Potential ecosystem services and disservices of arthropods associated with *Cyclopia* (Honeybush) species

By

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Declaration

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Abstract

Cyclopia species, commonly known as honeybush, are endemic to the Eastern and Western Cape of South Africa. Honeybush has historically been used as a tea, but has more recently been proven to have medicinal use properties. Honeybush biomass and extracts are used in the functional foods and cosmetics sectors both locally, and overseas. The growing demand for honeybush tea calls for further commercialization of the industry and a shift away from the predominantly (70%) wild harvested supply. The current study aimed to address the lack of baseline knowledge on insects associated with honeybush and serves to identify arthropods of importance for arthropod-mediated ecosystem services and disservices associated with honeybush cultivation.

The study was conducted on wild and cultivated *Cyclopia* species (*C. maculata and C. genistoides*) in the Overberg region. Sampling methods for recording honeybush phenology and monitoring insects were used on a monthly schedule, from April 2014 to April 2015. Phenology observations were conducted using qualitative methods recording seasonal change and plant feeding damage by insects. Arthropod monitoring techniques included suction sampling, sweep netting, pan traps and delta traps. Focal insect taxa (Coleoptera, Hemiptera, Thysanoptera, Lepidoptera and Hymenoptera) were sorted and identified to family and morphospecies level where applicable. Families and morphospecies were classified into functional feeding guilds relevant to honeybush biomass production. Functional guild classification was used to assess the relative predator-prey and parasotid-host composition of the arthropod assemblages associated with honeybush.

Qualitative phenology observations of wild *C. maculata* and cultivated *C. genistoides* indicated a high level of resemblance in seasonality of phenophase stages. The arthropod assemblage contained a diversity of families per functional feeding group relevant to biomass production, namely phytophagous, zoophagous and omnivorous taxa. Of the phytophagous arthropods a cohort of endopterygote and exopterygote taxa, among others, are noted as potential pest insects. A diverse collection of natural enemies (parasitoids and predators), from several Coleoptera and Hymenoptera families, were also abundant in wild and cultivated honeybush stands. Of the diverse natural enemy complex, parasitoids formed the predominant component with potential as valuable natural biological control agents. Disturbance caused by land management practices altered the functional composition of the arthropod assemblage significantly. This combined with

isolation from the natural vegetation, due to cultivation, had a negative synergistic effect on the natural enemy complex (parasitoid and predatory wasps) in cultivated honeybush stands.

The current research results highlight the importance of incorporating agroecological principles on fine- and landscape-scales for sustainable and ecologically sound honeybush cultivation. Research outcomes can be applied towards the development of land management practices, promoting a sustainable productive agroecosystem, for the commercialization of *Cyclopia* species. Considering the current biodiversity crisis and threatened ecosystem status of several honeybush species an ecologically-based approach is strongly recommended. Furthermore these findings form the basis for further research on the value of natural biological control agents for the integrated pest management of cultivated honeybush.

Opsomming

Cyclopia spesies, algemeen bekend as heuningbos, is endemies aan die Oos-en Wes-Kaap van Suid-Afrika. Heuningbos was histories en word tans gebruik vir die maak van tee, en dit is meer onlangs bewys dat dit medisinale gebruiks eienskappe bevat. Die groeiende vraag na heuningbostee vereis verdere kommersialisering van die bedryf en 'n verskuiwing weg van die oorwegende (70%) wild geoeste aanbod. Die huidige studie spreek die gebrek aan voldoende kennis van geleedpotiges wat geassosieer is met heuningbos aan. Die studie identifiseer geleedpotiges van belang vir geleedpotige-bemiddelde ekosisteem dienste en nadelige interaksies wat verband hou met heuningbos verbouing.

Die studie is uitgevoer op wilde en aangeplante *Cyclopia* spesies (*C. maculata en C. genistoides*) in die Overberg-streek. Steekproefmetodes vir die opname van heuningbos fenologie en monitering van grondvlak geleedpotiges is op 'n maandelikse skedule toegepas, vanaf April 2014 tot April 2015. Fenologiese waarnemings was met kwalitatiewe metodes gedoen om die seisoenale verandering en plant voedingskade deur insekte aan te teken. Geleedpotige moniterings tegnieke het behels die gebruik van opsuig monsterneming, swaai -net versameling, panvalle en deltavalle. Belangrike geleedpotige taksa (Coleoptera, Hemiptera, Thysanoptera, Lepidoptera en Hymenoptera) is gesorteer en geïdentifiseer tot familie en morphospesies vlak waar van toepassing. Familie en morphospesies was geklassifiseer volgends funksionele voedings groepe relevant tot 'n heuningbos biomassa produksie. Funksionele klassifikasie van eienskappe was gebruik om die relevante predatoor-prooi samestelling van die versameling geleedpotiges geassosieer met heuningbos te bepaal.

Kwalitatiewe fenologiese waarnemings van wilde *C. maculata* en aangeplante *C. genistoides* het 'n hoë vlak van ooreenkoms in seisoensgebondenheid van fenofase stadiums aangedui. Die geleedpotige versameling bevat 'n verskeidenheid families per funksionele voedings groep wat belangrik is vir heuningbos biomassa produksie, naamlik plantetende-, inseketende- en omnivoriese insekte. Van die plantetende-geleedpotiges is 'n groep van insekte van verskillende lewenssikluse aangeteken as potensiële plaag insekte. A diverse versameling van natuurlike vyande (parasitoïed en predatoor), van 'n paar Coleoptera en Hymenoptera families, was ook volop in beide wilde en aangeplante heuningbos. Van die diverse natuurlike vyandkompleks vorm die parasitoïede die oorheersende komponent met die potensiaal as waardevolle natuurlike biologiese beheer agente. Versteuring veroorsaak deur grond bestuurspraktyke het die

funksionele samestelling van die geleedpotige gemeenskap betekenisvol verander. Hierdie aspek tesame met die isolasie van die natuurlike plantegroei, weens aanplanting, het 'n negatiewe sinergistiese uitwerking gehad op die natuurlike vyand kompleks (parasitoïed en predatoor wespes) in aangeplante heuningbos lande.

Die huidige navorsingsresultate beklemtoon die belangrikheid van die integrasie van agro-ekologiese beginsels vir volhoubare heuningbosverbouing. Navorsingbevindings kan aangewend word vir die ontwikkeling van grond bestuurspraktyke vir die bevordering van volhoubare agro-ekologiese kommersialisering van *Cyclopia* spesies. Met inagneming van die huidige biodiversiteit krisis en ekosisteem-bedreigde status van verskeie heuningbos spesies word 'n ekologies-gebaseerde benadering vir die bedryf se uitbreiding aanbeveel. Die huidige navorsing vorm die basis vir verdere navorsing oor die waarde van natuurlike biologiese beheer agente vir die geïntegreerde plaagbestuur van aangeplante heuningbos.

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Dedication

To the communities of Genadendal and the surrounding outstations, who inspired and motivated me in undertaking and completing this thesis.

Table of Contents

List of figures

List of tables

CHAPTER 1.

GENERAL INTRODUCTION

1.1. Ecosystem functioning and associated ecosystem services

Biodiversity and the complexity of interactions among biotic and abiotic components within an ecosystem make up the life supporting systems mankind is dependent upon (Millennium Ecosystem Assessment (MEA) 2003; Kremen 2005; Naeem *et al.* 1999). Although the concept of gaining benefit from nature was already being considered by the late 1960's formalization of the term 'ecosystem services' (ESS) by 1970 (Hermann *et al.* 2011) was an important step toward realizing the extent and value of services mankind derives from the natural environment. The Millennium Ecosystem Assessment (2003) defines ecosystem services as the direct or indirect benefits mankind derives from ecological systems. These ecosystem services have been defined as fulfilling one or a combination of either 'provisioning' (e.g. water purification and timber), 'regulating' (e.g. pest and disease control), 'cultural' (e.g. aesthetic and recreational) and/or 'supporting' (e.g. nutrient cycling, habitats that support natural enemies) services (MEA 2003). The ecosystem functioning differs from that of ESS in that the concept does not directly imply that the ecological process at hand has a direct meaningful value/role toward human well-being (Naeem *et al.* 1999). The functionality of the process is rather a direct link to the characteristics of the organisms within an ecosystem. Ecological functioning relies on both the composition and identity of the individual components that make up a specific functional unit (Bihn *et al.* 2010; Naeem *et al.* 1999, Philpott & Armbrecht 2006). The concept of ESS or disservices (potentially detrimental impacts such as pest damage to crops) contrasts with ecosystem functioning in that the ecological interaction or process is rated according to the human-induced benefit or detrimental outcome derived from an ecosystem.

1.1.1. Value of arthropod-mediated ecosystem services

Arthropods form the largest volume of biotic organisms on earth and thus contribute the greatest proportion to life supporting ecological functions within ecosystems (Strong *et al.* 1984). These ecological functions provide important arthropod-mediated ecosystem services (AMES) such as crop pollination by bees and other pollinators, pest and disease regulation by predators and

parasitoids and decomposition and nutrient cycling by detritivores and other functional groups (Isaacs *et al.* 2009; Losey & Vaughan 2006; Power 2015). Threats causing biodiversity loss of arthropods, among other biodiversity, thus places these life-supporting ecological functions and processes under threat as well. Degradation of ecological functions would result in high economic losses due to the monetary value of the ecosystem services rendered by these processes (Altieri & Nicholls 1999). The economic implications for arthropod-mediated ecosystem services (including dung burial, pest control, pollination and wildlife nutrition) in the United States of America are estimated at $57 billion (Losey & Vaughan 2006).

Arthropod-mediated ecosystem services (AMES), such a pollination and pest control, fulfills an important part of agricultural productivity (Losey & Vaughan 2006; Power 2015). Natural enemies (predators and parasitoids) within agricultural landscapes make a substantial economic contribution to the success of commercial crops through population regulation of undesired organisms (Altieri & Letourneau 1982; Isaacs *et al.* 2009; Losey & Vaughan 2006). Losey and Vaughan (2006) estimated that natural predators and parasitoids of native crop pests contribute 33 – 39% to agricultural pest regulation within the United States, this averaging to the value of $7.32 – 13.6 billion per annum. Most studies on AMES within agroecosystems are from the Northern hemisphere (e.g. Dib & Libourel 2012), of those few studies that do exist for the Southern hemisphere (see Carvalheiro *et al.* 2011; Henri *et al.* 2015) even fewer are on indigenous crop species.

Several indigenous crops within South Africa are important for local and international trade; some of these include species such as rooibos (*Aspalathus linearis* (Brum.f) Dahlg.), buchu (*Agathosma betulina* (P.J.Bergius)), Cape aloe (*Aloe ferox* (Mill) and honeybush (*Cyclopia* Vent. species) (Cheney & Scholtz 1963; Joubert *et al.* 2008; Van Wyk 2011). The global trend towards 'healthy living' has opened up the market internationally and nationally for the introduction and establishment of natural and health products such as those made from these indigenous plants (Joubert *et al.* 2011; Van Wyk 2011). Honeybush is one of the indigenous crops that has more recently become established as a formal industry within the last decade, and has gained increasing popularity as a health beverage on both local and international markets (Coega Development Corporation (CDC) 2011; Joubert *et al.* 2011). There is an increasing need for the expansion of honeybush biomass production, in terms of cultivation, to meet the increasing demand, as well as ensure the sustainable development of this South African industry. Indigenous crops such as honeybush are often cultivated within the geographical region to which they are native to. Native cultivated stands are still subject to the natural ecological interactions within

these ecosystems, including, among others, the diversity of arthropod assemblages associated with honeybush species. These include phytophagous (herbivorous) arthropods that utilize the indigenous crop as a host plant as well and the natural enemy complex (predators and parasitoids) that regulate herbivorous arthropod populations. Indigenous crops, such as *Cyclopia* species, therefore, have several potential AMES and disservices that should be considered upon cultivation. Native herbivorous taxa, for example, could pose a pest threat (disservice) should the natural enemy pressure be disturbed through cultivation practices. On the other hand, indigenous crops also have a high potential for natural biological pest control due to existing predator-prey; parasitoid-host and pathogen-host interactions that could regulate population numbers of herbiverous taxa. In order for these arthropod related ecosystem functions and ESS and disservices to be understood and effectively managed within cultivated settings more needs to be known regarding both the host plant and the associated arthropod assemblage.

1.2. Honeybush (*Cyclopia*)

Cyclopia species [FABACEAE], commonly known as honeybush, make up 23 of the 20 456 floral taxa present in the Fynbos biome of South Africa (Goldblatt & Manning 2002, Raimondo *et al.* 2009). This vegetation type has a rich diversity of flora and fauna, the human value of which includes harvesting of four to six species of honeybush for commercial or livelihood purposes. These commercially important species include *C. genistoides*, *C. intermedia*, *C. sessifloria*, *C. maculata*, *C. subternata* and more recently *C. longifolia* (Joubert *et al.* 2011).

Honeybush is endemic to the coastal plains and mountainous areas of the Fynbos biome in the Western and Eastern Cape Provinces of South Africa (Joubert *et al.* 2011; Van der Walt 2000). The 23 species of *Cyclopia* vary in their distribution (Joubert *et al.* 2011; Kies 1951; Schutte 1997); some species occur over a wide range, while others have a fairly limited distribution due to their specific growth requirements (Joubert *et al.* 2011; Van der Walt 2000).

The genus is characterized by bold yellow flowers with a distinct round indent at the calyx base (Schutte 1997; Van Wyk & Gericke 2000). The generic name, derived from the Greek 'cyclops' (round-eyed), refers to this distinct feature. The common name, honeybush, bears reference to the sweet scent of the spring (September - October) flowers (Van der Walt 2000; Joubert *et al.* 2011). The genus is further characterized by having a trifoliate leaf, although the morphology of the individual leaves varies greatly between species (Bond & Goldblatt 1984; Kies 1951; Van der Walt 2000; Van Wyk & Gericke 2000). Honeybush species lie along a resprouter non-resprouter

(reseeders) continuum as part of their fire-survival strategy (Joubert *et al.* 2011; Schutte *et al.* 1995).

1.2.1. Historic and current stance of the Honeybush industry

Honeybush tea has long been used by local inhabitants of the Western and Eastern Cape to produce a hot beverage, subsequently also recognized for its medicinal value (Joubert *et al.* 2008; Joubert *et al.* 2011; Kies 1951; Van Wyk 2011). Honeybush tea as a fully fermented product is classified as a black tea. Some processing points have also entered the green tea market with unfermented honeybush tea (Joubert *et al.* 2011).

Unlike rooibos (*Aspalathus linearis*), honeybush has up to now enjoyed limited commercial interest, remaining as a cottage industry until the mid-1990's (Joubert *et al.* 2008; Joubert *et al.* 2011). More recently, the production and distribution of honeybush tea has undergone considerable growth and has now entered the market more formally. The globally increased interest in healthy living has thus opened up a large potential market for an upcoming product such as honeybush. Honeybush is recognised as a 'natural product' with the potential to expand exponentially as an internationally recognised health product (Department of Agriculture, Forestry and Fisheries (DAFF) 2014; Den Hartigh 2011; CDC 2011; Van Wyk 2011). Currently, the industry is valued at R10 million, forming part of the greater R400 million herbal tea market (Coetzee 2012).

The current honeybush industry has grown steadily over the past decade (DAFF 2014; Joubert *et al.* 2011) with great potential to expand even further in both local and international markets (DAFF 2014; CDC 2011). The complexity of the honeybush market value chain should in future provide the South African economy with added direct benefits besides expansion of this specific agricultural sector (DAFF 2014). Growth in the honeybush industry will create more job opportunities in several sectors, ranging from primary to secondary and tertiary production (Department of Trade and Industry 2007). The industry thus has the potential to provide a means of additional income for small- and large-scale farmers. In addition, the honeybush industry has 'lateral' growth potential for expansion at the secondary and tertiary processing levels (DAFF 2014; Khuzwayo 2011). Market related opportunities for increased processed honeybush produce are vast. This includes diversification of fresh tea fermenting to processing for convenience products or developing a range of health products (Joubert *et al.* 2008).

Currently 95% of the honeybush tea produced, is sold in bulk on the overseas market (Coetzee 2012; DAFF 2014; Joubert *et al.* 2011). The main buyers of honeybush are Germany and the United States, as well as the Netherlands and Bulgaria (Den Hartigh 2011; DAFF 2014). Wild-

harvesting still dominates the current supply to the honeybush market, with a rough estimate of 70% wild to 30% cultivated yield entering the market (CDC 2011; DAFF 2014; Joubert *et al.* 2011). It is speculated that extensive wild-harvesting has resulted in many natural population becoming locally extinct (Du Toit *et al.* 1998). Of the 23 species of *Cyclopia*, only six are recognized for their economic value, with four species most frequently harvested for commercial purposes. *Cyclopia intermedia* ('bergtee') is the dominant species harvested from wild mountain populations (Cape Honeybush Tea 2003), while other species, such as *C. genestoides* ('kustee') and *C. subternata* ('vleitee'), are mainly harvested from cultivated plantations (Joubert *et al.* 2011; South African Honeybush Tea Association (SAHTA) 2015). The species used in the production of tea varies depending on the species found locally in the various areas. In the Western Cape, the main species used for brewing tea in the 1920's was *C. genistoides* in the Cape Peninsula and for Caledon (Overberg) and the George area *C. subternata* was mostly utilized (Joubert *et al.* 2008; Joubert *et al.* 2011; Marloth 1925). *Cyclopia maculata* grows naturally in the Overberg region and along with several other species, is currently under evaluation for commercialization (Coetzee 2012; Du Toit *et al.* 1998; Joubert *et al.* 2011). Industrial growth has been hindered over the past 10 years by the lack of a consistent supply to the expanding market (DAFF 2014; SAHTA 2015). For the honeybush industry to expand and exploit its potential as a global herbal tea, a shift is needed from wild-harvesting to harvesting from cultivated stands (Den Hartigh 2011; Coetzee 2012). With a shift from a market supplied by wild harvested biomass to one produced from cultivated stands, the industry is expected to continue growing at a steady rate (Den Hartigh 2011; Coetzee 2012). Currently only approximately 300 ha of land is under cultivation (DAFF 2014), but recent economic research conducted by the Coega Developement Corporation (2011) suggests that the industry has the potential to expand its export volume ten-fold from the current average of 150 tons to 1500 tons per annum.

Honeybush is still considered a fairly new crop with many unknowns when it comes to the successful cultivation and processing of the crop. Several baseline questions have already been addressed while many are still under investigation by a cohort of research institutes. The diversity within the genus *Cyclopia* makes answering basic questions, for example the most effective seedling propagation and soil preparation methods (SAHTA 2012), more complex than with other novel crops. Different honeybush species have also been found to vary in their biological properties and active health properties (Joubert *et al.* 2008). The complexity of the multiple factors that need to be considered makes addressing these baseline questions a continuous challenge. Research has shown that successful honeybush cultivation requires not only careful planning, but also needs to consider the species and sites, each being specific (SAHTA 2012).

1.2.2. The importance of the Honeybush industry

The economic potential of the honeybush industry concurs with the South African governments' strategy to promote the agricultural sector and integrated rural development (National Development Plan (NDP) 2011). The agricultural development strategies have successfully identified the importance of having a sound scientific foundation of sustainable resource use, combined with a focus on capacity building of rural communities for successful agricultural and rural development. The implementation of such multi-facet strategies for the integrated development of agricultural and rural regions is challenging.

One of the four core strategies for this development concerns capacity building for sustainable resource management (Strategic Plan for the South African Agriculture, 2001). This strategy prioritizes the importance of agricultural biodiversity and the use of sustainable land-use practises for enhancing farmland productivity. The potential to further link natural resource management as part of development programmes (computer/software programs) has been identified as a focus point for promoting short- and long-term benefits for community development and growing gross domestic product (GDP) gained from natural resources. Complementary strategies for agricultural development also include the Integrated and Sustainable Rural Development Strategy (ISRDS) and the Knowledge and Innovation strategy (Strategic Plan for the South African Agriculture 2001). Both of these highlight the need to invest additional resources into developing biodiversity-friendly farming practises intertwined with local community innovation and active participation. The honeybush industry has shown great potential for addressing these development goals and holds promise for further exponential growth (CDC 2011). The industry has already created new job opportunities across primary and secondary production levels, including cultivation and production by local communities (DAFF 2014). The active research focused on various aspects of the industry is also making a valuable contribution toward the advancement of sustainable development within South Africa.

The growing need for the expansion of honeybush production in terms of cultivation is important to meet the increasing demand, as well as for the sustainable development of this unique South African industry. As the honeybush industry develops toward becoming more commercialized and as supply shifts over to cultivated biomass, it is important to consider how best to develop biodiversity-friendly farming practises. A trajectory toward a sustainable and biodiversity-friendly industry is especially of importance considering the threatened ecosystem status several honeybush species are endemic to (Holness & Bradshaw 2010). As the honeybush industry gears itself towards increased commercialized cultivation, it is now appropriate to incorporate

6

preliminary steps in guiding the industry toward maintaining a balanced/healthy agroecosystem approach. In doing so, the industry will be strategically positioned for sustainable production and biodiversity conservation in the near future.

1.2.3. Commercialization of honeybush: challenges and opportunities to learn from the rooibos industry

Commercialization of any crop carries certain inherent threats to biodiversity. The common practice of land clearing, intensive ploughing and planting of monocultures, are but a few of the threats biodiversity faces during agricultural expansion. This is potentially an even greater reality during the commercialization of indigenous crops such as honeybush (*Cyclopia* spp.). These indigenous crops are often cultivated within their native habitat range on areas previously disregarded as being unsuitable for commercial crop production. Since these indigenous plants are adapted to the regions climatic and abiotic conditions, as is the case for rooibos (Hansen 2006; Pretorius 2009), it is feasible to cultivate them on less prime agricultural land or previously marginalized land. The expansion of the rooibos industry is a tragic South African example of the commercialization of an indigenous crop that resulted in extensive habitat destruction and biodiversity loss (Green Choice 2009; Hansen 2006; Pretorius 2009).

Coupled to the drastic expansion of rooibos cultivation between 1994 and 2007, the level of endangered plant endemics has increased by 300% in the rooibos production area (i.e. the greater Cedarberg in the Western Cape) (Pretorius 2009). The monoculture-dominated rooibos industry has caused large tracts of natural vegetation to which the species is native to be ploughed up for selective cultivation (Hansen 2006; Pretorius 2009). In some areas, pristine land continues to be cleared (often illegally, Hansen 2006) for the establishment of 'organic' *A. linearis* plantations (Anonymous pers. com). The rooibos industry is also facing severe pest challenges along with rising input costs spent on pesticides to suppress crop infestations ((Erasmus 2013; Hatting *et al.* 2011) . Although detailed published research on *A. linearis* insect pests is limited, several rooibos pest where noted as early as the 1980's by Annecke & Moran (1982) as well as by Rust & Myburgh (1989). More recently, 13 insect pests where recorded by Justin Hatting, a researcher at the Agricultural Research Council, in the form of a detailed practitioners guide published by the Agricultural Research Council (Hatting 2009, Hatting 2015). Several of these correspond with those initially noted by Annecke and Moran (1982) and Rust and Myburgh (1989), while some have only more recently been noted by Hatting (2009). Of the pest taxa associated with rooibos, cicadellid leafhoppers (Hemiptera: *Molopopterus theae*), geometrid 'looper' larvae (Lepidoptera: *Isturgia exerraria*) and Sessidae (clearwing moth) larvae (Lepidoptera: *Monopetalotaxis candescens*) have been identified as the main pest taxa causing the high levels of crop damage

(Erasmus 2013; Hatting 2009). The larval phase of both the Lepidoptera utilizes *A. linearis* as a host plant during the early stages of their life cycle. The geometrid 'looper' feeds externally on the foilage while the Sesiidae larvae are internal root-borers causing severe damage to the plants' root system. Both of these lepidopteran pests have the potential to cause huge crop losses (Hatting 2009). Rooibos pests, such as the clearwing moth, are not all common agricultural pests (Hatting 2009), but have rather come onto the pest radar with the increase commercial cultivation of *A. linearis* as monoculture plantations.

Hatting *et al.* (2011) recorded clearwing moth infestation to on average occur within the first year of planting at levels as high as 28 ± 2%, which then increases drastically in successive years (53 ± 2% and 72 ±1% in the 2nd and 3rd year respectively). Root-borer infestation ultimately leads to the loss of plants, often at the time when bushes would normally be at the peak of their commercial yield. Approximately a quarter of one of the plantations monitored by Hatting *et al.* (2011) was lost due to root-borer infestation. Insect pest on *A. linearis* varies with seasonality according to weather conditions, but are commonly more abundant when plants are under some form of stress, either during summer drought conditions or after harvesting (Erasmus 2013; Hatting 2009). Producers are advised to make use of various monitoring techniques so that chemical control can be implemented at the correct time (Hatting 2009; Hatting *et al.* 2013). Preventative spraying is done by some farmers, whereas others only apply pesticides when pest numbers reach undesirable levels (Anonymous pers. com 2015; Erasmus 2013). The potential role of conservation-biological control has been noted, but is as yet not effectively implemented as an alternative management approach of pest control (Hansen 2006; Pretorius 2009).

