

Herbicide	Select	Clethodim	1	5	1.2
Herbicide	Simazine	Simazine	1	1	2
Herbicide	Sorgomil Gold	s-metachlor + terbuthylazine	1	1	1
Herbicide	TBZ	Terbuthylazine	1	2	1.4
Herbicide	Terbutylazine	Terbuthylazine	1	3	1
Herbicide	Terbuweed	Terbuthylazine	1	1	1
Herbicide	Tyllanex	Terbuthylazine	1	1	2
Insecticide	Chlorpyrifos	Chlorpyrifos	4	1	1
Insecticide	Lambda	Lambda-cyhalothrin	4	1	1
Insecticide	Movento	Spirotetramat	1	5	1.5
Insecticide	Pride	Fenazaquin	4	1	1
Insecticide	Ripple	Bromopropylate	2	1	3
Insecticide	Savage	Chlorphenapyr	4	1	1
Moluscicide	Ferramol	Iron phosphate	1	1	2

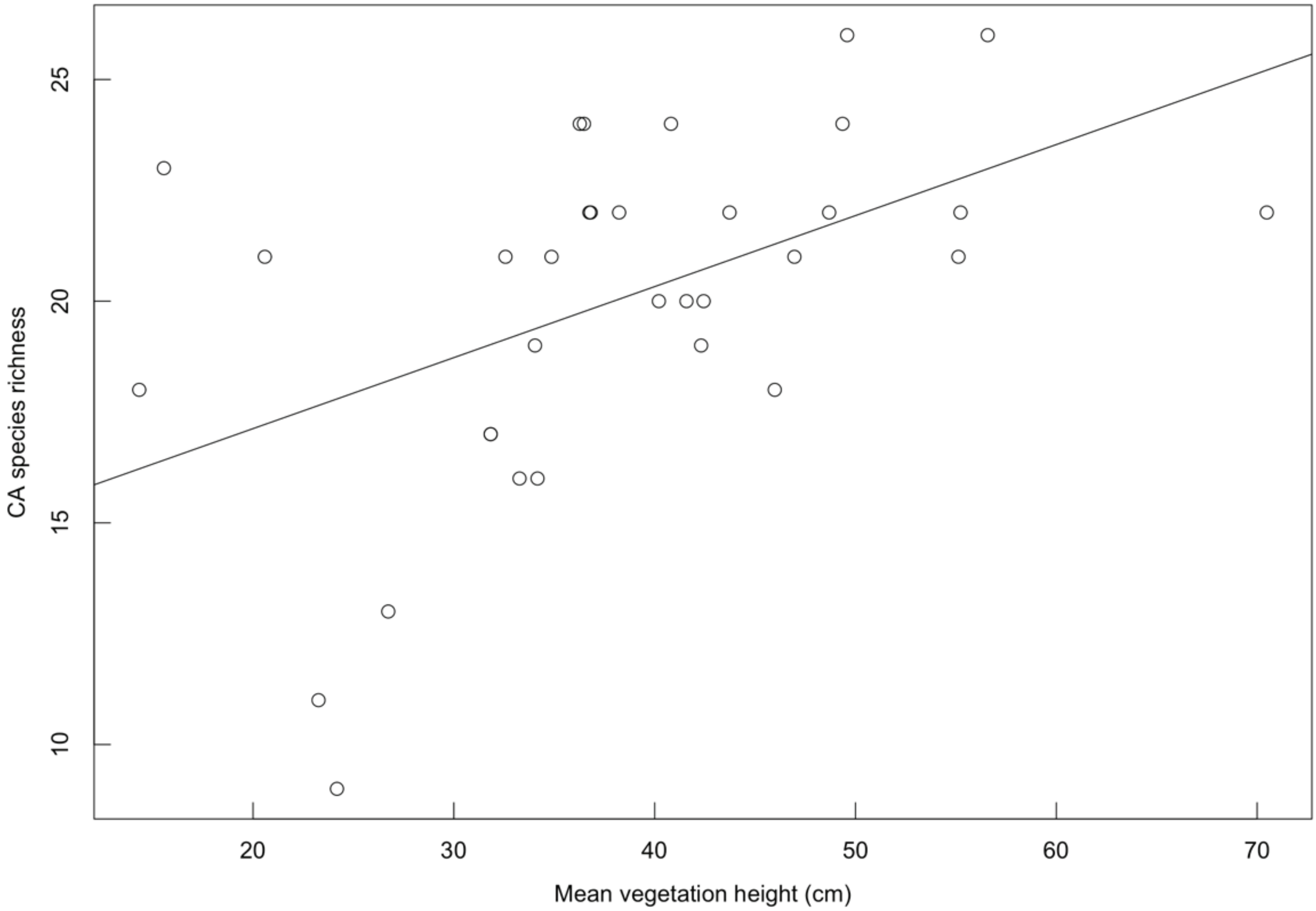
Organic farms

Class	Trade name	Active Ingredient	IP Coding	# Farms applied	Mean # applications per vineyard block
Fungicide	Agromos	N, CuS	N/A	1	3
Fungicide	Bio-Impilo	Metabolites of Trichoderma spp	0	2	4
Fungicide	Breakdown All	Fe, Mn, Cu, Zn	N/A	1	3
Fungicide	Copstar 120 SC	Copper hydroxide	2	2	11
Fungicide	Funguran-OH	Copper hydroxide	2	1	6
Fungicide	Kumulus	Sulphur	2	1	8
Fungicide	Striker	Sulphur	2	1	10
Fungicide	Sulfostar	Sulphur	2	1	11.67
Fungicide	Thiovit Jet	Sulphur	2	1	9