For responsible and sustainable commercialization of *Cyclopia* species to be successful, it needs to be guided towards a biodiversity-friendly sustainable industry, requiring a sound knowledge network in terms of not only its specific cultivation and sustainable harvesting, but also towards effective agroecosystem management of plantations.

1.3. Agroecosystems

An agroecosystem, in its simplest definition, is a managed 'ecosystem' for the purposes of agricultural production (Altieri 1995; Altieri 2004). These farming systems can incorporate a range of farming activities and land management practises. Most importantly to note, however, is that an agroecosystem is an ecological unit (Altieri 1995) that forms part of the broader landscape. Agrobiodiversity consists of the assembly of all biotic organisms within an agricultural landscape of potential economic benefit to the farmer (Altieri & Nicholls 1999). The concept of

agrobiodiversity originally comprised of organisms and processes from which humans obtained direct benefit. Natural resources that provided producers with food, fibre or any other tangible products were thus grouped under this umbrella term (Altieri & Nicholls 1999). The spectrum of these organisms usually focused on non-crop fauna and flora.

Modern approaches to agrobiodiversity consider this human and commercial value of resources as either planned or associated diversity (Costanzo & Bàrberi 2013; Perfecto & Vandermeer 2008; Vandermeer *et al.* 2002). Planned agrobiodiversity includes elements of diversity that have intentionally been incorporated by humans into the agroecosystem. Agrobiodiversity elements usually include aspects such as genetic diversity and selection of a mixture of crop cultivars or legume intercropping (Costanzo & Bàrberi 2013). Associated agrobiodiversity includes aspects of naturally occurring biodiversity still present within an agricultural landscape. These aspects range from the occurrence of natural enemies of pests to local soil biota (Costanzo & Bàrberi 2013).

The original definition of agrobiodiversity did not necessarily exclude aspects that are included in more modern definitions of this concept, but did not place an emphasis on these organisms as in the case of the current definition (Altieri & Nicholls 1999). From a production perspective, the main focus is on optimizing production for maximum economic return. It is therefore of great importance that ecologists and conservationists are able to identify and quantify the benefit that agrobiodiversity, in its extended definition, has for a producer or farm owner.

1.3.1. Agrobiodiversity and AMES

Agricultural expansion has led to high fragmentation and isolation of natural habitat within transformed landscapes which has resulted in the loss of many fundamental ecological functions and processes (Didham *et al.* 1996; Bu *et al.* 2014), many of these due to the loss of insect diversity (Bihn *et al.* 2010; Luck *et al.* 2003). The degradation and loss of fundamental ecological systems can lead to various consequences to the ecological balance within ecosystems and agricultural landscapes (Starý & Pike 1999; Wilby & Thomas 2007).

Incorporating agrobiodiversity, in its various forms and combinations, into an agricultural landscape can result in a cohort of production benefits to a producer (Costanzo & Bàrberi 2013). Insect communities, for example, play a vital role within agroecosystems in the ecological functions and AMES they provide within an agricultural landscape. These beneficial ESS includes insect pollination (e.g. see Melin *et al.* 2014), nutrient cycling (e.g. see Thiele-Bruhn *et al.* 2012) and natural biological control (e.g. see Henri *et al.* 2015). Natural biological control is an important AMES for regulating arthropod pest populations (thus preventing excessive biomass loss) and for

managing the spread of disease by insect vectors (e.g. see Roossinck & García-Arenal 2015). These ecological interactions within an ecosystem, and agroecosystem alike, are influenced by the structure of the ecosystem and surrounding landscape (Henri *et al.* 2015; Pickett & Cadenasso 1995).

Agroecosystems within a landscape do not function independently from the surrounding ecosystems. Management practises within an agroecosystem have an impact on the natural (existing) ecosystems adjacent to the agricultural area as well as the landscape as a whole (Altieri & Nicholls 1999). Similarly natural ecosystems also interact and influence adjacent agroecosystems (Henri *et al.* 2015; Gaigher *et al.* 2015). The study of landscape ecology considers the landscape as an ecological unit and emphasizes the role spatial ecology plays in shaping ecological systems (Pickett & Cadenasso 1995; Pryke *et al.* 2013). Insect response and their spatial distribution are altered, on a species specific basis, by different landscape mosaics and environmental variations (Didham *et al.* 1996; Pickett & Cadenasso 1995). Habitat transformation caused by agricultural practices thus also has an influence on the spatial distribution of insects within and between natural and managed ecosystems (Carvalheiro *et al.* 2011; Henri *et al.* 2015). The contrast created between natural and managed habitats due to habitat simplification, for example between vineyards and adjacent natural vegetation, limits movement of natural enemies (predators and parasitoids) into cultivated fields (Nicholls *et al.* 2001).

Temporal (Olesen *et al.* 2008) and environmental conditions (Gutbrodt *et al.* 2012) also influence how insects responsd to their immediate environment. Altered fluctuations in temperature can either promote or limit pest outbreaks and foraging efficiencies of natural enemies (Ascerno 1991; Forrest & James 2011; Yang *et al.* 2005). The occurrences of sporadic agricultural pests are closely synchronized with seasonal fluctuations and specific optimal weather conditions and corresponding resource availability of host plants (Forrest & James 2011; Sivertsen *et al.* 1999). Rooibos pests, for example, *Isturgia exerraria* (Lepidoptera: Geometridae) and *Molopopterus theae* (Hemiptera: Cicadellidae) have distinct seasonal fluctuations in population abundances (Hatting 2009).

1.3.2. Maintaining a functional agroecosystem

Ecosystems resilience and the reliability of ecosystem functioning, and associated ESS such as natural biological control, is determined by the complexity of an ecosystem, with respect to both the habitat heterogeneity and functional diversity of the natural enemy complex (Tilman 1999; Naeem 1998; Naeem *et al.* 1999). Therefore if agroecosystems are to maintain high ecological

functioning, and benefit from the related ESS, they should be managed in such a way that habitat heterogeneity and agrobiodiversity is enhanced or maintained. This can be done whereby the complexity of natural systems are either mimicked or re-established within an agricultural setting (Benton *et al.* 2003; Altieri 2004). Two important aspects for promoting biological control within agroecosystems would be to limit the application of nonselective pesticide and using cultural land management practices that conserve natural enemies effective as natural biological control agents (Aliniazee & Croft 1999; Schellhorn & Silberbauer 2002).

i.   Landscape elements and integrated pest management

Within an agricultural system various microhabitats can be created by the different landscapes elements within the system – remnant patches, gaps in hedges and corridors of natural vegetation intersecting and/or within the cultivated crop creates valuable niche habitats for invertebrates within the agroecosystem (Altieri & Nicholls 1999, New 2005). The nature of these microhabitats affects the occurrence, abundance and diversity of arthropods within agroecosystems and influence how these interact within the rest of the landscape (New 2005). The arthropods may be partly or solely dependent on the agro- or native landscape features for their survival – they may, for example, feed in the cropped area and overwinter in the adjacent hedge, or require the remnant patch for reproduction (larval or adult stage) or as an alternative food source or shelter when the crop is harvested (Altieri & Letourneau 1982; Gurr *et al.* 2011; New 2005). High-quality agricultural matrices thus serve as a valuable habitat passageway for species to move within a fragmented landscape (Perfecto & Vandermeer 2008) enhancing habitat connectivity. Several studies in the tropics have indicated the agricultural matrix to house high levels of biodiversity (Bu *et al.* 2014; Perfecto & Vandermeer 2008; Philpott & Armbrecht 2006) and have shown the significance of field margins in promoting within crop arthropod diversity (Altieri & Nicholls 1999; Balzan & Moonen 2014). Landscape elements enhance the mobility of arthropods between adjoining ecosystems, such as the agroecosystem and the surrounding natural vegetation.

These landscape elements provide refuge habitats for predatory and parasitoid arthropods that can serve as important components for Integrated Pest Management (IPM) within agroecosystems (Altieri 1995; New 2005). IPM, as first conceptualized in the early 1970's, is an attempt at more sustainable pest management (Altieri 1995). This pest management strategy aims to establish alternatives to the use of only chemical control methods to control pest (Altieri 1995; Hokkanen 2015). The IPM approach uses a combination of pest control tactics with the first line of defence falling to natural biological control and cultural management practises. These are combined with chemical control where pest populations exceed economic threshold levels.

11

Landscape elements can thus be used in advance, at a landscape level, for incorporating IPM strategies into an area to be utilized for agricultural production. Incorporating viable strips/patches of natural veld within the agricultural landscape can, for example, create a mosaic favouring natural pest control agents as the first pest control tactic (Altieri 1995; Nicholls *et al.* 2001). Landscape planning within agricultural systems can thus be geared both toward the benefit of production (IPM strategies for bottom-up pest management) and conservation.

ii.   Key natural enemies for integrated pest management

The natural enemy complex consists of a combination of arthropod taxa, pathogens and entomopathogens (Flint *et al.* 1999). For the purposes of this study insect natural enemies are the main focus. Several predator and parasitoid insect taxa present in natural enemy complexes have become well-known as effective biological control agents for use in IPM strategies (Aliniazee & Croft 1999; Stevens *et al.* 2007). Integrated pest management strategies can incorporate either the classical or natural biological control approaches. Classical biological control is the mass rearing and release of biological control agents (from the pests native home range) of specific agricultural pests, whereas natural biological control (also known as conservation biological control) optimizes on the predation pressure of the natural enemies already present within the agricultural landscape (New 2005). Predators and parasitoid arthropods used for IPM include, among others, lady beetles (Coleoptera: Coccinellidae) and predatory and parasitoid wasps and ants (Hymenoptera), as well as other taxa such as spiders (Arachnidae) and predatory mites (Acari).

Coccinellidae (lady beetles) are known for their regulation of aphids (Hemiptera: Aphididae) which are agricultural pests in crops such as wheat (Dong *et al.* 2012) and deciduous fruit (Aliniazee & Croft 1999). Lady beetles also form an important part of the natural enemy complex of other non-hemipteran prey (e.g. insect eggs and Coleoptera larve) and are widely used as agents for natural biological control (Evans 2009; Scholtz & Holm 1985) in IPM programmes. Hymenoptera are important predators and parasitoids and include both generalist and specialist feeders on a wide host range and are used for both classic and natural biological control (Stevens *et al.* 2007). Egg parasitoid wasps, for example, are extensively used for biological control within the deciduous and tropical fruit industries (Aliniazee & Croft 1999; Henri *et al.* 2015).

For natural biological control to be effective natural enemies need to be able to maintain arthropod pest populations below the economic threshold of crop damage (Altieri 1995). For this to be possible an adequate population of the desired natural enemies needs to be present and be actively foraging within the cultivated area. These requirements can be met through effective

12

habitat management (cultural management practices) of non-crop vegetation within and adjacent to agricultural fields (e.g. see Bianchi *et al.* 2003).

1.4. Agroecology in the Honeybush industry: the current perspective

The honeybush industry finds itself at an interesting point in its development as it continues to grow from the former modest cottage industry it used to be. As the industry gears itself towards further commercialization, it is of utmost importance that the agrobiodiversity available to the industry is further taken into account. The shift from wild harvested biomass to cultivated stands represents a challenge to the industry to heed the growing demand for honeybush. The question of its production being sustainable, and potentially an environmentally friendly supply remains uncertain. The end product will depend on how the current pioneers of the industry value the resource holistically and incorporate sustainability and agrobiodiversity principles into the future design of the industry – considering all aspects of the production chain, from its cultivation through to the processing and packaging of the final product.

Taking its cue from the rooibos industry, in terms of its current pest challenges and threat to the native vegetation, it seems only wise to intentionally and timeously develop the commercialization of *Cyclopia* spp. to understand its ecology in avoiding similar issues. Improved understanding of the ecology of honeybush can translate into shaping the industry accordingly, to maintain a functional proportion of the original, natural ecological balance within the agroecosystem.

Current research on insects associated with honeybush is limited (Joubert *et al.* 2011). The only reference available is an unpublished insect survey done by Knipe & Rosenberg (2008) as part of initial trials done by the Agricultural Research Council (ARC), Infruitec-Nietvoorbijl, Stellenbosch. The ecological role of insects (e.g. pollination and natural biological control) associated with honeybush remains greatly unknown. Similarly, research focused on incorporating agroecological principles into agricultural practices to promote natural biological control of potential pests is also lacking. Nature along with all its elements and role players is in an intricate balance (Krüger & McGavin 2001; Starý & Pike 1999). Much can be learnt from the composition and interactions of associated invertebrate communities. One of the many aspects that require considerable monitoring and management includes the determination of the potential and level of pest insects and their natural enemies. The potential arthropod-mediated ecosystem service and disservice that these groups of insects could render to a farmer are especially important to investigate.

1.5. Research aim and objectives

The suitable first step towards establishing the relevant ecosystem services available to a land user is to identify the local biodiversity, and to consider which component could potentially be of direct benefit to a producer. The aim of the current study was to address the lack of baseline knowledge regarding the insect assemblage associated with *Cyclopia* species. The first chapter (Chapter 2) is dedicated to describing the methodological approach and study areas. This sets the scene of the land management practices and farmer insights regarding the research aim and objectives. Research objectives included an investigation into the diversity and seasonality of the insect assemblage associated with honeybush (Chapter 3) and determining the potential arthropod-mediated ecosystem services and disservices available to a honeybush farmer (Chapter 4). Chapter 4 further highlights potential insect pests, and identifies the dominant insect families of the natural enemy complex within honeybush stands. The land management practices within agroecosystems are known to impact the composition and abundance of arthropods and the ecological functioning within the agricultural landscapes. It is therefore also important to understand how current land management practices affect the insect assemblage within honeybush stands (Chapter 5). Through a better understanding of the ecology of honeybush within natural and cultivated stands industry guide-lines for sustainable land management and expansion can be compiled. These insights, together with lessons learned from the pest challenges faced by the rooibos industry, can assist in guiding the honeybush industry towards a healthy agroecosystem that is agriculturally productive, economically viable, environmentally sustainable and socially valued.

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CHAPTER 2.

METHODOLOGICAL APPROACH

In this chapter the study areas are described in detail as the Honeybush (*Cyclopia* spp.) crop species under study are highly variable in phenology, growth patterns and distribution. Management practices amongst producers also varied. This description will support the following chapters, to avoid unnecessary lengthy repetitions in the materials and methods sections of each chapter. These will thus only be stated briefly, with reference to this chapter.

The methodological approach of the project took into consideration insight gained from engagement with a wide range of relevant stakeholders, including current and upcoming small and large scale honeybush farmers from the Western and Eastern Cape.

2.1. The greater Overberg District

The study was carried out in the Overberg District at three study areas; the nearest towns to the study sites were Genadendal, Bredarsdorp and Pearly Beach (Figure 2.1). The Overberg District Municipality comprises the Theewaterskloof, Overstrand, Cape Agulhas and Swellendam Local Municipality, and includes towns such as Grabouw, Hermanus, Caledon, Swellendam and Barrydale (Western Cape Government, 2015). The district covers an area of 12,241 km^2 with 215,734 inhabitants with a 74.3% level of literacy (WESGRO 2013).

The Overberg region has a Mediterranean climate characterized by wet winters with cold to moderate temperatures and hot, dry summers. Most of the annual rainfall occurs between April and September. Rainfall ranges between 400 - 650 mm/a (Bothma & Du Toit 2010). The driest season is from November to March when potential evaporation exceeds precipitation. The region is known to be extremely windy. The average annual temperature approximates 16.9°C, with a maximum and minimum temperature range of 26.6°C in January to 6.6°C during August. The natural landscape of the Overberg region has been transformed extensively by agricultural practices. Large stretches of the natural vegetation have been removed for the planting of canola, wheat and other cereal crops. Due to the high degree of landscape transformation, many of the remaining vegetation remnants are listed as threatened or critically endangered by the National Environmental Management Biodiversity Act (NEMA) and National Equivalent Ecosystem Threat Status for the district (Holness & Bradshaw 2010). Two species of *Cyclopia* occur naturally in the

Overberg, namely *C. maculata* and *C. genistoides* (Figure 2.2). Several *Cyclopia* spp. are under cultivation in the Overberg by small and large scale farmers alike supplying an additional means of income. The Agricultural Research Council (ARC) was one of the institutions to promote honeybush cultivation within this region. Several experimental trials were initiated under their guidance. Discontinued experimental trails in the vicinity of Genadendal were among those considered during site selection. The cultivated stands of *C. genistoides* were also part of pioneer plantations established in accordance with the ARC initiative.
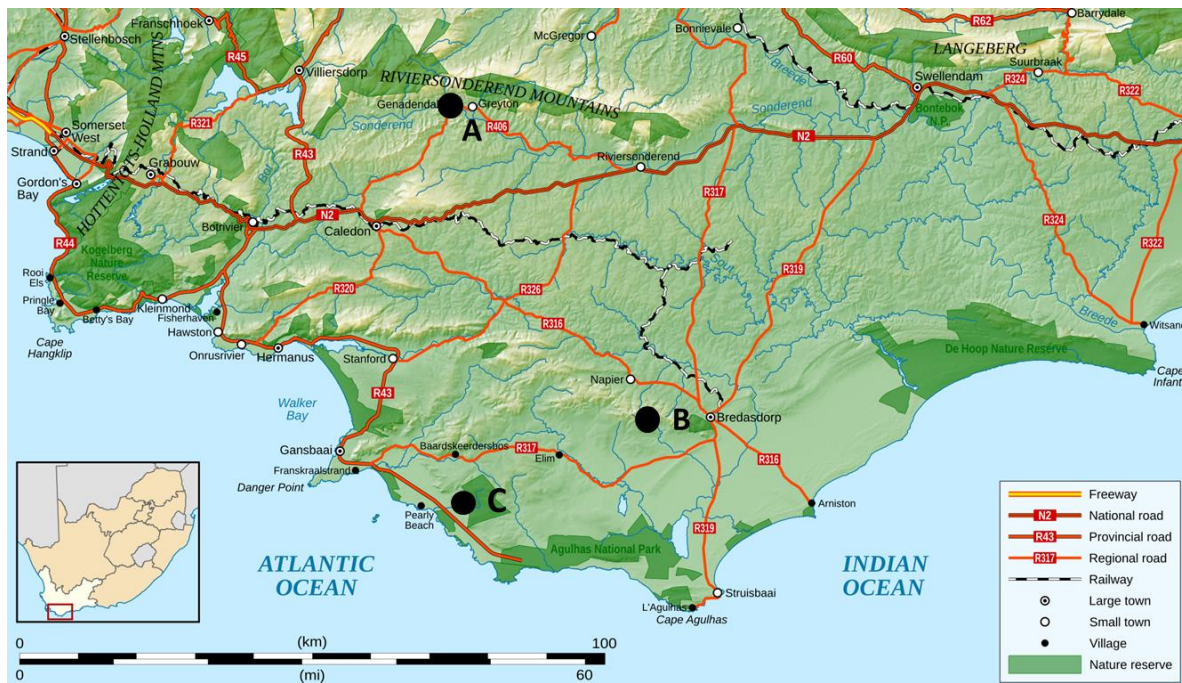
Figure 2.1. Study areas within the Overberg district in the vicinity of Genadendal (A), west of Bredasdorp (B) and south-east of Pearly Beach (C) (Htonl 2015).
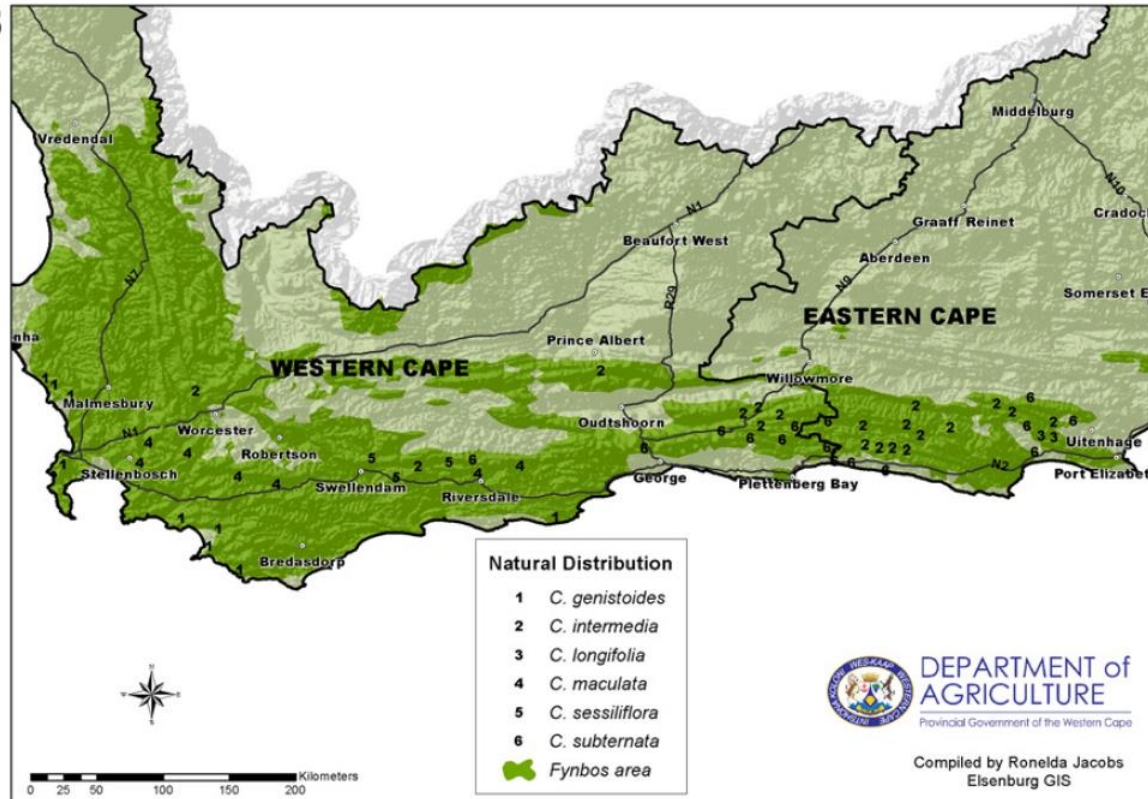
Figure 2.2. Natural distribution of *Cyclopia* spp. in the Western Cape (Joubert *et al.* 2011).

2.1.1. Study site selection and description

The three study areas selected included habitats with a combination of *C. maculata* and *C. genistoides*. *Cyclopia maculata* is a non-resprouter and *C. genistoides* a resprouter (Schutte 1997; see Box 1). Both of these species are of economic importance for current and future cultivation. Having two life-history types present in their natural habitats allowed a life history comparison to be made between a resprouter and a non-resprouter in terms of phenology and the related arthropod assemblage associated with these honeybush species.

> **BOX 2.1. Fire-survival for *Cyclopia* species: Resprouter vs. reseeder**
>
> Adaptation to recurring fires within the various habitats home to *Cyclopia* spp. has led to distinct fire-survival strategies and corresponding growth habits. Species that are resprouters post-fire use resources stored in a subterranean, woody rootstock to grow from buds at/just below ground level. Resprouters therefore have a multi-stemmed, often prostrate growth form, with shoots emerging from the rootstock. The non-resprouters perish post-fire and invest resources in mass seed production (obligate reseeders) as a means of fire-survival. No-resprouting species grow tall and erect like small trees with a single basal stem at ground level.
>
> Fire survival within the genus can be used as a means of distinguishing among species, but not for cladistics analysis as some species (e.g. *C. bowieana* and *C. alopecuroides*) vary in the fire survival strategy. Fire survival strategies for *Cyclopia* are thus rather considered to fall on a sprouter/non-resprouters continuum.
>
> These two fire survival strategies are common to fire prone vegetation types and are characteristic of other Fynbos taxa, specifically other legumes in the tribes *Podalyrieae* and *Liparieae*.
>
> (as summarized from Schutte (1997) and Schutte *et al.* (1995))

The study area incorporated three levels of disturbance created by either the *ad hoc* use of *Cyclopia* spp. in the wild or the management practices used on cultivated fields (Table 2.1). Study areas used were the only known sites available within the Western Cape suitable for investigating the insect assemblage associated with *Cyclopia* species. All three study areas are subject to a certain level of harvesting for tea production. Based on their disturbance level resulting from harvest events and/or land mnangement practices the three study areas are classified as having disturbance levels categorized as low (natural, wild sites), medium (semi-natural cultivation) and high (more traditional cultivation). This classification was only used in later chapters where the impact of disturbance on the insect assemblage composition was investigated. At each of the three study areas (Figure 2.3), four sites were selected for long term phenology observations and insect monitoring. The positions of sampling sites for the natural, 'wild' stands in the Genadendal/Greyton area were determined by the distribution of *Cyclopia* sp. in the study area. *S*ampling stations were placed within the immediate vicinity of the natural population, with control sampling stations 10 m into the Fynbos vegetation adjacent to honeybush stands. Sites could not be placed further due to a change in land use (e.g. apple orchard) or the proximity of invasive

trees such as Port Jackson (*Acacia saligna* (Labill.) Wendl), Pine (*Pinus pinaster* (Aiton)) and Black wattle (*Acacia mearnsii* (De Wild). In the cultivated fields, the sampling sites were placed at least 10 to 15 m into the plantation along the length of the field adjacent to the Fynbos vegetation. Due to their clumped distribution, sampling sites for the wild honeybush varied in size and the proximity of individual plants. Sites within the cultivated stands are planted uniformly in rows, and were thus sampling points were more evenly spaced within the cultivated area. Site selection within the cultivated honeybush stands were restricted to sections of the planted area that were adajcent to Fynbos vegetation. Sampling points were at least 10 to 15 m from the Fynbos edge as dictated by the layout of the plantation and presence of roads. Sites were spaced out as far as possible from each other over the length of the suitable section of the honeybush plantation to incorporate as much environmental variability as possible. Sites were between 50 to 100 m from each other. High temporal replication was also a restriction to the number of site replications that could be included in the study.