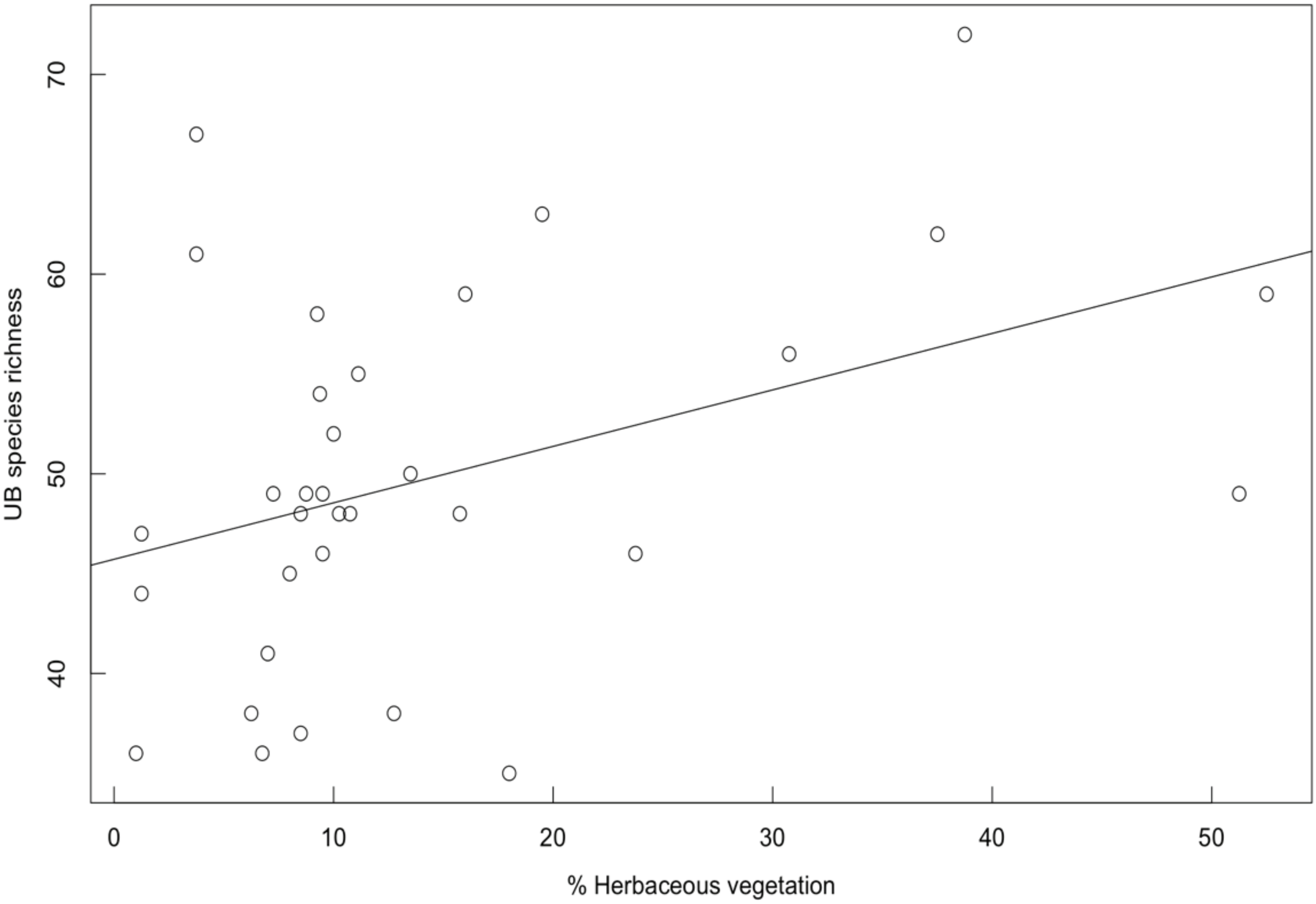
Appendix F: Total morphospecies richness and abundance of the sampled taxa for the overall assemblage, the taxonomic groups, microhabitats and feeding guilds (chapter 2).

		Morphospecies richness	Abundance
Total arthropods		486	21151
Taxonomic groups			
	Araneae	112	2861
	Coleoptera	218	6408
	Hemiptera	156	11882
Microhabitat			
	Soil surface	316	7933
	Cover crops	272	11174
	Vine	159	2044
Feeding guild			
	Detritivores	50	2562
	Herbivores	226	12577
	Predators	210	6012

Appendix G: Response of crop-associated arthropod species to mean vegetation height.

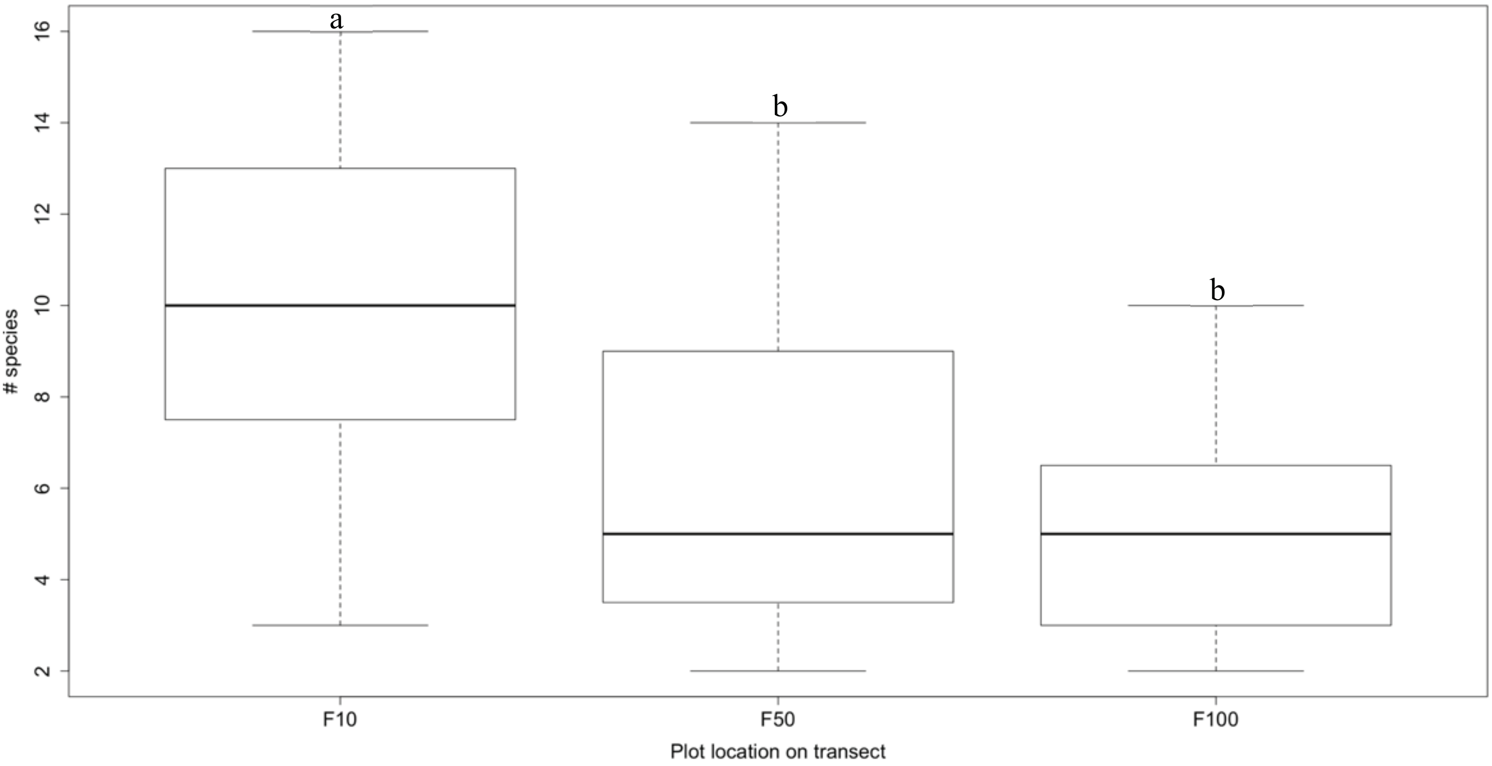


Appendix H: Response of ubiquitous arthropod species richness to the percentage of herbaceous vegetation present in vineyards.