Cyclopia maculata

This species of honeybush occurs naturally beside riverbanks and marsh areas along the Riviersonderend mountain range. *Cyclopia maculata* forms a tree-like bush that varies in size depending on the density of the honeybush stand. Bushes are mostly 2-3 m in height, and vary greatly in width (<0.5 – +2/3 m) depending on the density of the stand.

Study area #1

The study area near Genadendal and surrounding out-post stations had four study sites of wild *C. maculata*. The selection of study sites was based on the presence of *C. maculata* growing naturally in the area and the population being surrounded by natural/semi-transformed Fynbos vegetation. All four honeybush populations in the Genadendal and Greyton area are on Central Ruens Shale (FRs12) which has been classified with a conservation status of 'critically endangered' (Mucina & Rutherford 2006). Two of the wild populations of *C. maculata* sites are on Genadendal community land near Greyton (34°05' S; 19°41' E) (GPS locations are given at coarse resolution for protection of the communal resource). The other two populations are on private land between Bereaville and Villiersdorp, namely Middelplaas (34°03'33.91'' S 19°26'41.11'' E) and Meulrivier (34°03'35'' S 19°28'21'' E). All four wild populations consisted of large (1.5 – 2.5m), fully grown bushes generally not used for commercial production, while only some of the bushes at the Greyton sites showed evidence of selective *ad hoc* harvesting.

The populations on the Genadendal communal land consist of a mixture of very dense stands of *C. maculata* and other areas where bushes are more distant. The honeybush stands at the other two sites are more widely spaced; these bushes are generally much larger. The communal land is used for pastoral grazing and seasonal wood harvesting. A large area of the communal land is overgrown by alien invasive trees such as Port Jackson (*Acacia saligna*) and Pine (*Pinus pinaster*) trees. The Middelplaas site is within a low lying area that periodically becomes a marsh land during the winter months (especially June - July). The surrounding vegetation is dominated by vlei grass, with a patch of Fynbos 100 m west of the population. The population at Meulrivier Trust farm is situated along the riverbanks heavily invaded by Black wattle (*Acacia mearnsii*). Historically the land utilized was for vegetable cultivation, but the majority of the land is currently utilized for commercial apple orchards.

Cyclopia genistoides

Two farms on the Agulhas Plain where *C. genistoides* is cultivated were selected as part of the study. *Cyclopia genistoides* occurs naturally in the area, cultivated stands were established through selection from the natural population (Overberg strain) and/or from seed obtained of the Table Mountain strain. Plantation management differs in the harvest frequency and in the way ground cover vegetation in plantations is controlled. Both plantations are adjacent to Fynbos veld.

Study area #2

The farm Toekomst (34°33'22'' S 19°53'38'' E) is situated 20 km west of Bredasdorp, south of the Bredasdorp Mountains. The study area is on Overberg Sandstone Fynbos (FFs12) (Mucina & Rutherford 2008) which has a conservation status of 'least threatened' (Mucina & Rutherford 2008). The area under *C. genistoides* cultivation covers ± 45 hectares. Three of the four study sites are within honeybush plantations established in 2003 (12 year old stand), whereas the fourth site is a younger plantation established in 2008 (eight year old stand). The latter was harvested in January 2014 and has been sprouting new growth since February/March 2014; this site was omitted from the phenology comparison. The other three sites were also scheduled to be harvested in the first quarter of 2014, but due to unfavorable weather for processing the biomass, harvest was left over to the following year.

The honeybushes were established as seedlings and spaced approximately at one meter intervals along slightly elevated mounds formed after land clearing. Some bushes are, however, in clusters of closer proximity where more than one seedling was planted. The area between the honeybush plants harbours an assembly of weedy plants and early succession Fynbos shrubs

that have been left to reestablish naturally. These include a range of species belonging to the Ericaeceae and Poaceae as well as a variety of geophytes. The ground cover vegetation is left to grow and establish for several years before being brush cut to keep the veld in a prostate phase and to prevent ground cover out-competing the planted honeybush. The ground cover vegetation of the eight year old stand was subject to an alternative management technique where the vegetation is scorched serving as a 'chemical burn' to even out competition to the same level as the harvested honeybush. The adjacent veld is dominated by mature *Protea* and *Leucadendron*, their dominance enhanced since the area was several years ago used for the production of cut-flowers.

Study area #3

The farm Koksriver (34°41'43" S 19°35'04" E) is situated approximately 16 km south-east of Pearly Beach and 40 km from the other study area at Toekomst. The natural vegetation of the area is Agulhas Sand Fynbos (FFd7) which has a conservation status of 'vulnerable' (Mucina & Rutherford 2008). An area of approximately ± 25 hectares is under cultivation, with some of the area being planted as far back as 1996; this particular area of 5.2 ha is not actively harvested anymore and has been reported by the farmer to have high levels of bud mite infestation. The plantation was initially established as part of the trials set-up by the ARC in 2005/6. Most of the honeybush plantation still actively used is approximately eight years old. Seedlings were planted in a similar manner as at the farm near Bredasdorp. The honeybush is harvested, annually in late-January to February. After the honeybush is harvested, the ground cover vegetation is cut down with a tractor-drawn 'bossieslaner' (brush-cutter). Thereafter the natural vegetation is allowed to resprout among the honeybush during the months that the bushes are left to regrow post-harvest (January/February).This management action prevents the ground cover vegetation from becoming overgrown and out-competing the recently harvested honeybush. Due to the sandy soil and regular brush cutting, the ground cover within the plantations is not as dense as that in the adjacent areas or as at the Toekomst sites. The cut-down shrubs are left in the fields in an attempt to help prevent excessive wind erosion.

2.1.2. Land-user input and general field observations

A special feature of the research was the direction given by land-users who themselves showed an interest in the questions being asked. Land-users included small- and large-scale Western and Eastern Cape farmers. Several insects were noted by land-users to cause damage to honeybush species at various phenological phases.

Small scale farmers in Genadendal reported several insects feeding repeatedly on *C. maculata* seedlings, these included, weevils (Coleoptera: Curculionidae), Twig wilters (Hemiptera: Coreidae), Foam grasshoppers (Orthoptera: Pyrogomphidae) and several moth and/or butterfly larvae (Lepidoptera). Soft Brown scale (Coccidae) infestations were noted by one of the landowners on *C. subternata* at an abandoned ARC field trail site in the vicinity of Genadendal. These scale insects had completely infested the bush which, as a result of the infestations, was covered in sooty mildew. Several of these scale insects were, however, parasitized, an indication of biological control of this potential pest.

One of the more abundant hemipteran species (?Flatidae sp. 1) noted by a farmer on *C. genistoides* was not as abundant during the sampling period, possibly due to the decreased rainfall of that season. The landowners of the cultivated stands of *C. genistoides* noted that the past (2014/15) season was drier compared to the preceding year (2013), as was confirmed by weather data obtained from the Agricultural Research Council (AgroClimatology Staff 2015). One of the farmers also reported high levels of bud mite infestation in previous years, the infestation occurred in the oldest portion of his plantations now no longer actively utilized. Other potential pest insects noted by farmers on *C. genistoides* also included localized infestations of scale insects (Hemiptera: Sternorryncha), often tended by ants.

The bollworm, *Helicoverpa armigera,* was noted by a farmer to target the seed pods, although none were encountered during the sampling period. Seed pods are also prone to infestation by lygaeids (Lygaeidae) or bruchids (Bruchidae). These families are pests on other pod-forming plants such as *Acacia* species (Southgate 1983). Both of which were present during the sampling period. *Cyclopia subternata* seed pods have been found to be heavily infested by Bruchidae at an experimental plot of the ARC in the Stellenbosch area as well stands of *C. intermedia* in the Eastern Cape.

Additional taxa noted on *C. intermedia* by Eastern Cape land-users include the Silver-spotted Ghost Moth ('Keurboom mot') (Lepidoptera: Hepialidae), which causes severe damage as an internal root borer, as well as Ground Crickets (Tettigoniidae). The Silver-spotted Ghost Moth was previously recorded by Knipe & Rosenberg (2008) as a potential pest risk. The larvae of this endangered species, as reported by a small scale farmer in the Eastern Cape, caused fatal damage to large sections of a *C. intermedia* plantation. Heavily infested plants were also more prone to wind damage. Ground crickets were reported to feed on *C. intermedia* seed pods, but only a few of these were noted within the honeybush stands during the course of this study.

Other potential threats to the survival of honeybush plantations include herbivory of newly planted seedlings by snails, wind damage, damage to roots and dormant shoots during harvesting and land clearing post-harvest activities. Dune moles (*Bathyergus suillus*) are also a problem as these were reported to eat the central root base of *C. genistoides*, causing the plant to die.

Table 2.1. Study area descriptions of three sites with either wild or cultivated *Cyclopia* species.

Study area	*Cyclopia* spp. (common name)	Study area description	Harvest regime and management practice	Size of population	Natural vegetation (conservation status)	Nearest town	*GPS co-coordinates
A	*C. maculata* ('Vlei' tea)	Natural 'wild' populations with low disturbance. Sites are located on low lying land in vlei/marsh-type areas.	Wild population that is occasional harvesting on an ad hoc basis	± 0.2 - 0.5 ha	Central Ruens Shale (FRs12) ('critically endangered'). Several sites heavily invaded with Port Jackson.	Genadendal and surroundings	34°05' S 19°41' E
B	*C. genistoides* ('Kus tee'/coastal tea)	Semi-natural cultivated plantation with a moderate level of disturbance	Harvest events on a 2/3 year rotation. Ground cover occasionally managed by a chemical 'burn'	± 45 ha	Overberg Sandstone Fynbos (FFs12) ('least threatened')	Bredasdorp	34°33'22" S 19°53'38" E
C	*C. genistoides* ('Kus tee'/coastal tea)	More traditional cultivation practice with a high level of disturbance	Annual harvest (January/February). Regular clearing of ground cover vegetation	± 25 ha	Natural vegetation, Agulhas Sand Fynbos (FFd7) ('vulnerable')	Pearly Beach	34°41'43" S 19°35'04" E

*GPS locations are given at coarse resolution for Genadendal for protection of the communal resource

Figure 2.3 Study areas with *Cyclopia* species, natural (A) *C. maculata* (2 – 3 m x 1.5 – 3 m) near Genadendal, cultivated *C. genistoides* (1 - 1.5 m x ± 1 m) near (B) Bredasdorp and (C) Pearly Beach.

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CHAPTER 3.

CYCLOPIA (HONEYBUSH) SPP. PHENOLOGY AND ASSOCIATED ARTHROPOD DIVERSITY AND ABUNDANCE

3.1. Introduction

The Fynbos Biome is one of South Africa's eight biomes (Esler *et al.* 2014, Mucina & Rutherford 2006). Its Mediterranean-type climate along with recurring fires and nutrient-poor soils are some of the main driving forces that have shaped the fauna and flora within this biome (Esler *et al.* 2014). The rich biodiversity and high levels of endemism associated with Fynbos can be attributed to these biophysical conditions (Esler *et al.* 2014). Similar Mediterranean-type ecosystems are characterized by seasonal growth peaks in spring and autumn (Pilar & Gabriel 1998; Terradas & Savé 1992). The phenophase determinants of the Fynbos Biome are often interlinked and in synchrony, making it difficult to decipher the main causal relationships of abiotic and biotic factors at hand (Pierce 1984). Plant phenolgy and insect development are closely linked to biotic factors and often well synchronized (Ascerno 1991; Forrest & James 2011). Undertaking a phenology study of a new, indigenous crop, such as honeybush (*Cyclopia* spp.) is useful in better understanding the associated arthropod assemblage and determining when plantations would be the most vulnerable to insect attack and aid decision making for pest management activities.

Plant phenology

Plant phenological studies are based on observations of the current state of several phenophases of an organism's life history (Pierce 1984). Plant phenophases refer to one of several stages within a plant's life history, or its phenology. Examples of phenophases include, among others, active growth as indicated by leaf initiation and shoot elongation, flower bud development, flowering, and the various stages of seed development (Abdurahman 1991; Atkinson & Porter 1996; Pilar & Gabriel 1998). By using evaluative phenological methods over the course of a plant's

seasonal change, a better understanding will be gained as to when a species or vegetation type is active or dormant (Pilar & Gabriel 1998).

Another important aspect of phenology is the causal relationship of the onset or transition between phenophases and the interaction between plants and other biotic components (Pierce 1984). The transition between plant phenophases is governed by a combination of external, abiotic factors (Ascerno 1991; Atkinson & Porter 1996; Baumgartner *et al.* 1998) and internal physiological cues (Pierce 1984). Several environmental factors have been identified as useful for predicting plant and insect phenology (Atkinson & Porter 1996; Forrest & James 2011; Willmer & Stone, 2004). These include aspects related to temperature, photoperiod and soil moisture (Ascerno 1991; Baumgartner *et al.* 1998; Forrest & James 2011). The transition of phenophases and specific abiotic factors are considered to be strongly correlated (Ascerno 1991; Yang *et al.* 2005).

Plant phenology can be used as a predictive measure of insect development or migration within or between host plants (Ascerno 1991; Baumgartner *et al.* 1998). The relationship between plant and insect phenology helps to understand the complexity of ecological resource networks. Within the Fynbos Biome very few of the earlier ecological studies took these abiotic and biotic interactions into account (Pierce 1984). Some of the first studies capturing the interaction between arthropods and plants was done by Bond and Slingsby in the 1980's on myrmecochory, the ant dispersal of Fynbos plant seeds (Pierce 1984). Since then extensive research has been done on a wide range of biotic and abiotic factors that affect insect emergence and abundance (Ascerno 1991; Baumgartner *et al.* 1998; Forrest & James 2011; Olesen *et al.* 2008; Yang *et al.* 2005). Some of the factors that affect the timing and rate of insect development and emergence include seasonality of plant phenology, changing weather conditions and long term climatic conditions (Collinge & Louda 1989; Forrest & James 2011).

Plant-insect interactions and integrated pest management

Effective integrated pest management (IPM) relies on a sound understanding of the autology (species ecology) of the insect pest and the host crop (Ascerno 1991; Sivertsen *et al.* 1999). Several crop management approaches rely on weather variables and/or plant phenology as determinants for making predictions regarding the timing of insect development (Ascerno 1991; Baumgartner *et al.* 1998) and intervention measures agsinst pest outbreak. Insect emergence is closely coupled with temperature and host plant resources (Son 1999; Snodgrass *et al.* 2012; Willmer & Stone 2004). Thus plant phenology makes for a good indicator for determining the susceptible life stages of problematic insects (Ascerno 1991). By evaluating current weather conditions and observing plant phenology, predictions of the emergence of insects and the timing

34

of planned control measures can be made (Ascerno 1991; Forrest & James 2011). Results from this research are thus useful for land-users and other stakeholders interested in IPM within honeybush production systems.

Aim and objectives

Although *Cyclopia* morphology has been studied both in the wild (Schutte 1997) and in cultivated stands (Spriggs & Dakora 2009), only general observations are available about the phenology of the genus. Apart from implications for IPM, understanding the life histories of honeybush resprouters and non-resprouters is essential for making informed decisions regarding harvesting regimes and conservation actions. Accurately capturing and analyzing the phenology and life history of a species or vegetation type is not a simple task given the complex interaction between external abiotic and intrinsic biotic factors mentioned above. This study thus aimed to investigate and determine the phenology of two commercially relevant *Cyclopia* spp., namely *C. maculata* and *C. genistoides,* in correspondence with insect diversity and abundance across phenological stages. Results of this study should serve as a guideline for future, more detailed, phenology studies and form a baseline from which management decisions can be made regarding wild and commercial harvesting practices and conservation of the species. The detailed outline of phenological differences and similarities between the two *Cyclopia* species will aid in better understanding the variability and diversity of the associated insect assemblage. This will assist in understanding the potential arthropod-mediated ecosystem services and disservices available to a honeybush farmer.

3.2. Materials and methods

3.2.1. Study sites

Three study areas were selected within the Overberg area. Study sites harboured a combination of *C. maculata* and *C. genistoides* plants allowing for a life history comparison between a resprouter and a non-resprouter, more specifically by comparing between the phenology and related seasonal variation of the insect assemblage associated with the two honeybush species. Research sites comprised habitats of wild *C. maculata* in the vicinity of Genadendal, and two cultivated stands of *C. genistoides* near Bredasdorp and Pearly Beach (Chapter 2, section 2.1.1. , Figure 2.1).

At each of the three study areas, four sites were selected for long term phenology observations and arthropod monitoring (Chapter 2, section 2.1.1. , Table 2.1 and Figure 2.3). In short, the position of sampling sites for the natural 'wild' stands in the Genadendal/Greyton area were determined by the distribution of *Cyclopia* spp. in the study area. In the cultivated fields, sampling sites where placed at least 10 to 15 m from the edge of the plantation along the length of the field adjacent to the Fynbos vegetation. Site placement was determined by the occurance of roads or other regions of disturbance along the edge of cultivated areas. Sampling sites for the wild honeybush varied in size and proximity of individual plants whereas the sites within the cultivated stands were evenly spaced within the cultivated fields. Placement of sites within cultivated stands was restricted to areas were Fynbos vegetation was adjacent to the planted area. Site placement within wild honeybush stands was restricted by changes in land use or presence of dense stands of invasive trees (e.g. Port Jackson (*Acacia saligna* (Labill.) Wendl), Pine (*Pinus pinaster* (Aiton)) and Black wattle (*Acacia mearnsii* (De Wild)).

To determine the seasonal variation of the insect assemblages and to track the phenological changes of *C. maculata* and *C. genistoides,* field trials and observations took place on a monthly basis over a 12 month period. Experimental sites were demarcated during February and March 2014, with monitoring taking place between April 2014 and April 2015. Weather data were sourced from the Agricultural Research Council (AgroClimatology Staff 2015).

3.2.2. Honeybush phenology

Phenology observations were conducted with a two-pronged approach, using qualitative methods, as per Pierce (1984). Qualitative observations focused on the general phenology of *C. maculata* and *C. genistoides,* these were made throughout the course of the monitoring period (April 2014 to April 2015). More detailed descriptions of the two species' phenology were made

every second month of the 12 month period, rendering results for six months (mid-winter, July 2014 to autumn, April 2015), to determine the break of bud dormancy and the initiation of the reproductive and fruiting phases. For each of these detailed observations 10 plots, each equivalent to a single bush, were randomly selected within the demarcated sites. The relevant life history phases were recorded and average percentage new growth estimated from the top 10 centimeters of five branches per sample plot. To compare plant phenology between *C. maculata* and *C. genistoides,* only the unharvested honeybush stands near Genadendal (four sites) and Bredasdorp (three sites) were used. In total the phenology of 240 *C. maculata* and 180 *C. genistoides* bushes were recorded over the course of the study. From these observations, a phenology Gantt chart (phenogram) as well as a table detailing the average percentage new growth per bush was compiled, along with the percentage of the plant population currently in each respective growth phase (Pierce 1984). Observations of insect plant damage, including the recently harvested stands of *C. genistoides*, were also included in the study to identify pest risk periods along the phenological timeline of mature and recently harvested *Cyclopia species*.

3.2.3. Arthropod collection and identification

A combination of two sampling methods were used, namely suction sampling, using a leaf blower (Stihl, BG 55 model) with a reversed engine (hereon referred to as d-vac sampling) and sweep netting with an insect net (16 cm radius). Study sites were roughly divided in half with d-vac and sweep net sampling taking place within the respective areas. For both sampling methods ten bushes were sampled per study area with a sampling effort of ten sweeps per bush. Specimens were placed in labeled ziplock bags and stored in a cooler box subsequent to freezer storage. In the laboratory specimens were grouped into orders and identified to family level. To make the high abundance and diversity of arthropods collected more manageable focal taxa groups were selected pertaining to the research question of the current and subsequent data chapters.

Families were classified into functional feeding guilds according to Scholtz and Holm (1985), Hatting (2009), Stevens *et al.* (2007), Prinsloo (1980; 1984), Goulet and Huber (1993) and Guess and Guess (2014). The following functional feeding guild classification was used:

1. Zoophagous: Predators and parasitoids
   (dominated by Hymenoptera and some Coleoptera)
2. Phytophagous: Sap feeders, external (foliage) feeders, internal (stem, root and seed) feeders, other (nectar and pollen feeders)
   (combination of Hemiptera, Coleoptera, Lepidoptera and Hymenoptera)

3. Omnivorous: Diverse feeders of insects and plant material

(dominated by Formicidae (Hymenoptera), and Elateridae (Coleoptera))

4. Other: Fungivores, detritivores and scavengers (not included in analyses as these guilds do not directly impact on biomass production)

Lepidoptera and Coleoptera larvae were classified as either a defoliator, internal or diverse feeder, depending on the specific taxon's feeding characteristics.

Retained specimens were stored in 99% ethanol. A reference collection of relevant specimens are at the entomological museum at the Department of Conservation Ecology and Entomology, Stellenbosch University and the ARC-Plant Protection Research Institute, Roodeplaat.

3.2.4. Data analysis

Accumulation curves were drawn up to determine sampling effort for both d-vac and sweep net sampling to assess family richness. Appropriate curves were drawn using Estimate STM v.8.2.0 software (Colwell, 2006). Accumulation curves were drawn to family level identification with multiple sample-based rarefaction without replacement. Samples were then randomized 24 times; double the sampling effort (Colwell 2006).

Family richness and diversity indices were calculated to family level using PRIMER 6 (PRIMER-E 2008). Calculated estimate richness, evenness and diversity indices were used along with the standard family abundance and richness counts as these provide the opportunity to assess community complexity (DeClerck & Salinas 2011). The following indices were selected to describe family diversity (Heip *et al.* 1998; Hill 2015):

(1)   Estimated family richness (d):

$$d = (S-1)/\log(N)$$

where S is the total number of families and N the total abundance.

(2)   Simpson-inverse (1/D) :

$$1/D = 1/SUM\ p_i^2$$

with $p_{i,}$ as the proportional abundance of a family i in the sample. Evenness indices of 0 - 1, as the index increases toward the value of one, indicates a more even distribution of abundance within families represented in the sample. This measure of diversity is less sensitive to highly uneven species richness.

(3)   Shannon-Weiner diversity index (H'):

$$H' = - p_i \ln p_i$$

with p_i as the proportional abundance of a family i in the sample. An increase in the index indicates an increase of the richness and evenness of a community.

Count data are not generally normally distributed and are therefore often associated with a Poisson distribution. Plots of the raw residuals, however, showed normality for several of the data sets. Repeated measures ANOVAs were used with restricted maximal likelihood (REML) to test for significant differences in the abundance and richness of functional feeding guilds over the three study areas and over months. The sample plots (i.e. the four sample sites at each study area) were nested as random effects within the study areas. Where raw residual plots indicated non-normal distribution a square-root transformation was done on the observations or a bootstrap multiple comparison was done on the original results comparing the means. For the purposes of statistical analysis, sampling periods with missing data (due to harvest events) were omitted from the analysis. The tests for significant differences were followed by post-hoc Least Squares Distance (LSD) comparisons or bootstrap multiple comparisons on the original scores. The same statistical analyses were performed on the estimated richness, evenness and diversity indecies. ANOVA analyses were done in Statistica version 12 (Statsoft Inc. 2012).

3.3. Results

3.3.1. *Cyclopia* spp. phenology

Results indicated a high level of resemblance in seasonality of plant phenology for the duration of the observations made from April 2014 to April 2015 between wild C. *maculata* and cultivated *C. genistoides* (Table 3.1). Similarity is evident in the timing of the phenological cycles of the two honeybush species, with only slight variation in the duration of life history phases or the specific week in which transition between life history phases occurred, for example the transition from flower senescence to fruit set (Table 3.1).

Cyclopia maculata initiated floral budding much earlier (late autumn) than *C. genistoides* (early winter) (Table 3.1). Floral bud development was, however, delayed by several weeks with bud development only evident in June (Figure 3.1 a). Floral buds mature toward the end of winter. *Cyclopia genistoides* was observed to have a more rapid floral bud development, with floral buds first appearing in June and then maturing to pre-anthesis by early September (Table 3.1). The

delay in bud development in *C. maculata* prolongs this life phase doubling the time period in comparison to *C. genistoides.*

Both *C. maculata* and *C. genistoides* start their flowering period in September with a mosaic of bushes in early bloom or late floral budding (Table 3.1). *Cyclopia genistoides* was the first to start flowering (first week in September) and transitioned over into peak bloom over a shorter period of time than *C. maculata.* Despite the time lag for bud development in *C. maculata,* peak flowering period for both species was within the first two weeks of October (Figure 3.1 b and Figure 3.2 b). Both honeybush stands had 70 - 90% of the population in full bloom by the second week of October (Table 3.1 and Table 3.2). Floral senescence and seed set commenced approximately at the same time for both species forming swollen pods of ± 3 cm long from late October to November (Figure 3.1 c and Figure 3.2 c). *Cyclopia maculata* potentially commenced fruiting slightly earlier than *C. genistoides* as 20 - 30 % more of this population was already fruiting (seed set) by the second week of October (Table 3.2). For both honeybush species some seed pods were already ripe by mid-November. Ripening seed pods turn dark brown as the pods dry out (Figure 3.1 d and Figure 3.2 d). Once seed pods have ripened, they split open with a slight 'popping' sound to release the mature seeds within. This action of bursting seed pods aids in seed dispersal. The majority of ripened seed pods had already split open by early/mid-December (Figure 3.1 e).

Excessive leaf shedding is evident for both species, with several bushes becoming completely defoliated before new leaf growth forms a new canopy. The main growth period for *Cyclopia* spp. was during the summer month's post-seed release. New leaf growth was initiated as early as late July for *C. maculata*, followed by *C. genistoides* 4-6 weeks later (Table 3.1). *Cyclopia maculata* had a high level of leaf shedding, becoming evident as leaf buds developed and flowering peaked (Table 3.2). Newly formed leaves dominated the canopy volume soon after floral senescence (November to December). In contrast, *C. genistoides* retained its old leaf canopy for a longer period and only started to show signs of leaf shedding by November. The transition for *C. maculata* from a canopy dominated by old mature leaves to one dominated by new leaf flush overlapped in some cases. By January, *C. genistoides* had a restored leaf canopy of new growth. The average growth rate of new shoots was higher for *C. maculata* than that of *C. genistoides.*

Leaf bud dormancy was broken late winter for *C. maculata* and only in mid-spring for *C. genistoides* (Figure 3.3). Both of these events corresponded to temperature increases or fluctuations during the seasonal transition from winter to spring. New leaf growth was linked to average rainfall (Figure 3.3). For both *C. maculata* and *C. genistoides*, a distinct decrease was

seen in the average percentage new leaf growth per branch by late summer (February). This was followed by a doubling of the amount of new leaf biomass by April 2015.

Table 3.1. *Cyclopia* spp.: phenology and life history phases as observed in the Overberg for wild *C. maculata* and cultivated *C. genistoides* from April 2014 to April 2015.

C. maculata	Apr	May	June	July/Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	April
New growth				Initial leaf buds	Initial new leaf canopy							
Flower bud formation	Initial floral budding		Newly formed floral buds	Developing and mature floral buds	Mature buds							Initial budding
Flowering					Initial bud break	Early (1st wk) - peak (2nd – 3rd wk) bloom. Senescence (3rd - 4th wk)						
Seed set						Initial pod development (3rd/4th wk)	Pod development; mature green pod (2nd wk); pods ripen (2nd -3rd wk)	Ripened seed pods (1st wk)				
Seed release								All pods open by 2nd wk				
Senescence				Mature leaf canopy starts to thin out progressively at a fast rate			Varying % of old leaf canopy remaining					

C. genistoides	Apr	May	June	July/Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	April
New growth						Initial leaf buds	Canopy still dominated by old mature leaves					
Flower bud formation			Initial floral budding	Newly formed floral buds	Mature buds (1st wk)							
Flowering					Early bloom mosaic (1st wk), full bloom (3rd/4th wk)	Peak bloom (1st - 2nd wk), floral senescence (2nd - 3rd wk)						
Seed set						Initial pod development (2nd/3rd wk)	Pod development (1st - 2nd wk); pods ripen (3rd - 4th wk)	Ripened seed pods				
Seed release								All pods popped by 1st/2nd wk				
Senescence							Gradual onset of leaf shedding					

Table 3.2. Average percentage (± SD) / bush / phenology phase and percentage of the overall population within a specific phenology range of two honeybush species (wild *C. maculata* (n=240) and cultivated *C. genistoides* (n=180)). Honeybush species are representative of reseeder and resprouter fire-survival strategies, respectively. Phenology observations were made every second month from July 2014 to April 2015 in the Overberg.

	Phenology phase	Jul/Aug	%	Oct	%	Dec	%	Feb	%	Apr	%
C. maculata	New leaves	4 ± 8	10-30	42 ± 32	10-30	46 ± 19	60-80	33 ± 11	80-90	64 ± 47	70-90
	Mature leaves	99 ± 35	90-100	87 ± 3	90-100	63 ± 13	80-90	59 ± 42	80-90	16 ± 33	0-30
	Leaf shedding			8 ± 13	0-20	67 ± 58	0-10	64 ± 48	80-90	67 ± 50	60-80
	Early budding	38 ± 15	90-100							24 ± 31	20-30
	Mature budding	63 ± 16	90-100	24 ± 35	20-50						
	Late budding			6 ± 7	10-20						
	Initial flowering			3 ± 5	0-20						
	Peak flowering			33 ± 24	70-90	5 ± 10	0-20				
	Flower senescence			43 ± 41	60-80	99 ± 2	90-100				
	Seed set			26 ± 22	50-70						
	Popped seed					100%	100%				
	Dying/dead						0-10		0-20		0-30
	Phenology phase	**Jul/Aug**	**%**	**Oct**	**%**	**Dec**	**%**	**Feb**	**%**	**Apr**	**%**
C. genistoides	New leaves			20 ± 35	0-10	43 ± 4	80-100	18 ± 5	90-100	43 ± 42	80-90
	Mature leaves	100 ± 0	90-100	97 ± 35	90-100	61 ± 7	90-100	84 ± 2	90-100	10 ± 17	0-10
	Leaf shedding					29 ± 6	90-100	25 ± 22	90-100	23 ± 40	20-30
	Early budding	92 ± 7	90-100	12 ± 8	0-10						
	Mature budding			40 ± 49	10-30						
	Late budding			2 ± 3	0-10						
	Initial flowering			12 ± 13	0-10						
	Peak flowering			63 ± 16	70-90	11 ± 13	20-40				
	Flower senescence			32 ± 17	70-90	96 ± 5	90-100				
	Seed set			32 ± 28	30-40						
	Popped seed					100%	100%				
	Dying/dead						0				

Figure 3.1. Phenology of *C. maculata* (2 – 3 m x 1.5 – 3 m): The reproductive phases of (a) floral budding (June-August), (b) peak bloom (October), (c) fruiting and (d) pod ripening (November), (e) seed release, and growth phases of (f) leaf shedding and new growth starting with a (g) summer flush.

44

Figure 3.2. Phenology of *C. genistoides* (1 - 1.5 m x ± 1 m): The reproductive phases of (a) floral budding (June-August), (b) peak bloom (October), (c) fruiting and (d) pod ripening (November) and growth phases of (e) leaf shedding and new growth starting with a (f) summer flush.

45
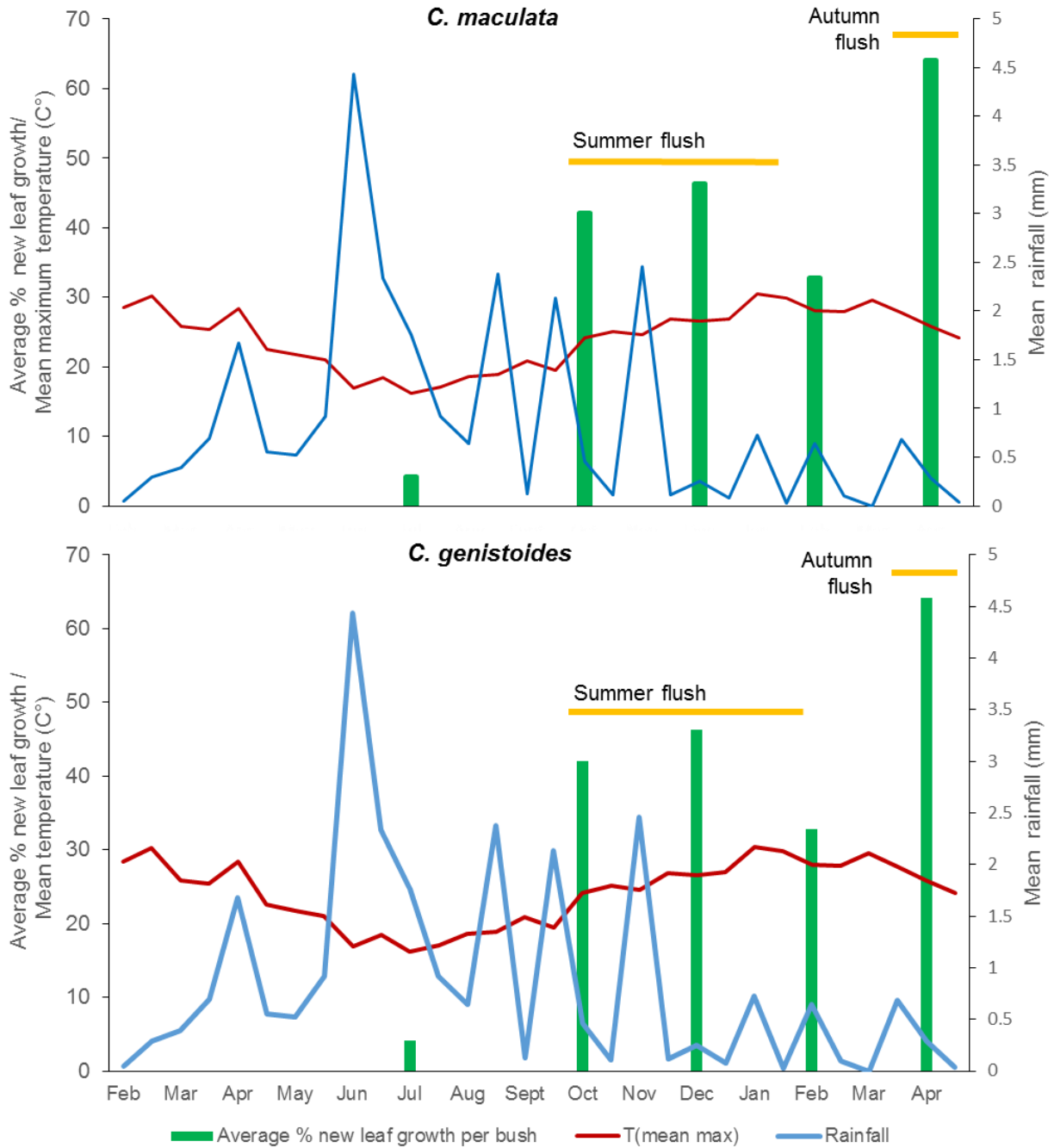
Figure 3.3. Average percentage new leaf growth (primary vertical axis) for *C. maculata* (top) and *C. genistoides* (below) with mean maximum temperature (C°) and mean weekly rainfall (mm) for the respective study areas. Mean maximum temperature ($T_{mean\ max}$) and rainfall are given on a bi-monthly basis. Phenological observations were made every two months from late July 2014 to April 2015.

3.3.2. Arthropods associated with *Cyclopia* spp. and their seasonality

Sampling effort

During the course of this study 21 538 specimens were collected by d-vac and sweep netting sampling, these included approximately 130 insect families. Focal group orders included in the analyses were selected due to their relevance to honeybush biomass production. These included Coleoptera (beetles), Hemiptera (leafhoppers and aphids), Thysanoptera (thrips), Lepidoptera (moths and butterflies) and Hymenoptera (predatory and parasitoid wasps, and ants). Family level species accumulation curves compiled per study area indicated that sampling effort for the mature stand of *C. maculata* and the recently harvested *C. genistoides* to be more representative of family richness than the mature stand of *C. genistoides* (Figure 3.4). The curve of the mature stand of *C. genistoides* is less asymptotic by 12 sampling periods than the other two study areas. The mature stand of *C. genistoides* appears to have the highest overall estimated family richness.
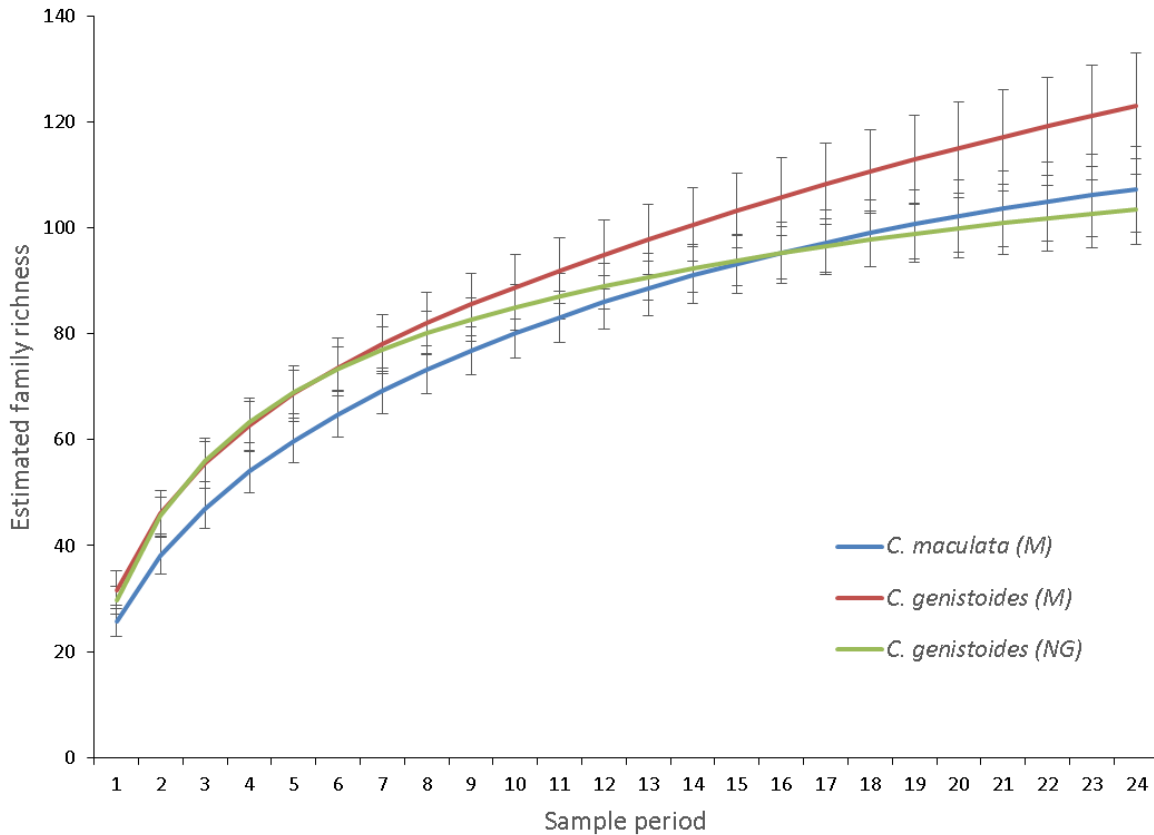
Figure 3.4 Accumulation curves (±SD) per study area for arthropods associated with *C. maculata* and *C. genistoides*; two sites comprised of mature (M) honeybush while the other consisted of new growth (NG).

Arthropod abundance and insect family diversity

Arthropod monitoring throughout the study revealed a diverse and abundant arthropod community associated with the *Cyclopia* species. Based on the diversity and richness indices, the mature stands of *C. maculata* and *C. genistoides* had high similarity in the recorded insect assemblages with regard to insect abundance (N), family richness (S), estimated richness (d), diversity (H') and evenness (1/D) (

Table 3.3). The recently harvested *C. genistoides* study area was significantly higher for all three calculated indices, namely estimated family richness ($F_{(2,9)}$= 11.013, p<0.01), family evenness ($F_{(2,9)}$=8.732, p<0.01) and diversity ($F_{(2,9)}$= 18.588, p<0.001).

Table 3.3. Descriptive statistics of the insect assemblage associated with *Cyclopia* species by d-vac samples collected from April 2014 to January 2015. Calculated mean abundance (N), richness count (S), estimated richness (d), diversity (H') and evenness (1/D) (±SE). Two study areas had mature (M) bushes of *C. maculata* and *C. genistoides*, respectively; the third study area consisted of *C. genistoides* recently harvested and in its new growth phase (NG).

Index	*C. maculata* (M)		*C. genestoides* (M)		*C. genestoides* (NG)		$F_{(2,9)}$	Sig
Mean abundance (N)	111.97 ± 19.43	a	90.81 ± 19.43	a	69.31 ± 19.31	a	1.206	NS
Family richness (S)	18.67 ± 2.43	a	19.47 ± 2.43	a	24.78 ± 2.43	a	1.872	NS
Estimated richness (d)	2.43 ± 0.21	a	2.82 ± 0.21	a	3.78 ± 0.21	b	11.013	**
Evenness (1/D)	0.70 ± 0.03	a	0.71 ± 0.03	a	0.83 ± 0.03	b	8.732	**
Diversity (H')	1.60 ± 0.08	a	1.73 ± 0.08	a	2.28 ± 0.08	b	18.588	***

Means within rows followed by different letters indicate significant differences (REML, LSD post hoc, confirmed with bootstrapping where necessary); * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Seasonality of arthropod assemblage

High seasonal variability for both *C. maculata* and *C. genistoides* was found within and between monthly sampling for family richness (S), abundance and evenness (1/D). To simplify the graphs, 95% confidence intervals have been omitted from most of the graphs, except for the first bar graph (Figure 3.5) depicting mean family abundance. Here the full sample set from April 2014 to April 2015 is illustrated with standard deviation to serve as a representation of the high variability found within sampling periods. Statistical analysis for d-vac sampling only are presented as the sweep net data set was not as comprehensive due to windy conditions or the inability to use sweep netting due to the shrubs' post-harvest regrowth being too short; the majority of these results showed non-significant differences.

Insect abundance peaked during the flowering period for the mature stand of wild *C. maculata* and cultivated *C. genistoides* (Figure 3.5). The peak in insect abundance occurred in October, with a gradual increase from September onwards.
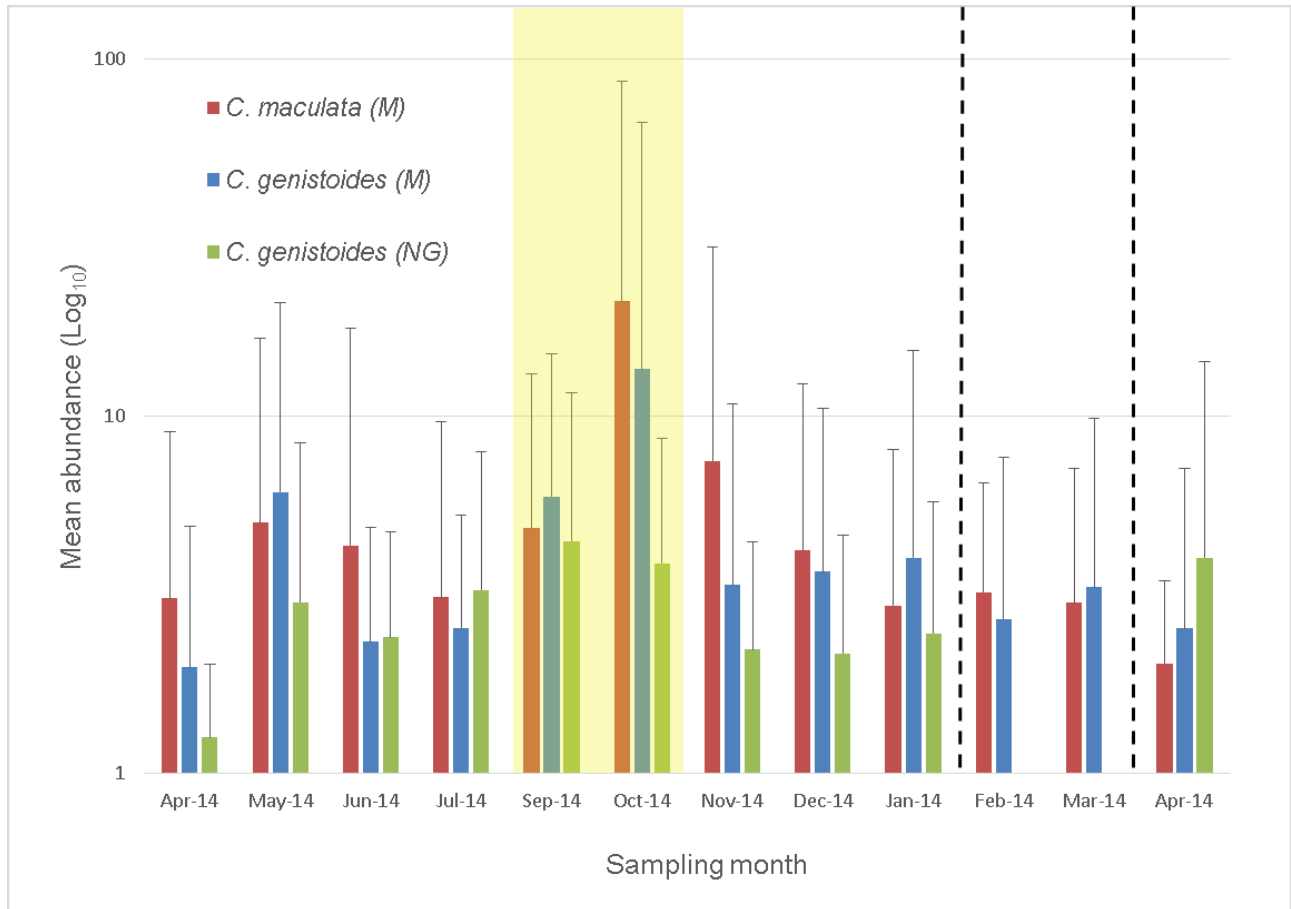
Figure 3.5. Mean arthropod abundance (± SD) for mature bushes of wild *C. maculata* (M) and cultivated *C. genistoides* (M) and the new growth stand of *C. genistoides* (NG) which was harvested prior to arthropod monitoring by d-vac sampling from April 2014 to April 2015. The yellow vertical band indicates the flowering period for the mature *Cyclopia* stands. Harvesting, indicated by the dotted lines, took place again the following January for *C. genistoides* (NG) and in March for *C. genistoides* (M).
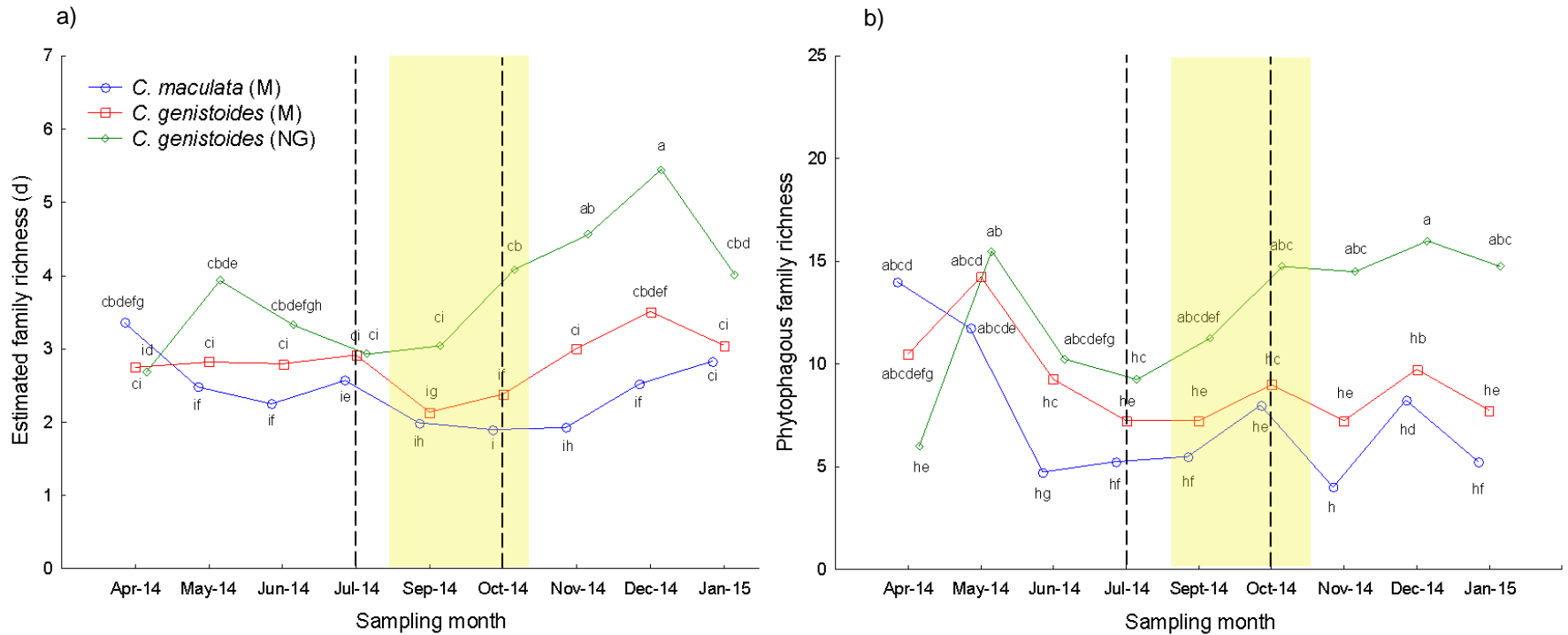
Figure 3.6 (a) Estimated family richness and (b) phytophagous family richness of the arthropod assemblage associated with *Cyclopia* spp. by d-vac sampling from April 2014 to January 2015. Two of the study areas were dominated by mature wild *C. maculata* (M) and cultivated *C. genistoides* (M); the third study area of cultivated *C. genistoides* (NG) was harvested shortly before arthropod monitoring commenced. Different alphabetical letters indicating significant differences within and across months (REML, LSD post hoc). To simplify graph interpretation, 95% confidence intervals have been omitted. The dashed lines indicate the initial leaf budding for *C. maculata* (Jul/Aug) and *C. genistoides* (Oct), respectively. Fruiting is initiated in October for both species after the flowering period (yellow band) in September to October.