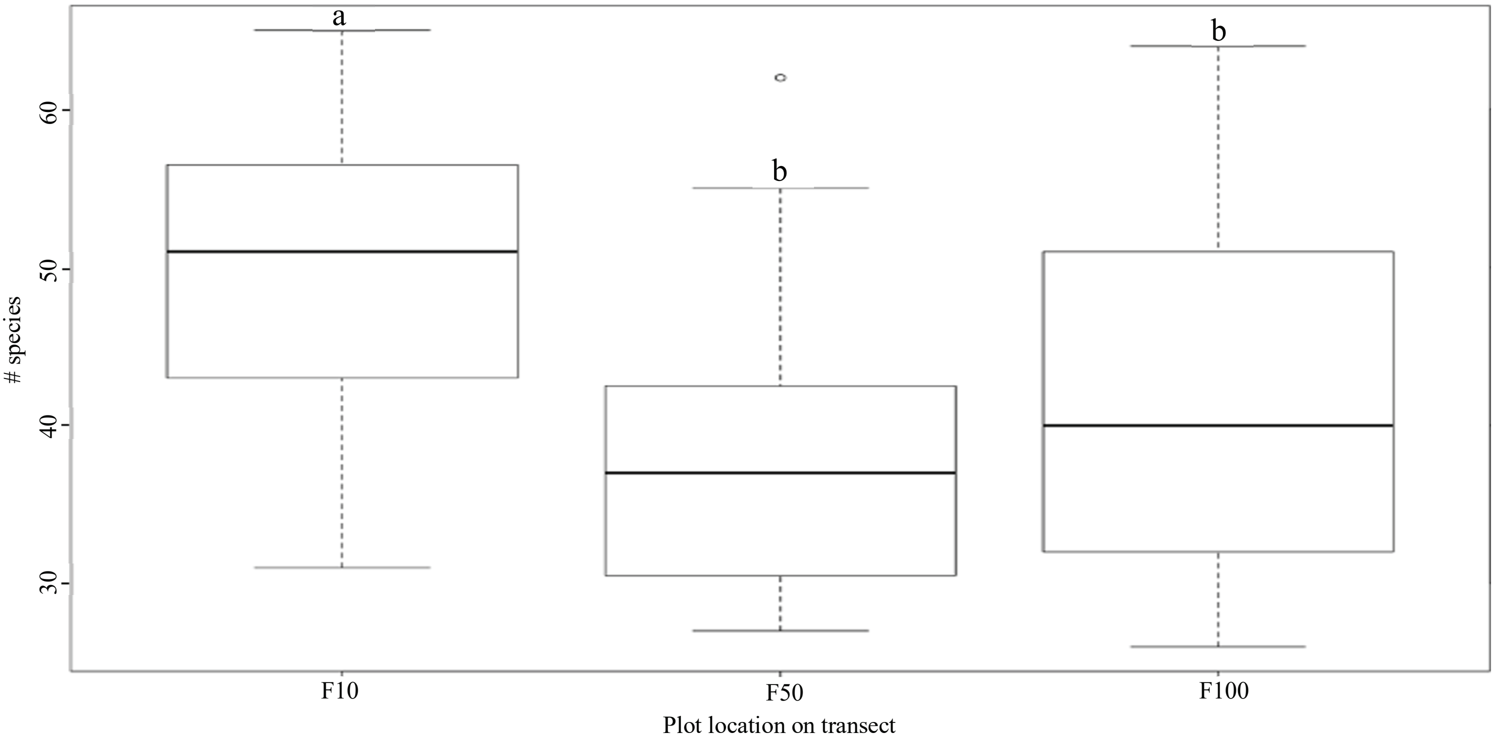


Appendix I: Species richness of arthropods across fynbos-vineyard transects.

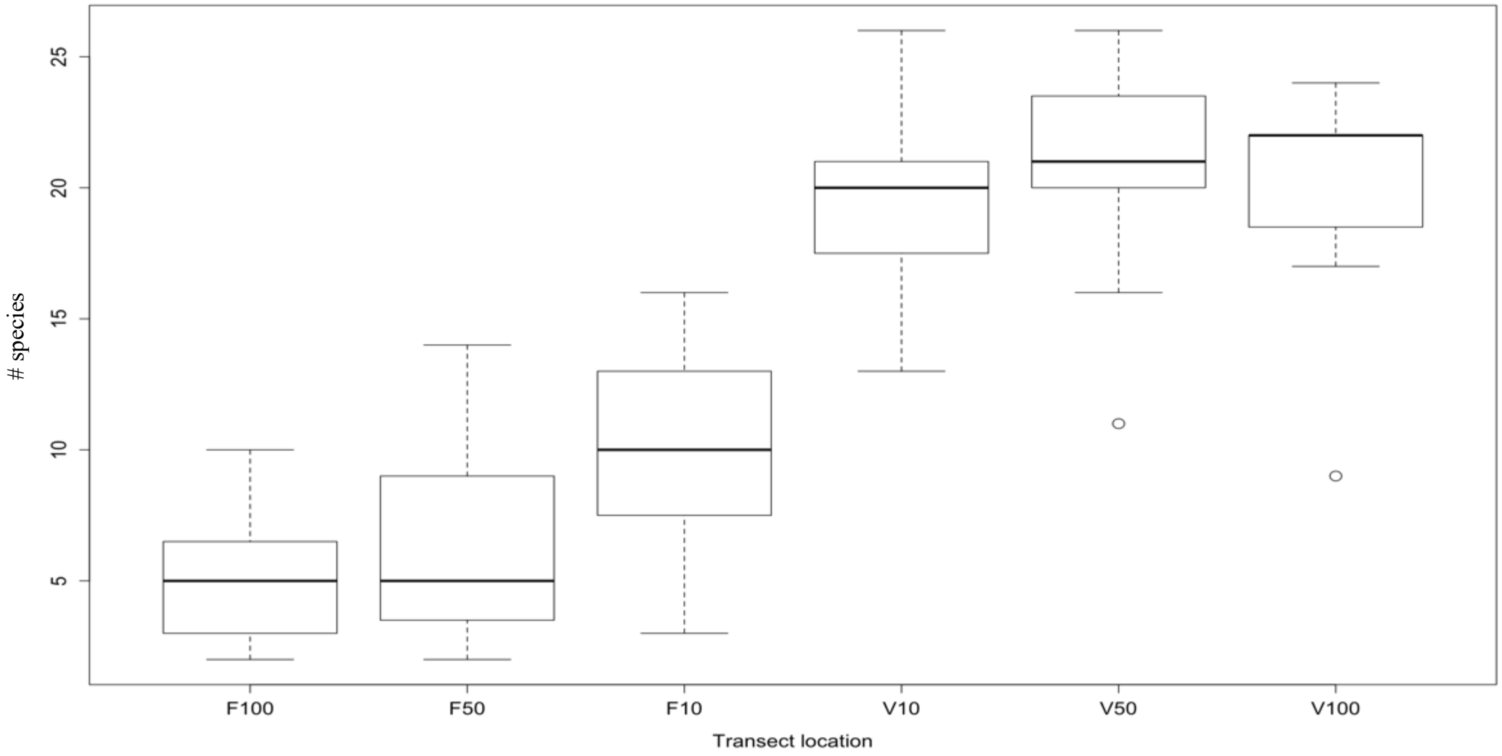
Species richness of crop-associated arthropods in fynbos at the 10 m, 50 m, and 100 m plot locations. Medians with letters in common are not significantly different.



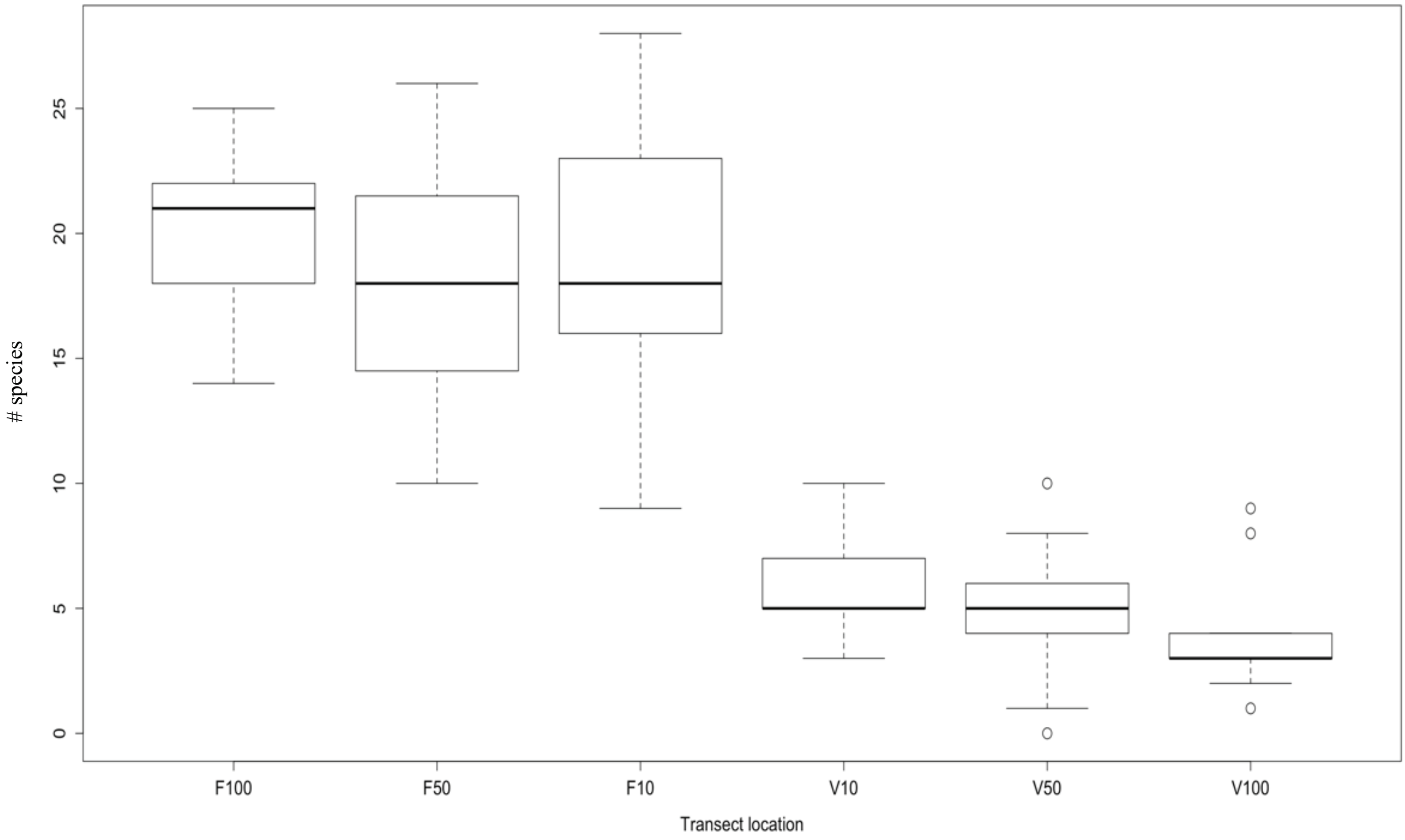
Species richness of ubiquitous arthropods in fynbos at the 10 m, 50 m, and 100 m plot locations. Medians with letters in common are not significantly different.

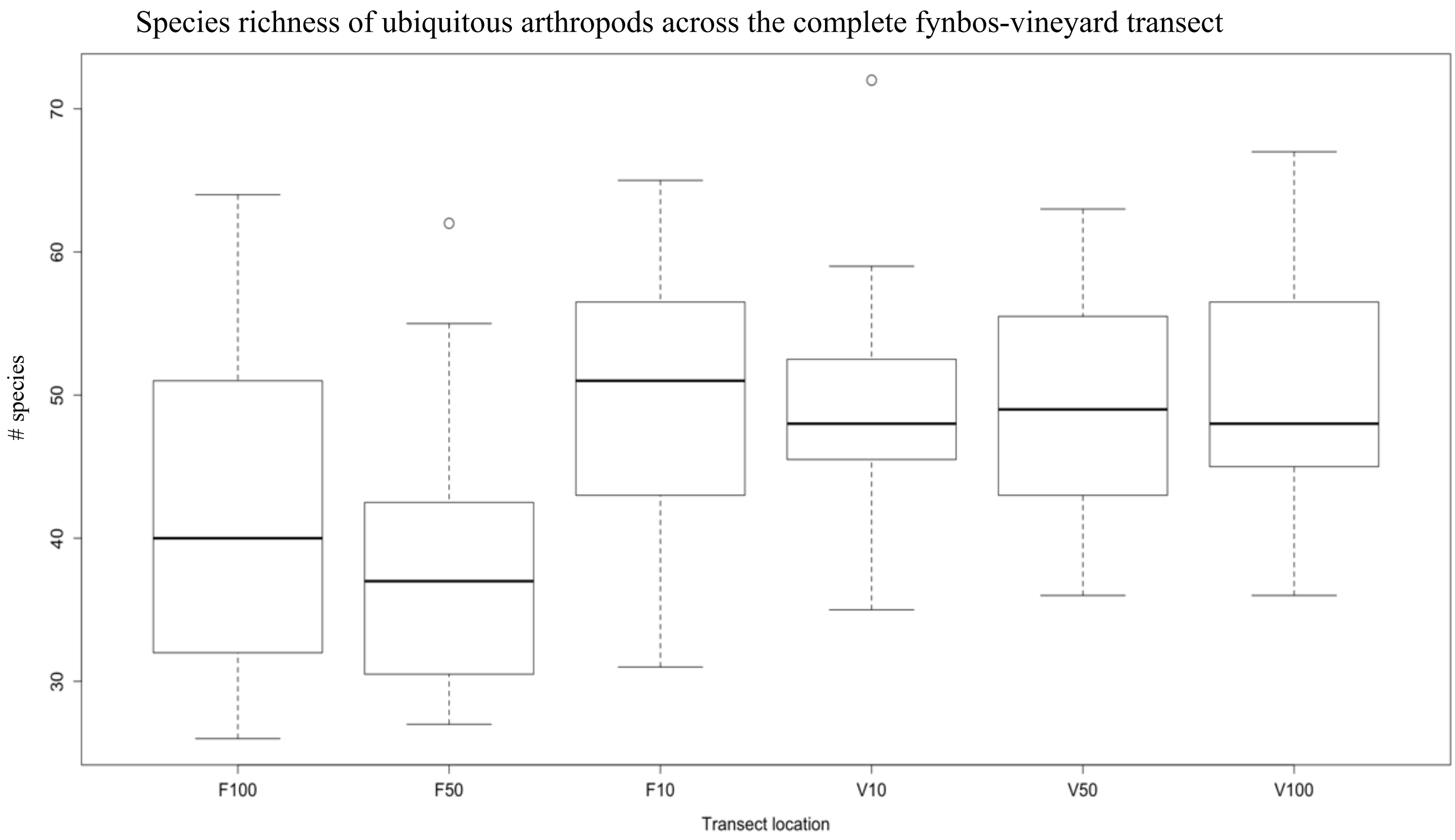


Species richness of crop-associated arthropods across the complete fynbos-vineyard transect