Overall family richness (S) ($F_{(8,72)}$= 2.262, $p<0.05$) of invertebrates across the study areas was significantly different across the sampling period. Family abundance (N) ($F_{(8,72)}$= 1.097, $p>0.05$) was not significantly different across the three study areas. Estimated family richness showed a similar trend across the three study areas ($F_{(16,72)}$= 1.243, $p>0.05$) (Figure 3.6 a). The mature *C. maculata* and *C. genistoides* stands generally had lower estimated family richness than that of the recently harvested *C. genistoides* stand (Figure 3.6). The zoophagous arthropod abundance ($F_{(16,72)}$= 1.590, $p>0.05$) and family richness ($F_{(16,72)}$= 1.316, $p>0.05$) was not significantly different between the three honeybush stands (Table 3.4., Appendix A, Figure A.1 a & b). Overall phytophagous family richness was significantly higher for the recently harvested *C. genistoides* ($F_{(2,9)}$= 9.807, $p<0.01$) study area in comparison to the mature stands of *C. maculata* and *C. genistoides*, respectively. Phytophagous arthropod abundance peaked during the flowering period for the mature stands of *Cyclopia*, but overall the three study areas were not significantly different ($F_{(16,72)}$= 1.423, $p>0.156$) from each other when comparing the combined means per months across the three study areas (Table 3.4., Appendix A, Figure A.2). Abundance and family richness of omnivorous arthropods was similar for all three study areas ($F_{(16,72)}$= 1.033, $p>0.05$ and $F_{(16,72)}$= 0.560, $p>0.05$).

Table 3.4. Combined mean family abundance and richness for zoophagous and phytophagous innesct collected on *Cyclopia* spp. across three study areas.

Functional feeding guild	$F_{(16,72)}$	Sig
Zoophagous abundance (N)	1.5895	NS
Zoophagous richness (S)	1.3156	NS
Phytophagous abundance (N)	1.4233	NS
Phytophagous richness (S)	9.807	**

Phytophagous insect families that were especially abundant during the sampling period from April 2014 to April 2015 included several species of sap feeders (Hemiptera: Aphididae, *Cicadellidae; Thysanoptera: Thripidae); external foliage and seed feeders (Coleoptera: *Buprestidae, Bruchidae, Chrysomelidae, *Curculionidae; Lepidoptera: Ctenuchidae, *Geometridae, *Lasiocampidae, *Noctuidae, *Pyralidae and Tortricidae); internal feeders (Coleoptera:

52

Apionidae, *Tenebrionidae); as well as diverse feeders (Coleoptera: Elateridae and Hymenoptera: Formicidae). Those marked with an asterix (*) are known pests on rooibos (Hatting 2009). Abundant predators included Coccinellidae, Anthicidae, and a diversity of spiders and predatory mites (personal observation - these did not form part of the statistical analysis as they were only identified to order level). A diversity of Hymenoptera were also part of the arthropod assemblage including both predator and parasitoid families, as well as Apoidae (personal observation - similarly these were only identified to order level and thus not included in statistical analysis).

Family evenness sampled from April 2014 to January 2015 was not significantly different among the three study areas ($F_{(16,71)}$= 1.192, p>0.05) (Figure 3.7). In October 2014 the family evenness is significantly lower (p<0.01) at the mature stand of *C. genistoides* than the recently harvested *C. genistoides* stand. Likewise, the mature stand of *C. genistoides* was also lower than the other two honeybush stands, albeit not significantly (p>0.05) so (Figure 3.7).
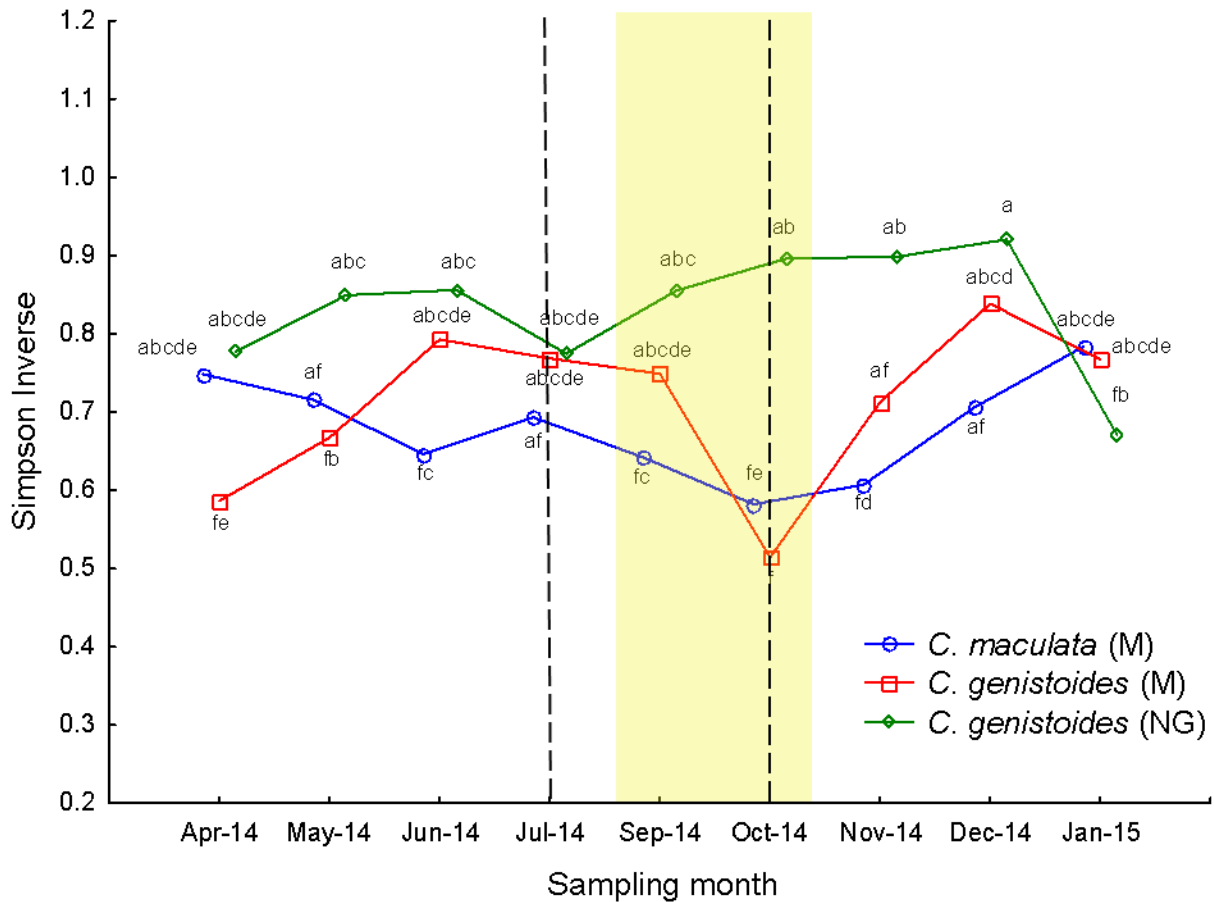
Figure 3.7. Family evenness across the sampling months for mature (M) and recently harvested (new growth: NG) *C. maculata* and *C. genistoides* for d-vac sampling from April 2014 to January 2015. Mean overall family evenness across study areas was not significantly different ($F_{(16,71)}$= 1.085, p>0.05); 95% confidence intervals have been omitted to simplify graph interpretation (different alphabetical letters indicate significant differences within and across months). The dashed lines indicate the initial leaf budding for *C. maculata* (Jul/Aug) and *C. genistoides* (Oct), respectively. Fruiting is initiated in October for both species after the flowering period (yellow band) in September to October.

3.4. Discussion

3.4.1. Honeybush phenology

The high resemblance of the two *Cyclopia* species, despite their different growth forms and fire-survival strategies, suggests some level of internal/endogenous cue for phenology transition. The potential of inherent cues in flowering events were first recorded in the 1980's where transplanted *Protea* species maintained their natural flowering period despite being removed from their accustomed climatic conditions (Vogts 1982 in Pierce 1984). Similarity in plant phenology could also be in accordance with the weather conditions observed at both study areas, where rainfall and temperature showed similar trends. Further in depth phenology studies are needed to determine the causal relationships between phenological phases, internal cues and climatic conditions for the *Cyclopia* genus. It would be especially helpful if co-occurring *Cyclopia* spp. of the same known age could be compared over time.

Differences in the growth habit and the slight variation in phenology turn-over between the two *Cyclopia* species could be ascribed to the distinctly different fire-survival strategies. *Cyclopia maculata* was observed to be relatively short-lived in comparison to *C. genistoides*, with a portion of the much younger *C. maculata* population dying off towards the end of the field trials. The *C. maculata* stand was less than five years old in comparison with the older 12+ year old *C. genistoides* plantation. Differences in plant longevity are also evident among other plant families with distinct fire-survival strategies (Allen 2008), for example Ericaceae and Bruniaceae (Mustart 2000). Current literature further suggests that the rate of development differs among and between fire survival strategies (Wardell-Johnson 2000, Pierce 1984). Longer-lived species such as resprouters generally have a slower rate of development (Wardell-Johnson 2000). Wardell-Johnson (2000) found this to be even more prominent for resprouters with subterranean storage organs, such as *C. genistoides*. The earlier onset and a higher rate of development for *C. maculata* could be due to the species' reseeding survival strategy (Wardell-Johnson 2000).

Overlap is seen in the various phenophases of both *Cyclopia* species. The resource limitations, such as low nutrient soils, have been coupled to several Fynbos species having synchronized or overlapping growth and flowering stages (Pierce, 1984). Adaptation to nutrient-poor soils, allowing for synchronised phenophases, however, does not necessarily suggest a resource limitation hindrance (Pierce 1984), but rather an adaptation to optimally utilize the limited resources available (Pilar & Gabriel 1998). Habitat preferences of *C. maculata* (Chapter 2, Table 2.1) suggest that it is well adapted to wetter conditions and seasonally waterlogged soils. Water resources are thus more readily available and explain the overlap of several high energy

demanding phenophases (Pilar & Gabriel 1998). *Cyclopia genistoides* has more compact reproductive stages suggesting adaptation to drier habitat conditions (Aronson *et al.* 1992). Synchrony and overlap of growth and flowering has also been recorded for several of the *Protea* and *Leucadendron* species, e.g. *Protea neriifolia* and *Leucadendron cuneiform*, among others (Le Maitre, pers. comm 1982 as referenced by Pierce 1984).

The overlap in flowering period for *C. maculata* and *C. genistoides* suggests that these two species could potentially hybridize within mixed cultivated stands (Mallet 2008; Rieseberg 1997; Rieseberg & Carney 1998). The cladistics analysis by Schutte (1997), based on morphology, suggested that *C. maculata* and *C. genistoides* are distant relatives, but more recent phylogenetic analysis revealed that most *Cyclopia* species are closely related (Boatwright *et al.* 2008). This suggests that morphology rather than phylogenetic relatedness are likely to have been the drivers of speciation. Several *Cyclopia* species, including *C. maculata* and *C. genistoides*, are currently being considered for cultivation (Joubert *et al.* 2011) which increases the potential risk of infield interspecific hybridization (Mallet 2008). Even though the genus is thought to have the same insect pollinators (presumably by Carpenter bees, Anthophoridae) every pollen transfer does not necessarily translate to a successful pollination event. Indeed, populations of these two species naturally occur in close enough proximity for cross-pollination to have been possible (considering dispersal limitations of the pollinator), yet no known viable hybrids have been recorded in the wild. Based on the known habitat preferences of these species (Joubert *et al.* 2011) it can be speculated that they are separated due to ecological speciation. Earlier *in vitro* studies (e.g. Bester & De Lange 2010) with various *Cyclopia* species suggest that there is a strong selection against hybrid formation (less than 2%: De Lange & Von Mollendorf, 2006). Nonetheless, should infield interspecific hybridization take place (across wild and cultivated populations) substantial losses to genetic diversity may occur (Laikre *et al.* 2010; Seehausen *et al.* 2008). Implications for potential hybridization of commercial honeybush species should be considered prior to cultivation beyond their natural range. Should hybridization occur between wild and cultivated species consequences would extend to jeopardizing the persistence of wild populations used for local livelihood purposes.

Patterns in new leaf growth suggests two main active leaf growth periods, namely a summer and autumn growth flush. These observations support the overall growth patterns of a summer and autumn growth flush as noted in studies by Pierce (1984) during the Fynbos Biome Project. The unique climatic conditions in the Cape (Esler *et al.* 2014) are potentially the cause for this deviation from the general trend observed in similar vegetation types (Cody & Mooney 1978). Bond (1980)

similarly found *Protea* species with a summer growth regimen to be more adapted to a summer rainfall or non-seasonal rainfall region. The Overberg is one such region with non-seasonal rainfall (Esler *et al.* 2014) and current phenology observations suggest that *C. maculata* and *C. genistoides* (whether wild or cultivated) are similarly adapted to these biophysical conditions.

3.4.2. Honeybush arthropod ecology

Insect phenology is determined by a complex relationship between internal life-history cues and external environmental factors (Danks 1994; Forrest & James 2011). Temperature and resource availability are critical factors in determining both insect and plant phenology (Ascerno 1991; Forrest & James 2011; Gilbert & Raworth 1996; Willmer & Stone 2004). As winter draws to an end and temperatures rise, both *Cyclopia* phenology and insect activity transitioned from a period of winter dormancy toward an active state of development in which growth took place. Insect emergence from a winter diapause correspond with an increase in temperature (Danks 1994; Forrest & James 2011; Snodgrass *et al.* 2012; Son 1999) and available food resources (Snodgrass *et al.* 2012; Willmer & Stone 2004). Insect activity, in terms of foraging and oviposition, are regulated by favorable temperature increases (Sivertsen *et al.* 1999) and the availability of food resources. As anticipated, *Cyclopia* phenology, such as active growth, was also found to be synchronized to increasing temperature (Ascerno 1991; Atkinson & Porter 1996), and could thus serve as an indicator of insect emergence (Ascerno 1991; Forrest & James 2011; Snodgrass *et al.* 2012). Insect infestation generally increase during susceptible crop growth stages (i.e. new leaf growth) and is accentuated by higher temperatures (Sivertsen *et al.* 1999). The summer and autumn growth flush phases are thus potential pest risk periods. Fruiting (Seed set), from October to November, is another pest risk period were by seed pods can become heavily infestation by various taxa, for example weevils and apionids.   With seasonal resource needs of insects as well as the suitability of the immediate surrounding habitat certain insect taxa could become problematic on cultivated *Cyclopia,* especially during new leaf growth or under stress conditions (e.g. drought) (Wilby & Thomas 2002; Kennedy & Storer 2000).

3.4.3. Arthropod richness and evenness

Arthropod richness and evenness was lower during the flowering period when the system was flooded by flower visiting insects, consisting predominatly of Coleopterans (Chrysomelidae and Scarabaeidae). The decrease in family evenness was more pronounced for the mature stand of cultivated *C. genistoides* due to the much larger area covered by flowering shrubs. The other flowering stand of *C. maculata* revealed less fluctuation in family evenness as the wild stands cover a smaller area and are not as densely populated as the cultivated field of *C. genestoides*.

The significantly higher family richness of phytophagous insects at the recently harvested *C. genistoides* study area suggests that new growth is targeted by herbivorous insects which could potentially negatively affect plant health (disease transmission) and decrease growth vigour (Collinge & Louda 1989; Sivertsen *et al.* 1999). Additional variability of weather conditions, such as temperature, could further increase risk of crop infestation during susceptible stages of new growth (Sivertsen *et al.* 1999). Several of the most abundant phytophagous insect families associated with *Cyclopia* could potentially become agricultural pests of cultivated honeybush considering the pest status that several of these families have within the rooibos industry (Annecke & Moran 1982, Hatting 2009, Hatting 2015, Rust & Myburgh 1989). Potential pests and biological control will be discussed in more detail in subsequent thesis chapters.

3.4.4. Conclusion and recommendations

When making decisions regarding when and how often to harvest *Cyclopia* species or how to manage crop production in the context of integrated pest management, ecological factors such as fire-survival strategies and phenology of the host crop are important to consider. *Cyclopia maculata* as a non-resprouter is less likely to respond favourably to excessive harvesting or insect damage, or any other disturbance, while *C. genistoides*, as a resprouter, is adapted to regrow after disturbance that results in the loss of its foliage biomass. This adaptation makes *C. genistoides* more suited for regular harvesting, and likely more resistant to insect pest damage, bearing in mind that plants require sufficient time to replenish their rootstock reserves after harvest. Regular annual harvesting is thus potentially not ideal for maintaining longevity, optimizing on biomass production and maintaining plant resilience against disease and insect pests. Management options and implications are discussed in more detail in subsequent thesis chapters.

Early monitoring of insect populations within plantations is recommended (Ascerno 1991), especially in view of the potential pests noted by land users and the increase in phytophagous richness at the one cultivated stand of *C. genistoides*. The abundance of several natural enemies suggests the potential value of arthropod-mediated pest control as an ecosystem service available within cultivated *Cyclopia*. A better understanding of potential pests along with long term records of insect emergence, coupled with plant phenology and weather data, can serve as a valuable database enabling future predictions regarding potential pest outbreaks. These can then guide decisions regarding integrated pest management strategies to prevent excessive damage to and loss of biomass production and promote sustainable cultivation practices.

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CHAPTER 4.

POTENTIAL ARTHROPOD-MEDIATED ECOSYSTEM SERVICES ASSOCIATED WITH *CYCLOPIA* SPECIES

4.1. Introduction

Ecosystem services and disservices are the positive benefits and detriments mankind derives from ecological systems and the components that they consist of (Kremen 2005; Millennium Ecosystem Assessment (MEA) 2003) (see Chapter 1 for more detail on ESS). The drastic global decline of biodiversity on multiple levels has a cascading effect on ecosystem functioning and associated ecosystem services (ESS) on a global and local scale (Naeem *et al.* 1999). Within agricultural landscapes numerous important ESS are mediated by arthropods (Aliniazee & Croft 1999; Altieri & Letourneau 1982; MEA 2003). Arthropod-mediated ecosystem services (AMES), such as pollination and pest control, are important ESS for agricultural productivity (Altieri & Nicholls 1999; Aliniazee & Croft 1999; Isaacs *et al.* 2009). Ecosystem services by natural enemies within agricultural landscapes in the United States, for example, were valued at $7.32 billion per annum; 33% of this contribution was ascribed to insect-mediated pest control (Losey & Vaughan 2006).

The potential role and value of AMES associated with South African crops has not been researched extensively. Even less is known regarding AMES associated with indigenous crops, such as rooibos (*Aspalathus linearis*) and honeybush (*Cyclopia* species). The honeybush industry, still being at its initial stages of cultivation, has the potential to incorporate effective land management practices into its commercialization process, and so promote sustained natural biological control within cultivated stands as best practice. Current literature on the ecology of *Cyclopi*a species is very limited, with the main reference to arthropods being an unpublished insect survey done by Knipe and Rosenberg (2008). From this survey several potential pest species were noted. Since then no further research has been done regarding the ecological interactions and potential AMES associated with *Cyclopia*. Rooibos, the industry perhaps most

comparable to honeybush, has been the focus of a larger body of research over a longer period of time. Considering the pest challenges the rooibos industry is facing (Erasmus 2013; Hatting *et al.* 2011) it is worth considering the potential pest risks that could arise through the commercialization of honeybush as a similar indigenous crop.

Agricultural landscapes are well documented to be subject to pest and disease outbreaks as plant diversity is lost within agricultural landscapes (Elmqvist & Maltby 2010; Schellhorn & Silberbauer 2002; Roossinck & García-Arenal 2015). Pest emergence is closely linked to the loss of functional species richness of natural enemies (Long & Finke 2014) within agricultural landscapes and the life-history traits (e.g. endopterogote verses exopterogote, see Box 1) of potential pests (Wilby & Thomas 2007). Species are usually first lost from the higher trophic levels, thus causing a cascading effect on the population dynamics of the lower trophic levels (Chaplin-Kramer et al. 2011; Estes et al. 2011). By implication, the likely effect of decreased predation pressure on potential pest emergence within cultivated *Cyclopia* stands would be determined by the life history of the phytophagous species associated with honeybush (Wilby & Thomas 2002; Wilby & Thomas 2007). The risk of pest emergence is also determined by the land management approach used (Kremen & Miles 2012; Tscharntke *et al.* 2005).

Box 4.1. Insect-life history traits and natural enemy complexes

Winged insect taxa can be grouped according to their developmental traits as either being Endopterygota (with internal wing bud development) or Exopteryogta (with external wing bud development). These two development characteristics correspond with distinct life-history traits. The life stages of endopterygotes are distinctly different based on morphology and behavior, and occupy different resource niches within a landscape. Exopterogotes, however, are similar in morphological and feeding behavior and thus utilize the same resource niche across their life-cycle. These life-history traits (among others), and other characteristics, determine the nature of the predation pressure of a specific insect group. Endopterygotes are subject to attack by specific natural enemies for each distinct life stage, whereas natural enemies of exopterygotes feed across nymph and adult stages. Theoretically species loss of natural enemies for endopterygotes results in a gradual decline in population regulation; whereas exopterogotes remain consistent until a tipping point is reached (i.e. the last natural enemy is lost) resulting in drastic population increases.

(as summarized from Wilby & Thomas (2002) and Wilby & Thomas (2007))

Population size of phytophagous arthropods is regulated by natural enemies (including arthropod predators and parasitoids, as well as insect diseaese and entomopathogens) within agroecosystems on both a field and landscape scale. Natural enemy complexes are composed of a diversity of predators and parasitoids of various taxa and functional feeding guilds (Hagler & Blackmer 2013; Wilby & Thomas 2007). Several insect taxa are considered effective biological control agents in agricultural landscapes, such as Carabidae (ground beetles), Coccinellidae (lady beetles), Syrphidae (predatory flies) and several predatory and parasitoid wasps (Hymenoptera) (Aliniazee & Croft 1999; Henri *et al.* 2015; Long & Finke 2014; Stevens *et al.* 2007). A few species within a natural enemy complex fulfill the key role in the natural biological control ESS (Larsen *et al.* 2005). It is, however, the collection of the natural enemy complex, rather than the individual species, that holistically maintains pest populations at adequate levels (Naeem 1998; Tscharntke *et al.* 2005).

Natural predators and parasitoids already present in landscapes where agricultural activities take place can serve as effective natural biological control agents (Aliniazee & Croft 1999; Henri *et al.* 2015). The presence and survival of these species in those agricultural landscapes is dependent on the diversity of non-crop vegetation within and adjacent to cultivated fields (Henri *et al.* 2015; Isaacs *et al.* 2009; Nicholls *et al.* 2001). Natural habitat adjacent to agricultural land serves as a reservoir for populations of natural enemies, and also provide these beneficial arthropods with essential supplementary resources, including, among others, alternative food resources and/or prey, and more favourable habitats for shelter and completion of their life cycle (Holzschuh *et al.* 2010; Isaacs *et al.* 2009; Landis *et al.* 2000). Native plants and cover crops within agricultural landscapes also promote connectivity between natural vegetation and cultivated fields, promoting foraging activities of beneficial arthropods within productive landscapes (Altieri & Letourneau 1982; Isaacs *et al.* 2009).