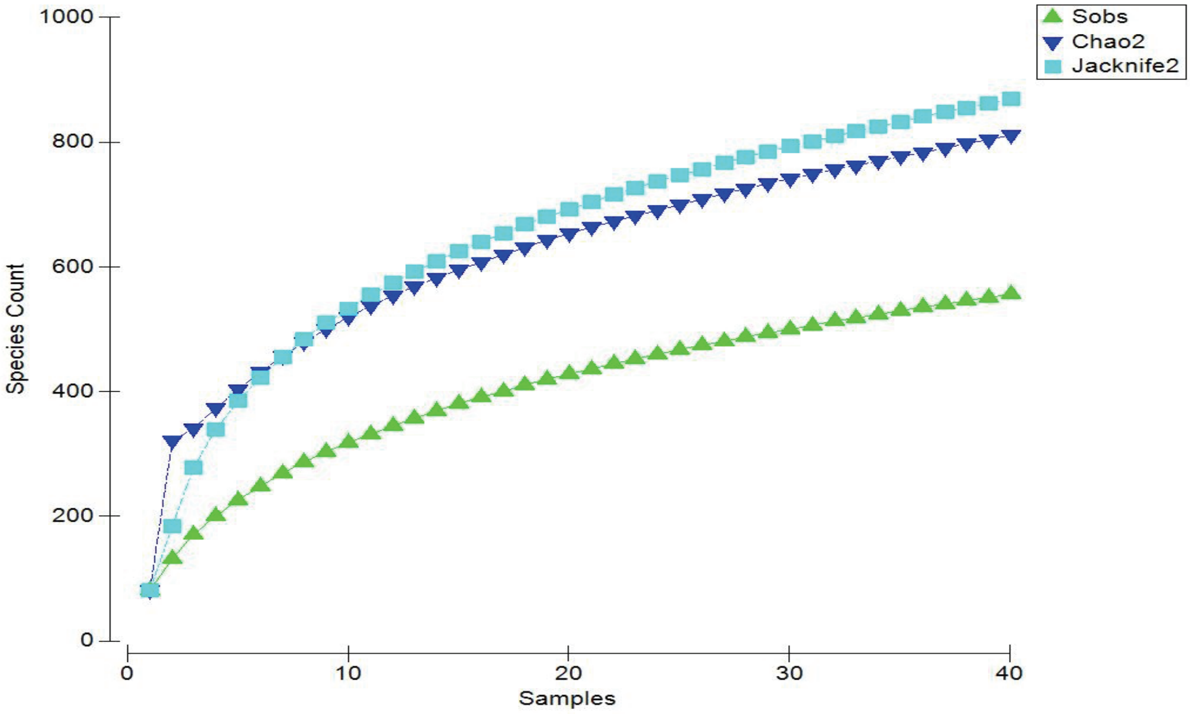
Species richness of fynbos-associated arthropods across the complete fynbos-vineyard transect



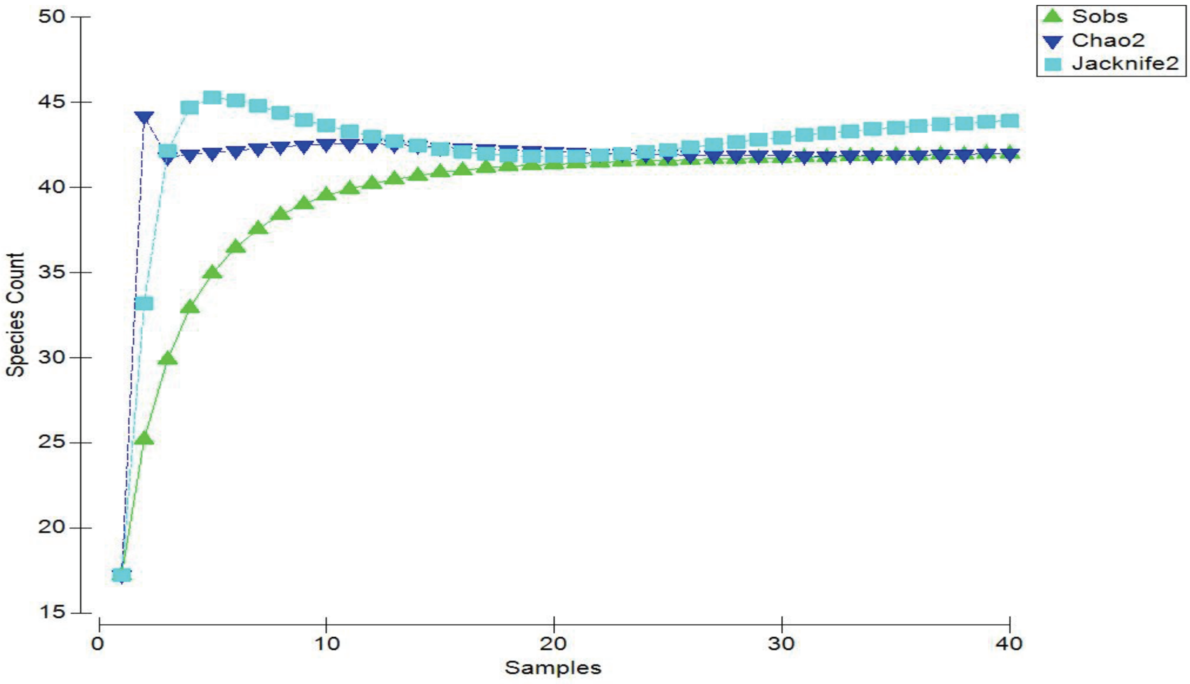

Species richness of ubiquitous arthropods across the complete fynbos-vineyard transect
species
70
60
50
40
30
F100
F50
F10
V10
V50
V100
Transect location

Appendix J: Species accumulation curves for overall arthropod assemblage and assemblages based on biotope associations.

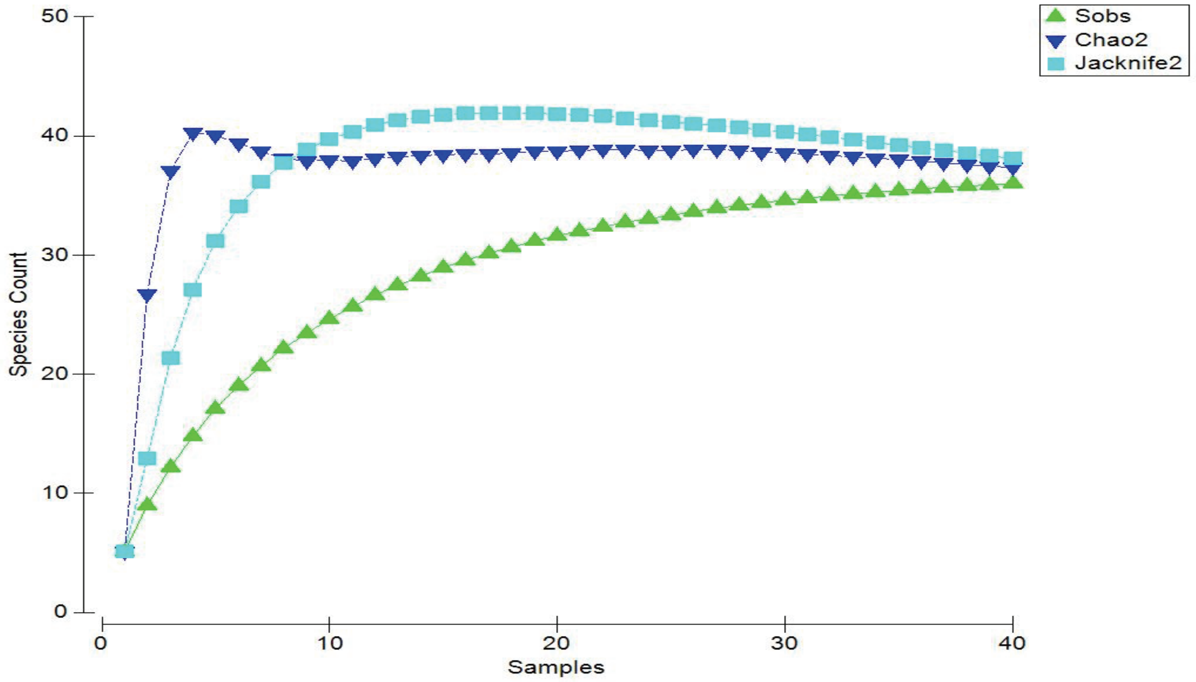
A species accumulation curve showing the sampling effort for the overall arthropod assemblage.



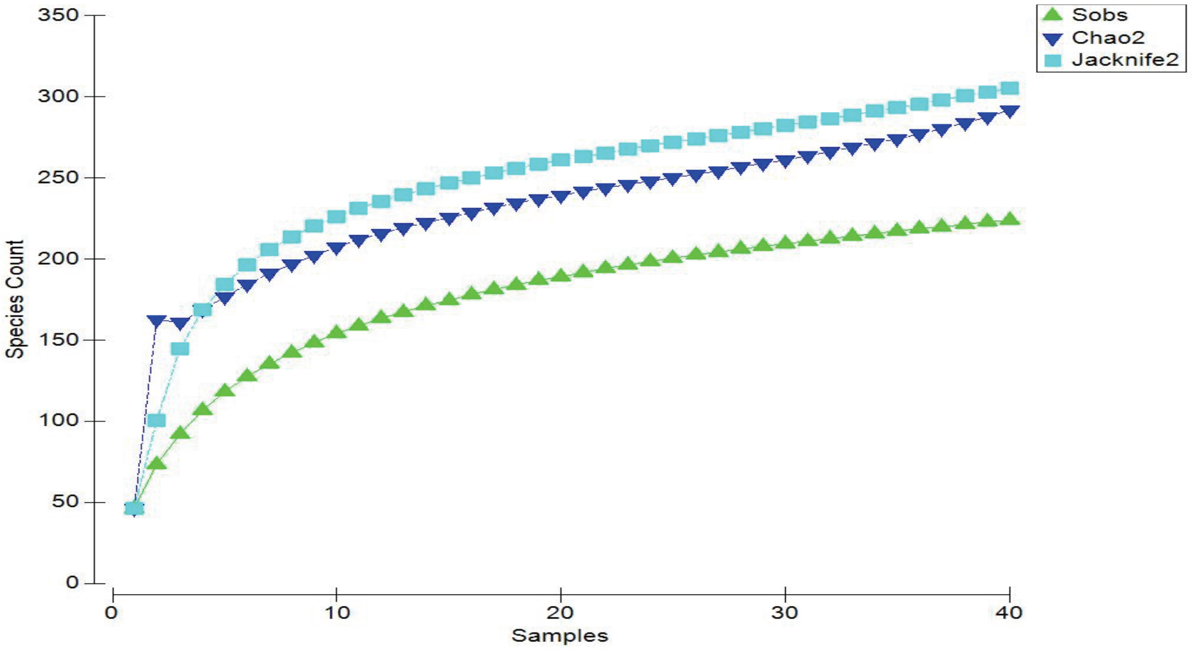
A species accumulation curve showing the sampling effort for the crop-associated arthropod assemblage.



A species accumulation curve showing the sampling effort for the fynbos-associated arthropod assemblage.



A species accumulation curve showing the sampling effort for the ubiquitous arthropod assemblage.