In order to identify the potential AMES available to a honeybush farmer the composition and ecological interaction of the arthropods associated with *Cyclopia* species needs to be better understood. The aim of the current study was to identify potential arthropod-mediated ecosystem services and disservices associated with *Cyclopia* species and the role of natural vegetation in maintaining the beneficial role of ESS such as natural biological control. This entailed identifying potential pest insect families (and specific species where possible), along with the natural enemy complex associated with *Cyclopia* insects. Focal insect taxa for the potential pest complex associated with *Cyclopia* spp. included Lepidoptera and Coleoptera, as these orders contain known agricultural pests for rooibos (Hatting 2009, Hatting 2015). For the natural enemy complex

the composition of the predatory and parasitoid wasps and predatory beetles were investigated within and across honeybush stands. Preliminary work was also done to determine direct parasitoid-host links. For a habitat comparison the composition of the Lepidoptera and predator and parasitoid wasps was compared between the honeybush stands (both wild and cultivated) and the adjacent Fynbos habitat. The change in family abundance and richness of the insect assemblage was also considered at increasing distances from the Fynbos vegetation. A better understanding of these ecological components and subsequent interactions associated with *Cyclopia* species will aid and inform decision-making processes regarding suitable land management practices and Integrated Pest Management strategies for the honeybush industry.

4.2. Material and methods

4.2.1. Study sites

Three study areas were identified in the Overberg region for long-term monitoring of the insect assemblages associated with *Cyclopia* species. They comprised sets of naturally occurring and commercially cultivated stands. Study areas were in the vicinity of Genadendal, Bredarsdorp and Pearly Beach (see detailed site descriptions in Chapter 2, Table 1 and Figure 2.3). At each of the three study areas, four sites were selected for long-term insect monitoring. Each site consisted of an internal honeybush section paired with an external section in the adjacent Fynbos. The Fynbos section served as the experimental control and allowed for a habitat comparison.

The external sampling points in the Fynbos vegetation were placed approximately 10 to 15 m from the periphery of the honeybush stands to avoid edge effects at the margins of Honeybush habitats or fields. Placement of external sampling stations were determined by the presence of alien invasive stands or cultivation near the *C. maculata* stands and by the proximity of Fynbos vegetation along the cultivated stands of *C. genistoides*. Sampling stations at the cultivated stands of Honeybush were roughly positioned in a grid layout at least 10 to 15 m from the field edge as determined by the occurance of roads or other regions of disturbance along the edge of cultivated areas. *Cyclopia maculata* sampling stations were placed within the immediate vicinity of the natural population, 10 m from the honeybush stands. Sites could not be placed further due to a change in land use (e.g. apple orchards) or presence of dense stands of invasive trees (E.g. Port Jackson (*Acacia saligna* (Labill) Wendl), Pine (*Pinus pinaster* (Aiton)) and Black wattle (*Acacia mearnsii*) (De Wild)).

4.2.2. Insect monitoring

Insect monitoring was done monthly over a period of a year from April 2014 to April 2015. To ensure an accurate representation of insect diversity and relative abundance various sampling methods were used to monitor insects within the honeybush and adjacent Fynbos habitat. These included suction sampling using a leaf blower (Stihl, BG 55 model) with a reversed engine (hereon referred to as d-vac sampling) pan trap sampling with three coloured dishes (yellow, blue and white, surface area ± 170 cm^2) containing soapy water and yellow delta traps baited with sticky pads and pear leaf roller (*Epichoristodes acerbella*) pheromone (all Chempac, (Pty) Ltd., Paarl RSA). Pear leaf roller pheromone was selected as Tortricid larva had been observed feeding on *Cyclopia* species during trial period field visits. Delta traps were mounted on a 1.2 m rod in the center of the honeybush and Fynbos sections of each sampling site. Pan traps were placed at the base of the delta traps for 6-7 hours during each subsequent sampling period. Additional *ad hoc* delta traps were also placed an additional ± 25-30 m into the center of the cultivated plantations of *C. genistoides* from July 2014 to April 2015. D-vac suction sampling was conducted on ten bushes, equivalent to a sampling unit, per study site with a sampling effort of ten suctions per sampling unit (Perner 2003; Schoenly *et al.* 2003). Collected specimens were transferred into labeled ziplock bags and stored in a cooler box prior to freezer storage.

To determine direct parasitoid-host links larvae, plant galls and shoot damage optentailly caused by insect were collected on *Cyclopia* spp., samples were collected on an *ad hoc* basis and brought to the laboratory for attempted parasitoid rearing.

4.2.3. Sorting and identification of insect specimens

Only certain orders were selected as focal points pertaining to the research question to simplify the high abundance and diversity of insects collected during the course of the sampling period. These included Coleoptera, Hemiptera, Thysanoptera, Lepidoptera and Hymenoptera (predatory and parasitoid wasps, and ants). Relevant specimens were sorted and identified to family and morphospecies where applicable. Non-focal taxa were only noted to order level. A reference collection of morphospecies was compiled for cross-referencing between sites and sampling periods. Identification keys and resources used for taxon identification included: Picker *et al.* (2004), Scholtz and Holm (1985), Prinsloo (1980; 1984), Goulet and Huber (1993) and assistance and use of reference collections at Iimbovane, Centre for Invasion Biology (De Morney pers. com) and the Department of Conservation Ecology and Entomology (Geertsema and Gaigher pers. com), both based at Stellenbosch University. Abundant insect taxa that were considered potential pest or key natural enemies were further processed to morphospecies level for five of the

sampling periods (altering monthly from April 2014) and then sent for species identification to relevant experts. These insects include taxa from the following orders: Hemiptera Sternorryncha, Thysanoptera (Thripidae), Coleoptera (Curculionidae, Apioidae and Elateridae), Lepidoptera (Pyralidae and Tortricidae) and Hymenoptera (several parasitoid wasps). Potential pests were identified to species level by the Plant Protection Research Institutes' Biosystematics division of the Agricultural Research Council (ARC) at Roodeplaat, Pretoria. Specimens that were retained were stored in 99% ethanol or pinned as part of a reference collection at the Department of Conservation Ecology and Entomology at Stellenbosch University.

Families and morphospecies were classified into functional feeding guilds as outlined in Chapter 3, section 3.2.3. Functional guild classification was used to assess the relative predator-prey composition of the arthropod assemblages (Thies *et al*. 2011; Tscharntke *et al*. 2012). The functional feeding guilds included four functional groups each with their respective feeding guilds. Taxa were classified as zoophagous (Predators and parasitoids), phytophagous (Sap feeders, external (foliage) feeders, internal (stem, root and seed) feeders, omnivorous (Diverse feeders of insects and plant material) and other feeders (e.g. fungivores, detritivores and scavengers). All taxa classified as 'other' feeders were not included in analyses as these guilds do not directly impact on biomass production.

4.2.4. Plant damage observations

Observations of insect plant damage were recorded on a two month basis from May 2014 to April 2015, resulting in percentage infestation records for the period of six months. Insect damage, similar to those observed on rooibos (*Aspalathus linearis*) (Hatting 2009) and other crops (Visser 2009), was recorded on a presence absence basis. Damage symptoms included evidence of sap feeders including leafhopper (Hemipetra: Cicalellidae) and thrips (Thysanoptera: Thripidae) spots, as well as galls and shoot damage caused by internal feeding of apionids (Coleoptera: Apionidae), as reared from collected samples. Plant damage observations were made on ten randomly selected bushes selected per site; for each bush the top ten centimeters of five branches were assessed for evidence of insect damage. From these observations the relative percentage infestation was determined per site for each season.

4.2.5. Data analyses

The pan and delta trap sampling were used for a habitat comparison between the honeybush and Fynbos vegetation. D-vac suction data were used for comparison of the functional composition of the insect assemblage (phytophagous and zoophagous guilds) collected within the honeybush

stands. Only orders identified to family or morphospecies level were included in analysis where applicable.

Overview of the insect assemblage and the impact of environmental variables

A summary of the functional composition of the insect assemblage was compiled as a cummulative graph in excel. The impact of enviroenemntal varaibles on the abundance and richness of insects within honeybush stands was assessed with the use of generalized linear mixed-effect models (GLMM). GLMMs were done in R (R Core Team 2015) using 'glmer' in the lme4 package (Crawley 2007).

Environemntal variables, noted as categorical variables, included the level of disturbance at the study areas and the weather conditions (temperature, cloud cover and wind condition) per sampling period. The environmental variables each had three to four factor levels, the first level for weather varaibles serving as the reference condition, e.g. temperatures four categories were 'cool', 'moderate', 'warm' and 'hot', the category 'cool' was used as the reference condition. The factor levels of the wind condition were grouped as being one of four; 'windstill', 'breeze', 'moderate' and 'strong wind'. Cloud cover categories included; 'clear sky', 'partly cloudy', 'overcast' and 'rain clouds'. For the study areas the 'moderate' level of disturbance was selected as the reference factor for ease of interpretation. GLMMs were conducted to determine the impact of these environmental variables on the abundance and richness of collected arthropods overall and per functional feeding guild. Temporal replication was taken into account by including sampling periods as nested random effects along with sampling plots (i.e. replicate sampling sites within study areas) per study area. The following 'glmer' structure was used:

> Abundance/richness of respective functional feeding group ~ study area + temperature + cloud cover + wind condition + (1|Honeybush species/plots), family = poisson.

A process of model simplification was not possible as most variables indicated significance on one or more factors per variable.

Habitat comparison

Count data are not generally normally distributed and are therefore often associated with a Poisson distribution (Zar 1999). Raw residual plots, however, indicated that several of the data sets were normally distributed. These data sets were statistically analyzed with Analysis of Variance (ANOVA) with Restricted Maximum Likelihood (REML) for testing significance in family abundance and richness between habitat types. The sample plots (i.e. the replicate sites at each study area) were nested as random effects within the study areas. If residuals were not normally

distributed a square-root transformation was performed on the regional variables to dampen the effect of highly stochastic abundance counts (for example dominant families) (Zar 1999). If the residual of the transformed data were normally distributed, an ANOVA was performed as before. If, however, the residuals were still not normal after square-root transformation, a bootstrap multiple comparison on the original results comparing the means was done (Hall & Wilson 1991). Family abundance and richness was compared between the two habitat types, Honeybush versus Fynbos habitat. The significant results from the ANOVA were followed-up by using appropriate multiple comparisons on the original scores, e.g. with Least Squares Distance (LSD) or bootstrapping.

Insect plant damage assessment

Multiple regressions were done to evaluate the relationship between observed insect feeding damage and the abundance of the insect causing the damage. Log (x+1) transformed percentage infestation (plant feeding damage) and insect family abundance were used to account for high variation (and zeros) in the data set.

The above ANOVAs with bootstrapping and multiple regression analyses were done in Statistica version 12 (Statsoft Inc. 2012).

Composition of the insect assemblage within and across habitat types

Cluster analyses using PRIMER 6 (PRIMER-E Ltd. 2008) were done on the composition of the zoophagous and phytophagous functional groups within the honeybush stands (Clarke & Warwick 2001). Similar analyses were performed on the composition of zoophagous wasps and predatory beetles using morphospecies level data to assess the consistency (and therefore the potential importance) of these natural enemies within honeybush stands. The analysis was done using a Bray-Curtis resemblance matrix with an additional dummy variable (as recommended by Anderson *et al.* 2008). A dendrogram was computed based on group averages and combined with a SIMPROF test (significant level of 5%) to assess the significance of clustering. Additionally a SIMPER (Similarity of Percentages) analysis was run to determine the dominant families or morphospecies represented per habitat type and within the study areas.

Results illustrated in the tables for the mean abundance and richness of insects per functional group are based on untransformed data for ease of interpretation. Statistical analysis was done on either the original data or squareroot transformed data as specified above.

4.3. Results

During the course of the study approximately 26 088 specimens were collected across the four sampling methods, these included roughly 168 families. Species level diversity was very high and the Hymenoptera wasps alone include more than 550 morphospecies or predator and parasitoid wasps.

4.3.1. Overview of the insect assemblage

The relative proportion of functional groups (zoophagous, phytophagous and omnivorous) was similar between the three study areas and varied proportionally between seasons (Figure 4.1). The increase of phytophagous insects in spring (October to September) corresponds with the peak flowering period of *Cyclopia* (Chapter 3, section 3.3.1, Table 3.1). The lower abundance of the zoophagous and phytophagous groups at the third study area (c) toward the end of the sampling period (early Autumn) corresponds with the decrease in plant biomass due to a harvest event that took place at this site mid-summer (January 2015).

The generalized mixed effects model indicated that environmental variables had a significant ($p < 0.05$) impact on the abundance and richness of the arthropod assemblage collected on *Cyclopia* species (Table 4.1). All three environmental variables influenced the abundance of arthropods per functional group; the impact had either a positive or negative outcome in comparison to the reference study area of mature *C. genistoides*. Family richness of zoophagous arthropods was significantly ($p < 0.05$) higher with higher temperatures and when it was windier. These weather conditions had the opposite effect on abundance of zoophagous taxa. The family richness of phytophagous arthropods was also significantly ($p < 0.05$) higher under warmer temperatures, but also so for cloudy conditions (Table 4.1). Abundance of phytophagous taxa was significantly higher ($p < 0.05$), but lower ($p < 0.01$) under various degrees of windiness. Comparison between the study areas indicated a significant change for two of the functional groups, namely phytophagous and omnivorous taxa. The abundance and richness of phytophagous arthropods was significantly lower ($p < 0.05$) at the recently harvested *C. genistoides* study area than the mature stand of *C. genistoides,* while the richness of the omnivores was significantly lower ($p < 0.01$) at the *C. maculata* study area (Table 4.1).
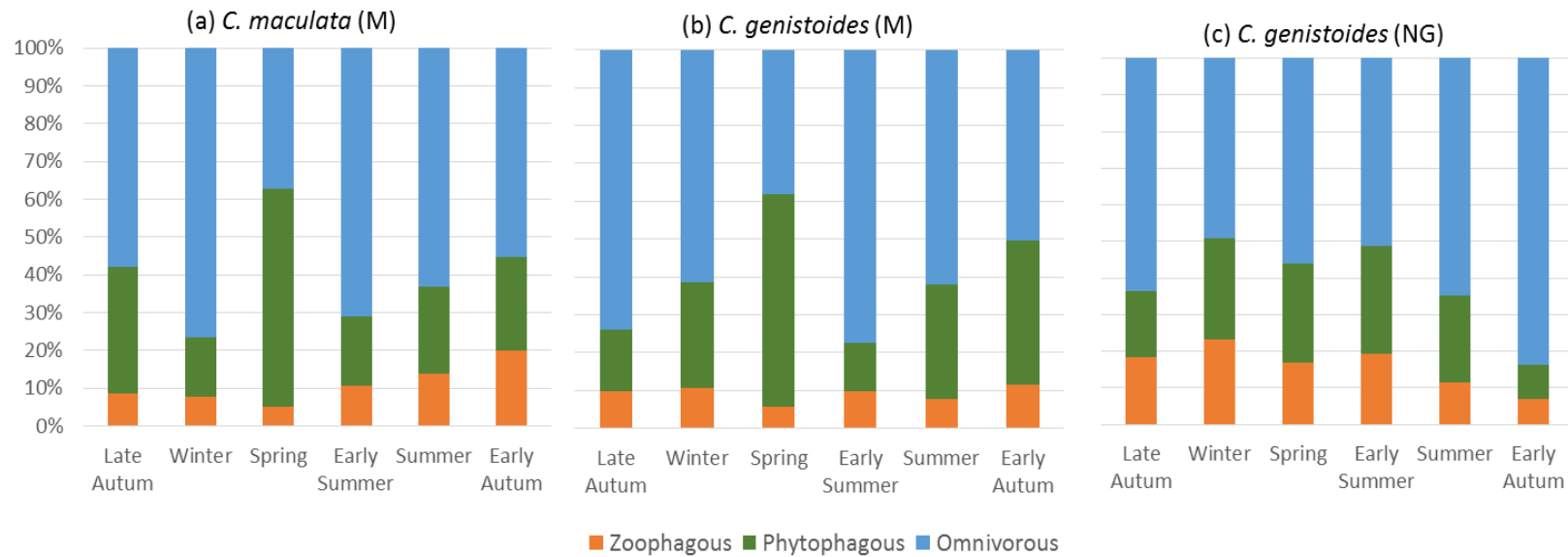
Figure 4.1. Composition of the arthropod assemblage associated with *Cyclopia* species by d-vac samples collected from April 2014 to January 2015. Two study areas had mature (M) bushes of *C. maculata* and *C. genistoides*, respectively; the third study area consisted of *C. genistoides* recently harvested and into its new growth phase (NG).

Table 4.1. Results from the generalized mixed-effects model of the impact various environmental factors had on family abundance (N) and richness (# families) of arthropods collected on *Cyclopia*. Sampling periods were nested as random effects along with sampling plots at each study area.

Functional group	Index	Study area [a]	Temperature [b]			Cloud cover [c]			Wind condition [d]		
			Moderate	Warm	Hot	Partly cloudy	Overcast	Rain clouds	Breeze	Moderate	Strong wind
Overall	N	1 < 2 > 3	(+) ***	(+) ***	(+) ***	(+) ***	(+) ***	(+) *	(+) ***	(+) ***	(+) ***
	# families	1 < 2 > 3	ns	(+) ***	(+) ***	ns	(+) *	ns	ns	(+) **	ns
Zoophagous	N	1 > 2 < 3	ns	(-) *	ns	ns	(+) *	ns	(-) ***	(-) **	(-) ***
	# families	1 > 2 > 3	ns	(+) **	(+) ***	ns	ns	ns	(+) **	(+) **	ns
Phytophagous	N	1 < 2 >*3	(+) ***	Ns	ns	(+) ***	(+) ***	(+) *	(-) ***	(-) **	(-) ***
	# families	1 < 2 >*3	ns	(+) **	(+) *	(+) *	(+) **	(+) *	ns	ns	ns
Omnivorous	N	1 < 2 > 3	ns	(+) ***	(+) ***	(+) ***	ns	ns	(+) ***	(+) ***	(+) ***
	# families	1**< 2 > 3	ns	Ns	ns	ns	ns	ns	ns	ns	ns

Study area: #1, *C. maculata;* #2, *C. genistoides;* #3, recently harvested *C. genistoides*.

Reference levels per factor: (a) study area #2, (b) temperature, 'cool', (c) cloud cover, 'clear sky', (d) wind condition, 'wind still'.

Positive (+) or negative (-) impact per variable, with significance level: ns, not significant; *, p<0.05; **, p<0.01; ***, p<0.001.

4.3.2. Potential ecosystem services and disservices

Habitat type comparison: Honeybush versus Fynbos

There was a significantly higher mean abundance and family richness of zoophagous (predatory and parasitoid) wasps within the honeybush stands than the adjacent Fynbos habitat for pan trap sampling from April 2014 to April 2015 ($F_{(1,239)}$= 11.879, p<0.001 and $F_{(1,239)}$= 14.76, p<0.001, respectively) (Figure 4.2). Average family abundance of zoophagous wasps was more than 40% higher within the honeybush stands (3.75 ± 0.29) than the adjacent Fynbos (2.19 ± 0.29) and +30% higher with regards to family richness (Honeybush: Fynbos; 2.08 ± 0.13: 1.45 ± 0.13).
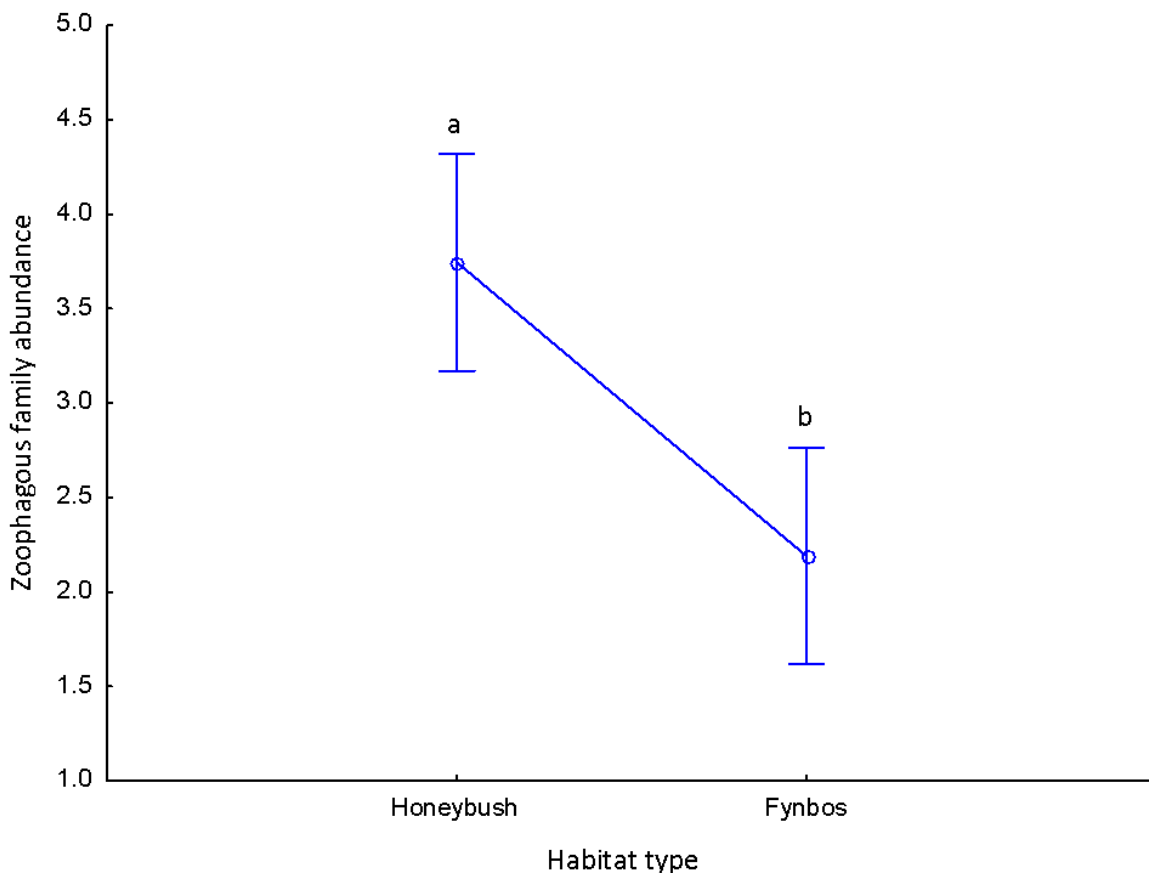
Figure 4.2. Mean family abundance of zoophagous wasps within the two habitat types, namely the honeybush stands and adjacent Fynbos by pan trap sampling from April 2014 to April 2015. Letters indicate significant differences (REML, LSD post hoc, with 95% confidence intervals).

Parasitoid wasp abundance and richness of pan trap sampling from April 2014 to April 2016 was significantly higher within the honeybush stands than the adjacent Fynbos habitat ($F_{(1,239)}$= 23.55,

p<0.001 and $F_{(1,239)}$= 17.34, p<0.001, respectively) (Table 4.2). Average family abundance of parasitoid wasps was nearly twice as high within the honeybush stands (3.00 ± 0.27) than the adjacent Fynbos (1.24 ± 0.26) (Table 4.2). Family richness of parasitoid wasps was more than 80% higher within the honeybush stand. Abundance and richness of predatory wasps was similar between the two habitat types, while diverse feeders, dominated by ants (Formicidae) were significantly ($F_{(1,239)}$= 13.25, p<0.001) more abundant within the Fynbos habitat. Abundance of ants was more than 60% higher within the Fynbos habitat (Table 4.2).

Family abundance and richness of zoophagous wasps collected in delta traps from July 2014 to April 2015 were not significantly different between the two habitat types ($F_{(1,180)}$= 0.10, p>0.05 and $F_{(1,153)}$= 1.43, p>0.05, respectively).

Table 4.2. Mean abundance and family richness of Hymenoptera per functional feeding guild as collected by pan trap sampling from April 2014 to April 2015.