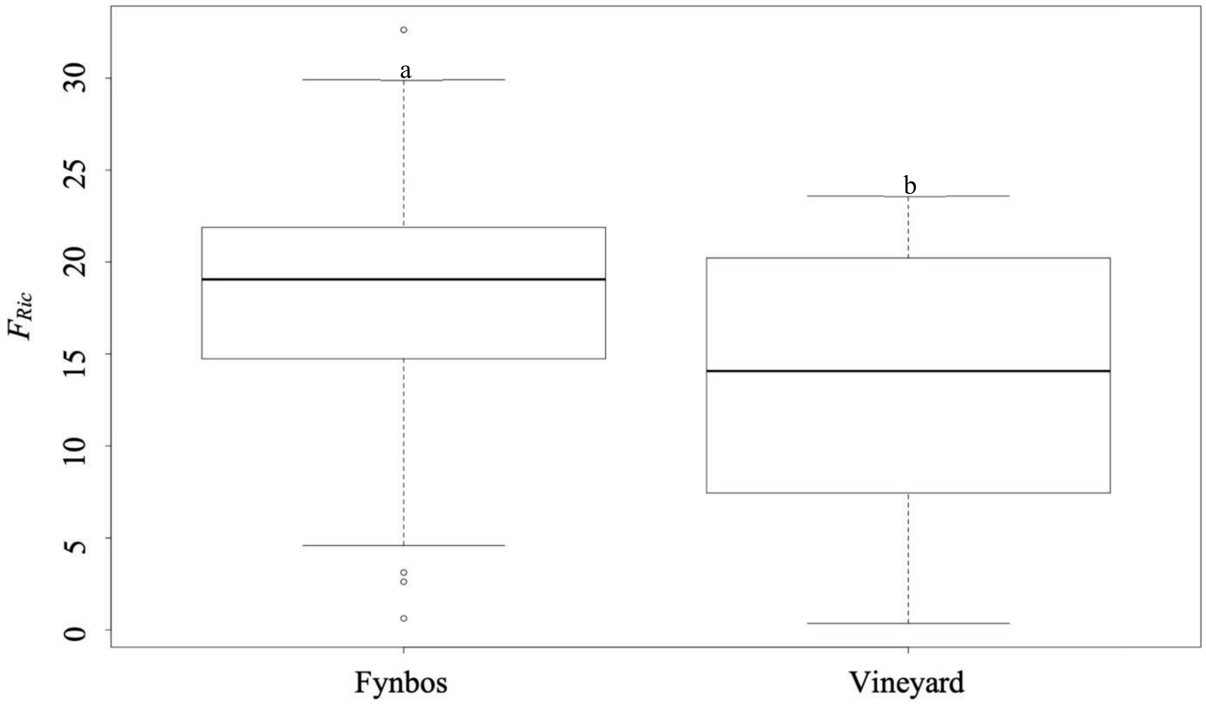


Appendix K: Summary of the two local-scale variables and the landscape complexity present at each plot. Cut-off values for classifying different landscape complexities were: x ≤ 18% = '*Low*', x > 18% and ≤ 36% = '*Intermediate*', and x > 36% = '*High*'.

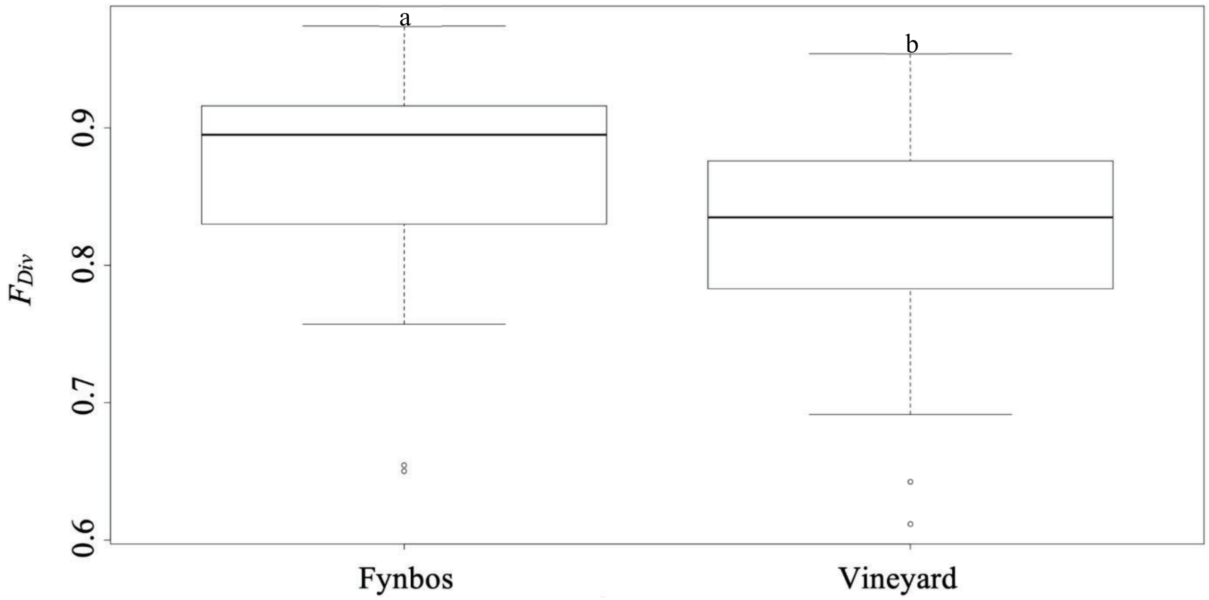
Plot code	Farming approach	% Herbaceous vegetation	Landscape complexity
Farm1P1	Integrated	9.38	Low
Farm2P1	Integrated	3.75	High
Farm2P2	Integrated	1.75	High
Farm2P3	Integrated	13.75	Intermediate
Farm3P1	Organic	6.25	High
Farm3P2	Organic	13.75	High
Farm3P3	Organic	5.25	Intermediate
Farm4P1	Integrated	9.4	High
Farm4P2	Integrated	4.5	High
Farm4P3	Integrated	2.25	Low
Farm5P1	Integrated	28.13	Low
Farm5P2	Integrated	13.25	Low
Farm6P1	Integrated	11.13	High
Farm6P2	Integrated	2.5	Low
Farm7P1	Integrated	14.0	High
Farm7P2	Integrated	41.25	High
Farm7P3	Integrated	23.75	Intermediate
Farm8P1	Integrated	4.5	Intermediate
Farm8P2	Integrated	6.0	Low
Farm9P1	Organic	7.5	Intermediate
Farm9P2	Organic	26.25	Intermediate
Farm10P1	Integrated	1.25	Low
Farm10P2	Integrated	12.0	Intermediate
Farm11P1	Organic	2.5	Low
Farm11P2	Organic	36.0	Low
Farm12P1	Integrated	15.73	High
Farm12P2	Integrated	3.75	Intermediate

Farm13P1	Organic	33.75	Low
Farm13P2	Organic	6.5	Low
Farm14P1	Integrated	1.25	Intermediate
Farm14P2	Integrated	3.75	Intermediate
Farm14P3	Integrated	2.75	Low
Farm15P1	Integrated	5.75	Low
Farm15P2	Integrated	7.25	Low
Farm16P1	Integrated	37.5	Low
Farm16P2	Integrated	8.0	Low
Farm17P1	Integrated	6.75	High
Farm17P2	Integrated	5.5	Low
Farm18P1	Organic	9.25	High
Farm18P2	Organic	2.63	High

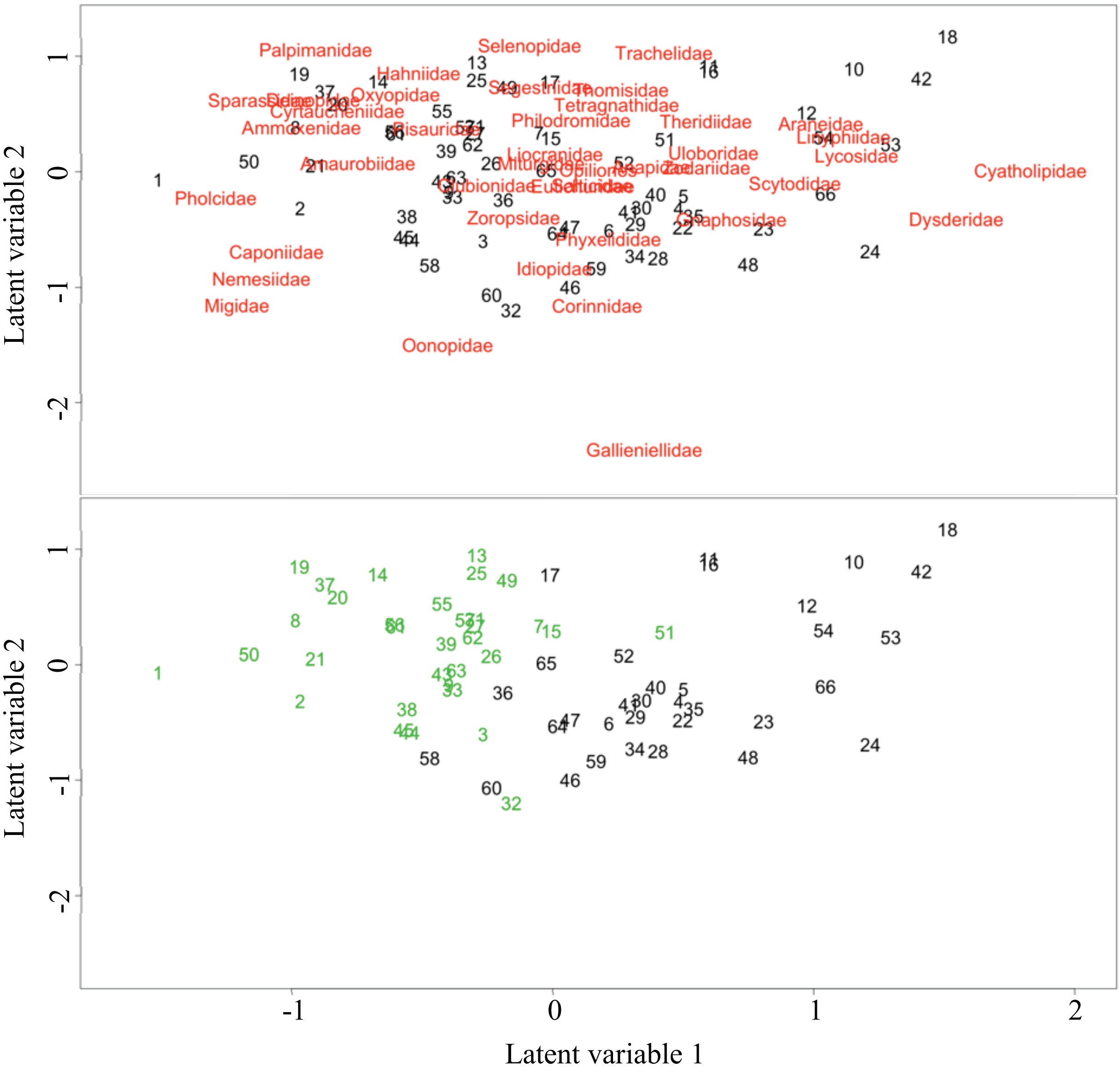
Appendix L: The functional richness of spiders among fynbos and vineyard sites. Different letters indicate significant differences of medians.



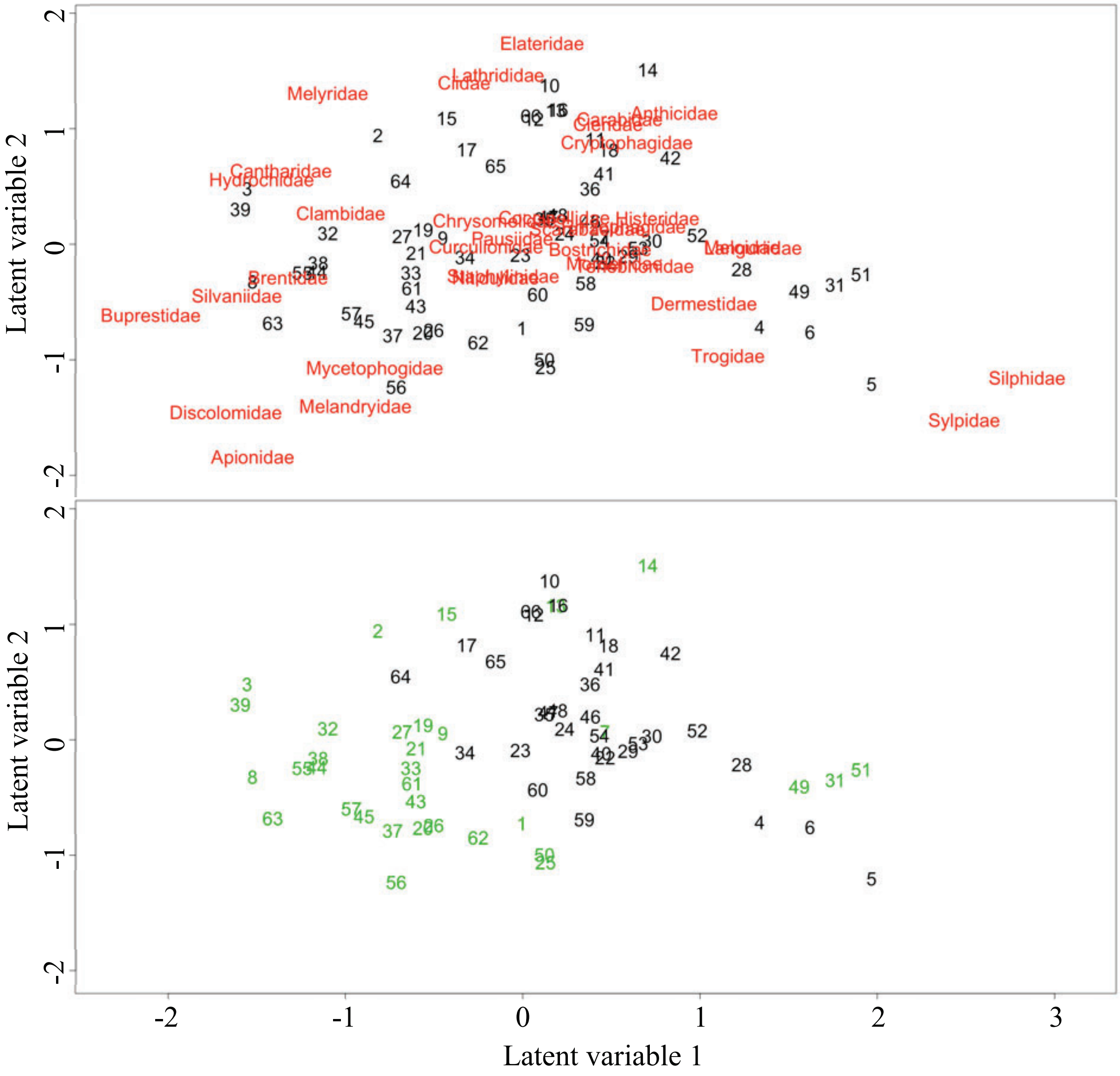
Appendix M: The functional divergence of beetles among fynbos and vineyard sites. Different letters indicate significant differences of medians.



Appendix N: Bayesian ordination and regression analysis of the spider family-level assemblage structure across vineyard (black) and fynbos (green) sites.



Bayesian ordination and regression analysis of the beetle family-level assemblage structure across vineyard (black) and fynbos (green) sites.



Appendix O: Species accumulation curves for the grand total of sampled spiders, beetles, and true bugs.