Functional feeding guild		Habitat type			
		Honeybush	Fynbos	$F_{(1,239)}$	Sig
Parasitoids	Abundance	3.00 ± 0.27	1.24 ± 0.26	23.55	***
	# families	1.67 ± 0.11	0.92 0.11	17.34	***
Predators	Abundance	0.75 ± 0.12	0.95 ± 0.12	1.59	ns
	# families	0.41 ± 0.05	0.51 ± 0.05	1.78	ns
Diverse feeders (Formicidae)	Abundance	1.45 ± 0.68	3.82 ± 0.68	13.25	***
	# families	na	na	na	na

REML on transformed data with LSD post-hoc (ns, not significant;*, p<0.05; **, p<0.01; ***, p<0.001; na, not applicable).
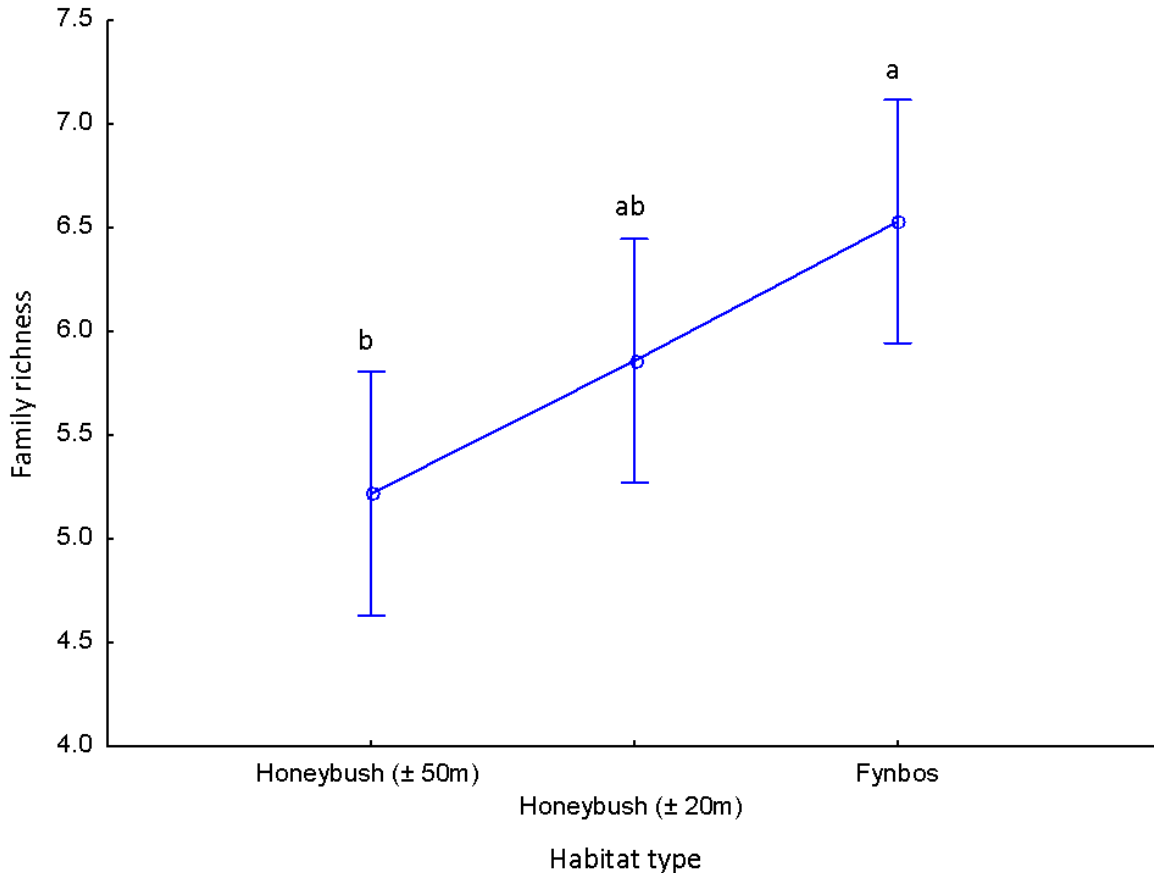
Figure 4.3. Mean family richness of zoophagous wasps within cultivated stands of *C. genistoides* and the adjacent Fynbos habitat for delta traps placed out from September 2014 to April 2015. Letters indicate significant differences (REML, LSD post hoc, with 95% confidence intervals).

Within the cultivated stands of *C. genistoides* the abundance of zoophagous wasps collected in delta traps (from September 2014 to April 2015, at increasing distances from the Fynbos habitat) was not significantly different from the adjacent Fynbos habitat ($F_{(2,168)}$= 2.58, p>0.05). The overall trend did, however, indicate an increase in the abundance of zoophagous wasps from the center of the cultivated stands toward the Fynbos habitat (Figure 4.3). Family richness of zoophagous wasps decreased significantly with an increase in distance from the adjacent Fynbos habitat ($F_{(2,168)}$= 4.90, p<0.05), and was significantly lower ± 50 meters into the center of the honeybush plantations ($F_{(2,134)}$= 4.87, p<0.001) (Figure 4.3).

4.3.3. Composition of the arthropod assemblage within Honeybush and Fynbos stands

Natural enemies (predators and parasitoids):

The natural enemy complex recorded on *Cyclopia* species consisted of a diversity of functional guilds from various insect orders, the dominat orders represented include Hymenoptera and Coleoptera.

Hymenoptera (wasps and ants as omnivours)

Both habitat types had a combination of predatory and parasitoid wasps as collected by pan trap sampling from April 2014 to April 2015, the latter being more dominant within both habitat types (Appendix A, Table 4.3). During the course of the sampling period more than 550 morphospecis of zoophagous wasps were recorded, more than 95% of these were parasitoids.

The composition of zoophagous wasps within the honeybush stands was 55.47% similar among samples (SIMPER analysis), and was dominated by ten parasitoid and two predatory wasp families. Zoophagous wasps in the Fynbos habitat had a 51.27% similarity with nine dominant families, a third being predators. There was a moderate level of similarity of 48.35% between the zoophagous wasp assemblages of the two habitat types. The most abundant predator wasp families encountered within both habitat types included Pompillidae and Sphecidae (Appendix A, Table A.1 and A.2). These two families were more abundant within the Fynbos, contributing the first 43.02% cumulative percentage toward the similarity between the Fynbos samples (Appendix A, Table A.1). Tiphiidae was also recorded more frequently within the Fynbos habitat than among the honeybush stands, and contributed 6.03% toward the dissimilarity between habitat types.

The dominant parasitoids within both habitat types included Platygastridae, Encyrtidae, Bethylidae and Ichneumonidae, along with Mymaridae and Eulophidae for the honeybush stands. Several of these parasitoids were found to be directly associated with some of the abundant Lepidoptera species or scale insects, reared parasitoids are listed in Table 4.3 (Appendix B, Figure B.1 – B.4). The abundance of ants within the honeybush and Fynbos habitats will be discussed in more detail in the following chapter.

Table 4.3. Parasitoids and prey/host species (phytophages) reared from samples collected on *Cyclopia* species.

Order	Parasitoid	Lepidoptera larvae	Tortricidae larvae	Lasiocamphicade larvae	Pyralidae larvae	Coccidae (Soft Brown Scale)	Eriophyt (gall-inducing) mites	Apionidae larvae within galls	Larvae of internal feeder	Phytophagous, Gall-inducers	Phytophagous, Internal feeder	Braconidae
Hymenoptera	Braconidae spp.		x		?x							
	*Eurytomidae sp. 1											X
	*Eurytomidae sp. 2											X
	Ichneumonidae sp. 1		x									
	Ichneumonidae sp. 2		x									
	Proctotrupidae sp. 1		x									
	Proctotrupidae sp. 2			x								
	*Eupelmidae sp. 1											X
	Eupelmidae sp. 2						?x	?x		?x		
	*Eulophidae sp. 1											X
	*Eulophidae sp. 2											X
	*Proctotrupidae sp. 3											?x
	Aphelinidae sp. 1					x						
	Aphelinidae sp. 2					x						
	Aphelinidae sp. 3					x						
	Bethylidae sp. 1		x									
	Eupelmidae (*Anustatus* sp. 1)		x									
	Eupelmidae (*Anustatus* sp. 1)	x										
	Eulophidae sp. 3						?x	?x		?x		
	Eulophidae sp. 4								?x		?x	
Diptera	Tachinidae sp. 1		x									
	Tachinidae sp. 2		x									

(*) Hyperparasitoids reared from wasp cocoons, (?) uncertain host status.

Predatory Coleoptera

A diversity of Coccinellidae (lady beetles) was sampled by d-vac sampling from April 2014 to April 2015. The composition and abundance of coccinellids varied within and between study areas, but mostly consisted of five to six dominant species (Appendix A, Table A.3). The wild *C. maculata* sites had the lowest similarity at 37.51% in the composition of Coccinellidae species across the sampling period, followed by the mature (44.71%) and the recently harvested *C. genistoides* study areas with the highest similarity of 54.51% (SIMPER analysis). There was a low level of similarity (12-20%) between the predatory beetle assemblages of the two habitat types. Some of the dominant species included Coccinellidae sp. 1[1], *Exochomus flavipes* (Black Mealy Bug Predator), Coccinellidae sp. 1[1], *Cheilomenes lunata* (Lunate ladybird) and Coccinellidae sp. 1[1] (Appendix A, Table A.3). Several other predatory beetles were also frequently collected on *Cyclopia* species; these included three species of Anthicidae (ant-beetles) and seven species of Carabidae (ground beetles) (Table 4.4). Although present at all three study areas, not all three predatory beetle groups were equally abundant across honeybush stands. The composition of the predatory beetles is discussed in more detail in the next chapter.

Table 4.4. Predatory Anthicidae and Carabidae species collected on *Cyclopia* species in the Overberg region from April 2014 to April 2015.

Order	Species
Anthicidae	*Formicomus coerulens* (Thunb)
	Formicomus spp. 1
	Formicomus spp. 2
Carabidae	*Acupalus* spp. 1
	Anthicus stygius (Laf.)
	Boeominmetes spp. 1
	Caminara spp. 1
	Microlestes capensis (Molsch.)
	Notoxus cucullatus (Laf.)

Phytophagous insects:

Hemiptera and Thysanoptera

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[1] Awaiting species identifications from the Plant Protection Research Institutes' Biosystematics division of the ARC.

The three study areas had varying levels of similarity in species composition of Hemiptera; the *C. maculata* study area had the highest similarity at 63.19%, followed by the mature stand of *C. genistoides* with 55.93% similarity (SIMPER analysis). The composition of hemipteran species varied the most at 51.26% within the recently harvested *C. genistoides* study area. Two of the hemipterans were dominant within all three honeybush stands, namely Aphididae sp. 1[2] (Aphididae) and Cicadellidae sp. 1[2] (Cicadellidae) (Appendix A, Table A.4). The two cultivated study areas of *C. genistoides* also had ?Flatidae sp. 1[2] (?Flatidae) as one of the most dominant hemipteran species. The recently harvested *C. genistoides* had several additional hemipteran morphospecies that were also prominent, these included additional families such as Delphacidae, Fulgoridae and Cercopidae. Thysanoptera species noted on *Cyclopia* species are listed in Table 4.5, Thripidae were the most abundant.

Table 4.5. Thysanoptera noted on *Cyclopia* species

Family	Common name (feeding guild)
Phlaeothripidae	Tube-tailed thrips (PS NE)
Thripidae	Common thrips (PS)
Thripidae (*Frankliniella occidentalis* (Pergande))	Western Flower Thrips (PS)
Thripidae	Thrips (PS)
Thripidae (*Franklinella schultzei* (Trybom))	Kromnek thrips (PS)
Thripidae (*Thrips tabaci* (Lindermann))	Onion thrips (PS)
Aeolothripidae	Banded thrips (PS NE)

Feeding guilds: (PS) sap feeder, (NE) natural enemy/predator.

Coleoptera

Apionids (Apionidae) and curculionids (Curculionidae) were the most dominant phytophagous Coleoptera families within the honeybush stands. At the two mature unharvested sites of *C. maculata* and *C. genistoides* two coleopteran species contributed 90 – 100% of the variation within study areas for Coleoptera morphospecies (recorded by d-vac sampling from April 2014 to April 2015). Apionidae sp. 1[2] (Apionidae) was dominant within both of these sites, but more abundant within the *C. maculata* study area (Appendix A, Table A.5). The other dominant species of *C. maculata* was *Baris* sp. 1, and Curculionidae sp. 1[2] for *C. genistoides*. The levels of similarity

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[2] Awaiting species identifications from the Plant Protection Research Institutes' Biosystematics division of the ARC.

and abundance of recorded coleopteran morphospecies was low across all three study areas, the mature stand of *C. genistoides* was the lowest at 12.22% similarity, followed by *C. maculata* (40.88%) and the recently harvested *C. genistoides* study area with a similarity of 41.22%. This study area included seven dominant coleopteran morphospecies of which the most prominent was also Apionidae sp. 2[2] (Appendix A, Table A.5). Additional coleopteran species that were dominant within this study area included Apionidae sp. 2[2] , *Tanyrrhynchus* sp. 1 and Curculionidae sp. 3[3] among others. Several Elateridae (click beetles) species were also more abundant at the recently harvested *C. genistoides* study area; these are listed in Table 4.6[3].

Table 4.6. Several Elateridae (click beetles) often encountered at the recently harvested *Cyclopia* genistoides study area.

Species
Elateridae sp. 1.
Elateridae sp. 2.
Elateridae sp. 3.

Lepidoptera

Several Lepidoptera families were abundant among delta trap sampling from April 2015 to April 2015, some of which are known pests on other crops including rooibos. These, together with specimens reared from larvae regularly encountered on honeybush during plant damage observations, are listed in Table 4.7.

The SIMPER analysis indicated considerable consistency in the composition of Lepidoptera encountered within the two habitat types, the Fynbos habitat had a similarity of 64.44% and the honeybush a 58.25% similarity. The two habitat types were 37.84% dissimilar with respects to family diversity of recorded Lepidoptera (Appendix A, Table A.6); the cluster analysis (with SIMPROF test) confirmed these findings with no significant (p>0.05) clustering between habitat types. The abundance of potential pest families was not significantly different between the honeybush and Fynbos habitat types ($F_{(1,153)}$= 0.00, p>0.05).

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[3] Awaiting species identifications from the Plant Protection Research Institutes' Biosystematics division of the ARC.

Table 4.7. Lepidoptera families that were frequently encountered on *Cyclopia* species, several of these families contain known pests on Rooibos ('*').

Family	Genus/Species	Feeding damage
Tortricidae	*Epichoristodes acerbella* (Walker)	Defoliator/Internal feeder
	Lozotaenia capensana (Walker)	Defoliator/Internal feeder
*Noctuidae	Variety of spp	Defoliator
*Pyralidae	*Crambidae* spp.	Defoliator
	Phycitidae sp. A	Defoliator
	Phycitidae sp. B	Defoliator
*Geometridae	Variety of species	Defoliator
Syntomidae (previously Ctenuchinae as a subfamily of Arctiidae)	*Amata cerbera* sp.	Defoliator (grass feeder)
*Lasiocampidae	*Coryphodema tristis* (Drury)	Internal borer
Cossidae	Variety of species	Defoliator/Internal feeder

4.3.4. Plant damage and insect abundance

The percentage insect feeding damage noted on the mature stands of *Cyclopia* species was positively correlated to the abundance of the respective insect families known to cause the damage symptoms. The mature stand of *C. maculata* showed closely correlated leafhopper feeding damage (Appendix B, Figure B.5) to the number of leafhoppers (Cicadellidae) recorded (regression analysis, $F_{(1,4)}$= 18.126, r^2= 0.82, p<0.01). The presence of thrips feeding damage, as noted by the presence of 'thrips-spots' on the underside of leaves and brown leaf tips of new growth, were both significantly correlated with seasonally recorded thrips abundance (regression analysis, $F_{(2,1)}$= 1069.6, r^2= 0.99, p<0.01). Apionidae (Appendix B, Figure B.6) abundance and damage symptoms indicated non-significant (p>0.05) regression with a positive slope.

Additionally two of the Lepidoptera species were noted to cause considerable plant damage to *Cyclopia* species. These included the Cape Lappet moth, *Eutricha capensis* (Linnaeus), and the

Quince borer, *Coryphodema tristis* (Drury). The Cape Lappet moth was found to be a heavy defoliator on cultivated *C. genistoides,* and was especially abundant in a densely planted section of the cultivated area. The Quince borer is an internal stem borer and was noted to cause severe (potentially fatal) damage to several *C. maculata* bushes at one of the study sites (Appendix B, Figure B.7). A species of Handmaidens, *Amata cerbera* sp. (Syntomidae) was also noted to be a regular visitor to *C. genistoides* at one of the study areas. Seed feeding damage was noted to be caused by Bruchidae sp. 1 (as previously noted on *C. subternata*) and Apionidae sp. 1 (on both wild *C. maculata* and cultivated *C. genistoides*) (Appendix B, Figure B.8)

4.4. Discussion

The arthropod assemblage associated with *Cyclopia* contains a diversity of phytophagous and zoophagous taxa that could render potential ecosystem services and disservices to honeybush producers. Several of the potential pest families are known agricultural pests, but many of these were recorded to have a range of potential natural enemies present within the honeybush and adjacent Fynbos habitat. The balanced proportions of functional feeding groups, relevant to honeybush biomass production, suggest that the current honeybush stands contained the necessary components for a functioning ecosystem that naturally regulates the abundance of potential pest taxa (Krüger & McGavin 2001; Warren & Gaston 1992; Wilby & Thomas 2007). Krüger and McGavin (2001), for example, found that predator-prey ratios within *Acacia* tree canopies were proportionally similar. The authors suggested that this (one of several factors) was due to the same conditions acting upon the respective feeding guilds and therefore resulted in a functionally balanced assemblage. The seasonal variability of the arthropod assemblage's functional composition can be attributed, among other factors, to the seasonal niche availability of resources and different responses to changing environmental conditions (Altieri & Nicholls 1999; Schmidt *et al.* 2014; Snodgrass *et al.* 2012). Schmidt *et al.* (2014), for example, found high variability between arthropod predators of the squash bug (*Anasa tristis*, Hemiptera) with population increases and changes in the composition of the natural enemy complex corresponding with the seasonal availability of prey.

Different functional feeding groups associated with *Cyclopia* were found to respond differently to various environmental conditions. Temperature, for example, is seen to increase the abundance and richness of arthropods collected on *Cyclopia* species (Table 4.1). Zoophagous and phytophagous taxa were more diverse at warmer temperatures, indicating increased insect activity under higher temperatures (Ascerno 1991; Forrest & James 2011; Yang *et al.* 2005). Phytophagous and omnivorous arthropods were more abundant under either moderately warm

and/or partly overcast weather conditions. Previous studies have also found that predatory taxa forage more actively at higher temperatures, for example wasps (Stevens *et al.* 2007) and predatory beetles (Evans 2009), while other taxa, such as agricultural pest insects, are more active under cooler, overcast weather conditions (Ascerno 1991). These responses to weather variables hold true also for arthropods associated with honeybush. The efficiency of biological control can thus be affected if predator-pest activities are not well synchronized within *Cyclopia* stands across various weather conditions.

4.4.1. AMES associated with *Cyclopia* species

Potential pest complex

The potential pest complex associated with *Cyclopia* species includes both endopterogote (e.g. several Lepidoptera spp. and a variety of Coleoptera families), and exopterogote (e.g. Aphids (Hemiptera), leafhoppers (Ciccadelidae) and Thrips (Thysanoptera)) insect taxa. Examples of Coleoptera families include Curculionidae, Apionidae and Elateridae. These were the most abundant phytophagous arthropods noted during the course of the study. The cohort of abundant Lepidoptera includes a range of known agricultural pest families. However, not all of the species noted are necessarily potential pest threats for honeybush, but several could become so if natural ecological balances are disrupted as was the case in the rooibos industry. One of the primary rooibos pests, for example, is a native clearwing moth, *Monopetalotaxis cadescens* Felder and Felder (Lepidoptera: Sessidae) (Hatting 2009; Hatting *et al.* 2011). While other frequently noted *Amata cerebra* sp. (Syntomidae), for example, are not considered as potential pests on *Cyclopia* as these are predominantly grass feeders (Geertsema pers. com). The Quince borer noted on *C. maculata* is, however, a potential pest risk for this and other *Cyclopia* species with a woody basal stem. The level of internal infestation by the Quince borer became notably higher (<10% to ± 45%) between May/June 2015 and February 2016. Heavily infested bushes were more prone to wind damage (due to structural damage), and it is speculated that several of the bushes died off due to the direct or indirect damage caused by this internal feeder. Infestation by this internal borer could additionally result in secondary pest infestations or cause physiological stress and increase the risk of disease (e.g. see Hatting *et al.* 2011). A variety of weevils and apionids also form part of the potential endopterogote pest complex for *Cyclopia* as several weevil species have been noted as agricultural pests on rooibos (Hatting 2009, Hatting 2015).

The leafhoppers (Cicadellidae sp. 1[4]), aphids (Aphididae sp.1[4]) and thrips (Thripidae) are potential sporadic pests noted on *Cyclopia* species. Although Cicadellidae sp. 1[4] was not

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[4] Awaiting species identifications from the Plant Protection Research Institutes' Biosystematics division of the ARC.

abundant during the summer of 2014/15, it was noted by a farmer to be highly abundant in previous cropping seasons (e.g. 2013/14) and it is thus also considered to be a potential sporadic pest on *Cyclopia* species. Since another of the major rooibos pests is a leafhopper (*Molopopterus theae* Theron, Cicadellidae) (Hatting 2009; Hatting *et al.* 2011, Hatting 2015), these abundant hemipterans are also noted as potential pests on *Cyclopia* species as a similar indigenous crop. The hemipterans within agricultural fields pose the additional risk as agricultural pests to be potential vectors of viral diseases (Fereres 2015).

The current study was only able to note initial associations between insect feeding damage of sap feeding taxa (leafhoppers and thrips), shoot damage by internal feeding of apionids (Apionidae sp. 1[4]), and the abundance of these taxa. Further long-term monitoring is recommended to investigate the effect of varying seasons and the extent to which these and other forms of insects cause damage to honeybush. Results of these kinds of studies would also point to the impact this has on biomass production (Omer *et al.* 2007).

Predatory and parasitoid wasps

The diversity of zoophagous wasps recorded in wild and cultivated honeybush suggest a high level of foraging activity by these natural enemies within honeybush stands.

Parasitoid wasps, in comparison to predatory wasps, are seen to be especially diverse, suggesting that the natural enemy complex with respect to wasps is dominated by this functional feeding guild. Although predatory wasps are seen to be present in both habitat types (Honeybush and Fynbos) they are more abundant within the Fynbos habitat. This suggests a shift in the composition of the natural enemy complex within the honeybush stands whereby parasitoids are favoured.

The dispersal patterns of zoophagous wasps into cultivated stands of honeybush decreased toward the center of the cultivated field (i.e. with an increased isolation from the adjacent Fynbos vegetation). This suggests that although predator and parasitoid wasps actively forage within honeybush stands they are still highly dependent on the natural vegetation adjacent to the honeybush (Henri *et al.* 2015; Landis *et al.* 2000; Wilby *et al.* 2006). The significant decrease in abundance of predatory and parasitoid wasps toward the center of a honeybush plantation could consequently cause a sharp decrease in the rate of predation and parasitism within these regions of a cultivated honeybush stand. In recent research on mango pests in the southern region of South Africa, it was found that an increase in distance from natural vegetation results in a significant decrease in the rate of predation and parasitism of two key pests (Henri *et al.* 2015). Henri *et al.* (2015) suggested that the efficiency of natural biological control within cultivated crops

is dependent on the proximity of natural vegetation to the cultivated area. Two of the main factors enhancing biological control closer to natural vegetation is the increased dispersal of natural enemies (especially parasitoids) into agroecosystems (Henri *et al.* 2015) and the supply of alternative food resources, such as floral nectar, required by many natural enemies (Henri *et al.* 2015; Isaacs *et al.* 2009). The impact isolation, as caused by cultivation, requires more in-depth investigation within honeybush stands to consider how to best layout plantations to promote effective natural biological control.

The prey preferences of dominant predatory and parasitoid wasps associated with *Cyclopia* species include a wide spectrum of arthropod taxa. Taxa included from this study were Coleoptera (e.g. Chrysomelide and Curculionidae), Diptera (e.g. Cecidomyiide), Hemiptera (e.g. Aphididae and Coccidae) and Lepidoptera (e.g. Tortricide and Pyralidae), among others. The level of specialization of predation or parasitism was diverse among the recorded Hymenoptera wasps. Several of the families are known to be effective biological control agents of arthropod pests in agricultural landscapes (Aliniazee & Croft 1999; Evans 2009). These included Encyrtidae, which are parasitoids of Lepidoptera; Bracondiae, which are egg parasitoids of scale insects (e.g. Aphidiinae); Encyrtidae and Aphelinidae as parasitoids of red scale, soft brown scale and other Coccoidea, and Myrmaridae are parasitoids of various weevil pests (Prinsloo 1980; Stevens *et al.* 2007). Platygastridae, Encytidae and Mymaridae were some of the dominant parasitoid families found in honeybush stands (wild and cultivated). Several of these were also reared from arthropod samples collected on wild and cultivated honeybush (Table 4.3). The parasitism associations noted on several Lepidoptera larvae and scale insects (Addendum, Figure 1 and 2) are indicative of beneficial ES functions through biological control taking place within wild and cultivated honeybush stands. The diverse collection of predators and parasitoids recorded on wild and cultivated honeybush stands suggest that there are both generalist and specialist predator-prey and parasitoid-host interactions taking place amongst the arthropod assemblage associated with *Cyclopia* species.

Predatory beetles

The abundance and diversity of predatory beetles (Table 4.4) within the honeybush stands suggest that these form an important portion of the natural enemy complex associated with *Cyclopia* arthropods. The natural enemy complex of predatory beetles include diverse feeding guilds and foraging habits. The diversity of Coccinellidae recorded on *Cyclopia* form part of the predation pressure on the hemipteran insects that could be potential pests (e.g. Aphids and scale insects) (Scholtz & Holm 1985), as well as other non-hemipteran insects such as various

coleopterans (Evans 2009; Stevens *et al.* 2007). Conservation of predacious lady beetles within honeybush stands would therefore be advantageous for managing hemipteran and other herbivorous Coleoptera (e.g. flower beetles (Chrysomelidae) and weevils) found within stands of *Cyclopia*.

The difference in abundance and diversity of these predatory beetles across the study areas suggest that land management potentially alters the composition, and consequently, the ecological functioning of this natural enemy complex. The impact of land management on natural enemy complexes is discussed in more depth in the next chapter.

4.4.2. Natural biological control within *Cyclopia* stands

Considering the abundance and diversity of natural enemy guilds found within honeybush stands it is likely that honeybush producers are already being rendered an ecosystem service in the regulation of undesired phytophagous insect populations. Often the value of natural biological control is only realized once population numbers of natural enemies reach a tipping point in the efficiency of biological control of potential pest taxa (Altieri & Nicholls 1999). Currently no insecticides are registered for the industry, which is an important aspect contributing to the high diversity of the natural enemies recorded within the honeybush stands. Should pesticide programmes be initiated for commercial plantations of honeybush many of these natural enemies and their potential pest control ES would be significantly reduced or lost (Fouche *et al.* n.d.).

The parasotid-host interactions recorded through the course of the study suggest active parasitism of several of the abundant lepidopteran species. Some of the parasitoids included known biological control agents such as parasitoid wasps (e.g. two *Anustatus* sp. (Eupelmidae), Proctotrupidae and Ichneumonidae) and two parasitoid flies (Tachinidae) (Table 4.3). Aphids and scale insects were also observed to be actively parasitized by wasp parasitoids; these included two Aphelinidae species (Table 4.3). Leafhopper populations are also known to be effectively controlled by egg parasitoids within agroecosystems (Sayedoleslami & Croft 1980 in Aliniazee & Croft 1999); dominant leafhopper parasitoids recorded within honeybush stands included Platygastridae, Encyrtidae, Mymaridae, Eulophidae, Pteromalidae, Braconidae and Diapriidae.

The loss of predation pressure on the potential pest complex associated with *Cyclopia* species would have different outcomes for the various potential pest groups. The potential impact on endopterogote insects would be limited in comparison to that of exopterogote taxa. Population regulation of endopterogote taxa is determined by a diversity of predator guilds whereas exopterogote taxa predation is more uniform (Wilby & Thomas 2007). A decrease in species

richness of exopterogote predators would therefore have a more immediate effect as the release of predation pressure is more holistic across the life cycle of the taxa.

Factors impacting on potential ESS associated with *Cyclopia* species

Environmental factors such as climate and habitat conditions affect the potential occurrence of pest outbreaks (Kremen 2005; Letourreau & Goldstein 2001). The phytophagous arthropod assemblage was more abundant under moderate and overcast days, while the zoophagous taxa were not specifically favored by either of these weather conditions (Table 4.1). Windy conditions caused a significant decrease in abundance of both of these functional groups, potentially due to the hindrance of effective foraging activity. The significant decrease in abundance and richness of phytophagous taxa at the third study area (near Bredasdorp) could potentially be an outcome of the difference in land management practices between study areas. However, it may well also be a consequence of the frequency of windy conditions during sampling periods. These possibilities are discussed in more detail in the next chapter.

4.4.3. Conclusion

This study aimed to assess the current ecological condition of the arthropod assemblages associated with wild and cultivated *Cyclopia* and to determine the potential arthropod-mediated ecosystem services and disservices available to a honeybush farmer. The current ecological functioning within *Cyclopia* stands was found to be balanced with regards to the abundance of the three main functional feeding groups within the arthropod assemblage, namely phytophagous, zoophagous and omnivorous taxa. Several potential arthropod pests, similar to those found on rooibos, were identified along with highly diverse natural enemy complexes within the *Cyclopia* stands. The potential arthropod pests included a cohort of endopterogote and exopterogote phytophagous taxa. These could become problematic should the predation potential of natural enemies associated with *Cyclopia* be significantly undermined, either through isolation from the natural habitat (e.g. typically as a result of conventional monoculture establishment), or disruptive land management or pest control practices. A diverse natural enemy complex of zoophagous wasps (dominated by parasitoids) and predatory beetles were identified as potential biological agents for regulation of undesired arthropod taxa within honeybush stands. The natural vegetation adjacent to cultivated fields of *Cyclopia* were found to fulfill an important role in maintaining a high diversity of zoophagous wasps toward the centre (± 50 meters form the edge) of cultivated *Cyclopia* stands.

In light of the current reality of climate change, it is important to ensure the integrity of ecological systems as a means of maintaining ecosystem functioning and beneficial services such as

biological control of arthropod pests within agroecosystems. Application of the outcomes of this study in better understanding the diversity and complexity of the arthropod assemblage associated with *Cyclopia* species can aid in the development of sustainable agricultural guidelines for the honeybush industry. One of the ways this can be done is through incorporating suitable land management practices for the conservation of biodiversity within agricultural landscapes.

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CHAPTER 5.

IMPACT OF DISTURBANCE ON THE FUNCTIONAL COMPOSITION OF ARTHROPODS

5.1. Introduction

Anthropogenic change to agricultural landscapes and managed ecosystems, such as crop lands or grazing pastures, drastically alters the species richness and compositional structures within these landscapes (Naeem *et al.* 1999). Numerous studies have shown that as cropping systems expand and intensify (toward monocultures) in an attempt to improve yield output, biodiversity is lost in the process, and along with it important ecosystem services (Altieri & Nicholls 1999; DeClerck & Salinas 2011; Wilby & Thomas 2007). Reduced heterogeneity or ecosystem simplification in agricultural landscapes causes a decrease in ecological functioning and associated biological processes and services that are important for agricultural productivity, for example crop pollination and pest control (Carvalheiro *et al.* 2011; Isaacs *et al.* 2009; Letourneau *et al.* 2011). Ecosystem simplification has also been found to increase the risk of viral plant diseases in agricultural landscapes (Roossinck & García-Arenal 2015).

Within productive landscapes, one of the consequences of reduced habitat heterogeneity is the emergence of pests that are no longer under natural predation pressures (Crowder *et al.* 2010; Kruess & Tscharntke 1994). Cultivation of indigenous crops, such as rooibos (*Aspalathus linearis*) and honeybush (*Cyclopia* species), has increasingly occurred on previously marginalized or fallow lands to which the species are native (Raimando *et al.* 2009). The commercialized cultivation of these endemic species could, however, result in several negative outcomes should a certain degree of habitat heterogeneity not be maintained within these productive landscapes. One potential issue would be the emergence of arthropod pests native to the region (Hatting 2009). The high intensity and monoculture approach used by commercial rooibos producers has resulted in extensive habitat degradation (Pretorius 2009), and consequently severe arthropod damage by several native arthropod species that utilize rooibos as a host plant (Hatting 2009; Hatting *et al.* 2011, Hatting *et al.* 2013). The rising interest and demand for honeybush over the last decade has resulted in the increasing need for commercialization of this industry as well. Currently the industry is still predominantly dependent on wild harvested biomass, but is in the process of

advancing commercial cultivation to meet rising international demands (Coega Development Corporaton (CDC) 2011; Joubert *et al.* 2011). The potential cultivation and land management approaches employed in this developing industry, in both small and large scale production systems, will determine whether this industry will have a less harsh ecological foot-print than its sister industry as it expands toward increased commercial cultivation. One of the key factors that need to be considered is the incorporation of agroecosystem (Altieri & Letourneau 1982) and landscape ecology (Pickett & Cadenasso 1995; Wiens 2009) principles into the commercialization process. The value of agrobiodiversity within agricultural landscapes, among others, promotes ecological functioning and the associated ecosystem services (e.g. natural biological control of pest, Kean *et al.* (2003)) these interactions could render a honeybush farmer.

Ecosystem and function is vulnerable to adjustments of the species richness and evenness of the functional components within the ecological community (Bihn *et al.* 2010). The unique characteristics and functional identity of organisms play an important role in the functioning of that community (Bihn *et al.* 2010; Naeem *et al.* 1999). The changes to biodiversity and habitat heterogeneity within agricultural landscapes could thus lead to the loss of ecological functioning that would increase the frequency of pest outbreaks (Crowder *et al.* 2010; Kruess & Tscharntke 1994), or in the case of a novel crop such as honeybush it increases the risk of new pest outbreaks. Maintaining agrobiodiversity within agricultural landscapes thus plays an important role in sustainable pest management. For effective natural biological control within an agroecosystem, functional complementarity of the natural enemy complex should be conserved. This will maximize the predation pressure derived from functionally diverse natural enemy complexes and increase the efficiency of natural biological control within an agroecosystem (Bihn *et al.* 2010; Tscharntke *et al.* 2005; Wilby & Thomas 2007).

Determining the interactions within arthropod communities and the impact of disturbance on trophic level interactions is complex as many of the interactions are interlinked and often react differently under various land management practices and ecosystems (Estes *et al.* 2011; Griffen & Byers 2006; Hemptinne *et al.* 2012; Larsen *et al.* 2005). The efficiency of ecological functions such as pest control is determined by the community composition (i.e. predator and parasitoid diversity) of the arthropod assemblage not necessarily only the species richness of the predator/parasitoid complex (Bihn *et al.* 2010; Naeem 1998; Wilby & Thomas 2007). The more diverse the natural enemy complex the higher the diversity of functional feeding guilds acting upon the phytophagous assemblage which increases the overall stability and resilience of the

ecosystem (Tscharntke *et al.* 2005; Jackson *et al.* 2007) to managing population levels of undesired organisms.

The current status of the rooibos industry, with respect to its negative ecological impact (Pretorius 2009) and pest infestations (Hatting 2009; Hatting *et al.* 2011) highlights the need for more environmentally sound commercialization practices to be adopted within the honeybush industry in avoidance of the same ecological devastation. This study aimed to assess the impact different management practices within honeybush stands have on the functional composition of the insect assemblage associated with *Cyclopia* species. The three management practices assessed created varying degrees of disturbance (low, moderate and high) within the honeybush stands. The low disturbance study area were natural stands of honeybush, while the other two were cultivated stands with moderate to high disturbance level caused by the land management practices within the honeybush stands. Insect monitoring across these disturbance levels will allow for an effective comparison of the impact land management practices have on the potential arthropod-mediated ecosystem services available to a honeybush farmer.

5.2. Materials and methods

5.2.1. Site selection

Long-term insect monitoring took place at three study areas in the Overberg region where *Cyclopia* species were either naturally present in the landscape or through cultivation (Chapter 2, Figure 2.1). Sampling took place over a period of a year from April 2014 to April 2015. The study sites near Genadendal contained wild *C. maculata,* while those near Bredarsdorp and Pearly Beach were of cultivated *C. genistoides* (Chapter 2, Table 1 and Figure 2.3). At each of these study areas four sites were selected for insect monitoring as detailed in Chapter 4, section 4.2.1 (Genadnedal: site A – D; Bredasdorp: Site E – H and Pearly Beach: Site I – L). Additonal replication was not possible due to the lack of suitable sites and high seasonal sampling effort.

The sites selected incorporated different management practices for assessing the impact of disturbance on the insect assemblage. Based on the land management practices and field observations the arbitrary classification of 'low', 'moderate' and 'high' disturbance level categories were used. The natural honeybush stands near Genadendal were considered to have a 'low' (L) level of disturbance, while the study area near Bredasdorp was considered to have a 'moderate' (M) level of disturbance due to the semi-natural appearance of the cultivated stands (Chapter 2, Figure 2.1). The study area near Pearly Beach had the highest level of disturbance in comparison

to the other two study areas; it was thus classified as the study area with a 'high' (H) disturbance level.

The natural stands of honeybush were considered to have a low level of disturbance as only selective harvesting took place on an *ad hoc* basis on a few bushes, whereas the cultivated stands were harvested more regularly for tea production. The cultivated sites at Bredasdorp were within a semi-natural setting as natural succession of the native vegetation is maintained within the cultivated area and only managed selectively. Harvesting took place systematically within sections of the plantation, with a set block being harvested on a rotational basis of two to three years. One of the sites at this study area was harvested shortly before insect monitoring commenced, and will be omitted from the final analyses due to the difference in disturbance level at this site in comparison to the study area as a whole. The land management approach of the other cultivated study area near Pearly Beach follows more traditional cultivation practices as outlined in Chapter 2, section 2.2.1. This study area is harvested annually and regular management on the native plants within the cultivated field occurred.

5.2.2. Insect monitoring

A range of sampling techniques was used to ensure that an accurate representation of insect diversity and abundance are recorded over the 12 month monitoring period from April 2014 to April 2015. Insect monitoring was based on the same sample techniques outlined in Chapter 4, section 4.2.2.

With each sampling period the delta traps were re-set and pan traps put out for approximately six to seven hours. D-vac sampling was done within the honeybush stands as outlined in Chapter 4, section 4.2.2.

5.2.3. Sorting and identification of insects

Insect samples were processed and identified as specified in Chapter 3, section 3.2.4. Formicidae from pan trap monitoring were identified to genus and morphospecies level with assistance and use of reference collections at Iimbovane, Centre for Invasion Biology (CIB) (De Morney pers. com).

Based on family level identification, insects were assigned to a functional feeding group, as listed in Chapter 3, section 3.2.4. Classification of insects according to their functional feeding guilds allowed comparative analyses of land management practices (i.e. disturbance levels) on the functional ecology and composition of the insect assemblage associated with *Cylopia* species. Hymenoptera (ants and zoophagous wasps) and predatory Coleoptera were
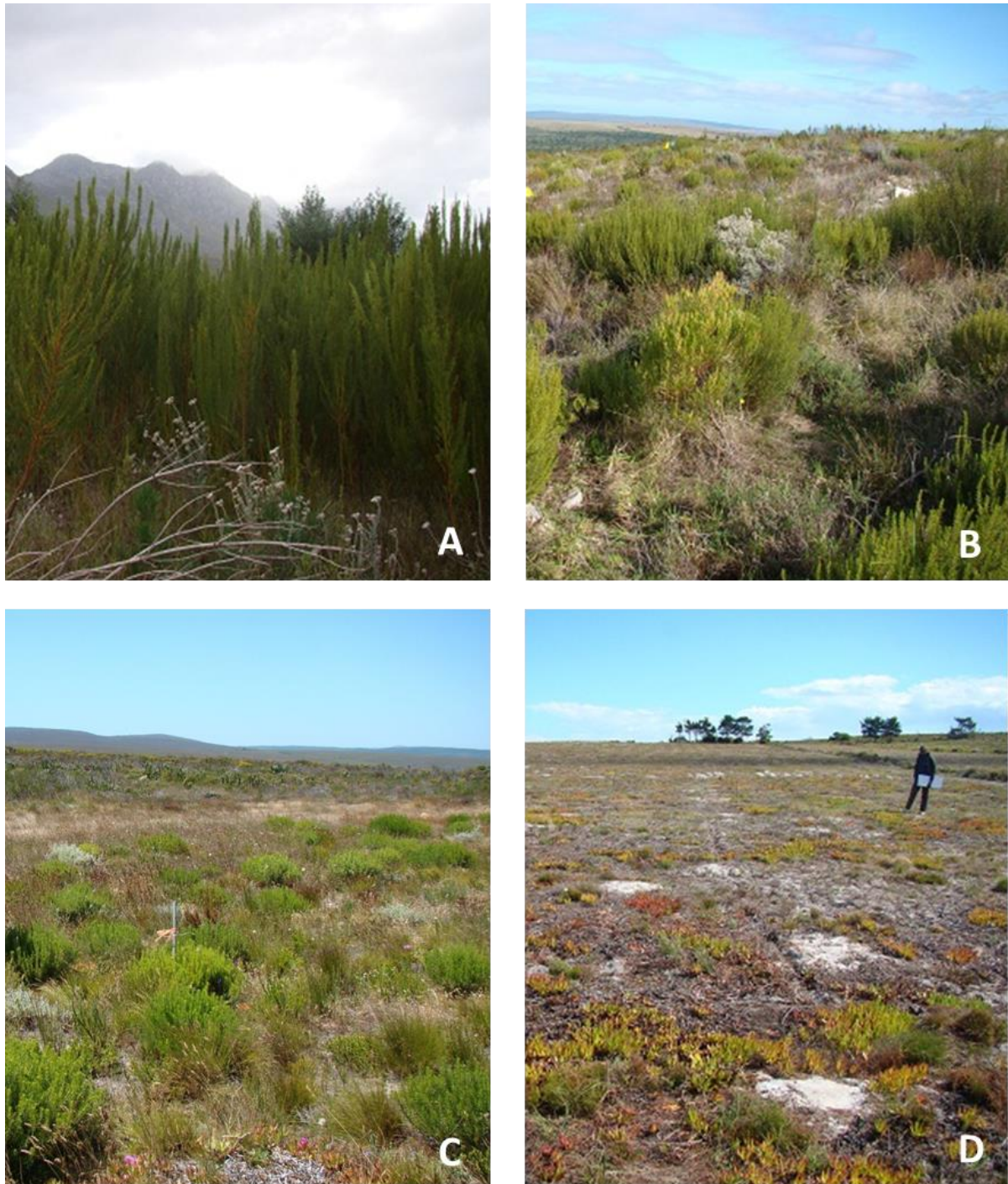
Figure 5.1. Study areas with *Cyclopia* species, natural (A) *C. maculata* (2 – 3 m x 1.5 – 3 m) near Genadendal with low habitat disturbance, cultivated *C. genistoides* (1 - 1.5 m x ± 1 m) near Bredasdorp with moderate levels of disturbance (B) and high disturbance study area near Pearly Beach (C & D, before and after a harvest event and clearing of native vegetation within the plantation).

the main focus for addressing the research aims as these orders are known to be valuable natural biological control agents within agricultural landscapes.

5.2.4. Data analyses

Composition and diversity of the insect assemblage

The species composition of various functional insect groups were assessed between the three levels of disturbance using cluster analyses (with SIMPROF test of significant clustering at 5%) and SIMPER (Similarity of percentage) analyses in PRIMER-E Ltd. Dendograms with SIMPROF analyses indicated non-significance of clustering in red. Calculated diversity and evenness indices were performed on the phytophagous and zoophagous portions of the insect assemblage. Species accumulation curves were compiled in PRIMER to determine efficiency of sampling effort for pan trap Formicidae.

Impact of environmental factors and isolation on the abundance and family richness of insects

Statistical analyses for this chapter followed a similar approach as outlined in Chapter 4, section 4.2.5. Analysis of variance was performed to compare the abundance and richness of zoophagous wasps between the three levels of disturbance and isolation distance from the Fynbos habitat. If the residuals, were were non-normal a square-root transformation to normality was performed, before again subjecting the variables to an ANOVA. If transformation was unsuccessful, bootstrapping multiple comparisons were run on the original data set.

The abundance of predatory beetles across and within the three disturbance levels were statistically compared by performing a Kruskal-Wallis non-parametric ANOVA, with multiple comparisons where significant differences occurred.

A generalized linear mixed-effect model was used to assess the impact of various environmental factors on the abundance and family richness of functional feeding guilds associated with *Cyclopia* species. The same reasoning outlined in Chapter 4, section 4.2.5 was applied. The nested design of the generalized mixed-effect models had the following structure:

Abundance/richness of respective functional feeding guild ~ disturbance level + temperature + cloud cover + wind + (1|Honeybush species/plots), family = poisson.

5.3. Results

5.3.1. Composition of the insect assemblage

Cluster analysis with (SIMPROF tests) showed that there was distinct clustering based on the composition of the phytophagous insects sampled from the three stands of *Cyclopia,* as collected by d-vac sampling from April 2014 to April 2015. The cultivated fields of *C. genistoides* formed two distinct clusters at 60% similarity, with the exception of site H (a recently harvested site at the moderately disturbed study area) that clustered closer toward the high disturbance study area (Figure 5.2). The composition of phytophagous arthropods at the low disturbance sites were more distinct, with sites A and B, however, clustering more closely with the moderate and high disturbance sites than with the other two low disturbance sites (C and D) (Figure 5.2). The cluster analyses of the zoophagous portion of the arthropod assemblage showed similar results, the SIMPROF test, however, indicated less distinct clustering for the cultivated stands of *Cyclopia.*
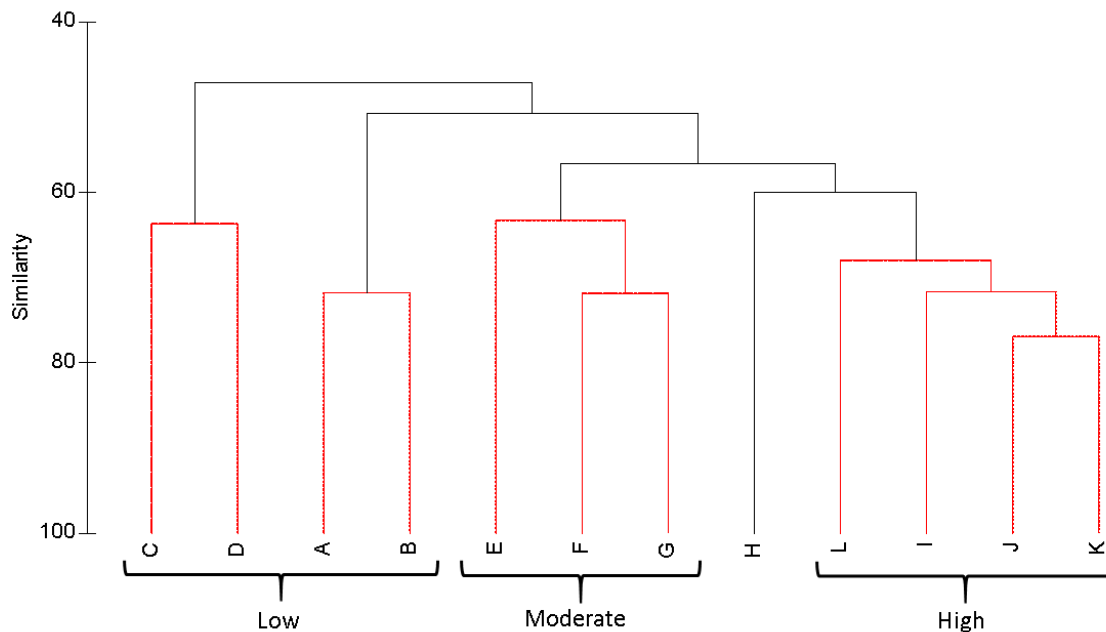
Figure 5.2. Dendrogram of phytophagous family abundance (square-root transformed) per site with grouping indicated per disturbance level, namely low (site A - D), moderate (E – G, with H as an outlier) and high (site I - L) disturbance.

These dendogram clusters, with the exception of site H as an outlier, supports the arbitrary grouping of the sites per study area according to the level of disturbance caused by land

management practices. Site H deviates from the rest of the moderately disturbed study area due to a recent harvest event at this site and based on this deviation in disturbance from the rest of that study area this site was omitted from further statistical analysis assessing the impact of disturbance on arthropod composition.

Family diversity of functional feeding groups

Family richness of phytophagous taxa was higher within the cultivated stands of *Cyclopia* with moderate and high disturbance levels than the natural stands of honeybush. The 'moderate' and 'high' disturbance study areas both had richness levels between 28 - 30 families in comparison to the 20 families at the 'low' disturbance study area (Table 5.1). The diversity and evenness of the phytophagous assemblage were, however, highest within the 'high' disturbance study area (moderate vs. high diversity: 1.6 ± 0.3 vs. 2.7 ± 0.1). Zoophagous family richness was similar across the three disturbance levels, but diversity of this functional group was proportionately lower at the 'high' disturbance study area (Table 5.1).

Table 5.1. Average (± SD) diversity indices of phytophagous and zoophagous families on *Cyclopia* species under three levels of disturbance (low, moderate and high).

Functional group	Index	Disturbance level		
		Low	Moderate	High
Phytophagous	S	20 ± 3.6	28 ± 2.4	28 ± 1.1
	H'	1.4 ± 3.6	1.6 ± 0.3	2.7 ± 0.1
	1-λ	0.6 ± 3.5	0.6 ± 0.1	0.9 ± 0
Zoophagous	S	20 ± 1.9	21 ± 1.6	20 ± 2.7
	H'	2.4 ± 0.2	2.4 ± 0.2	2.0 ± 0.1
	1-λ	0.9 ± 0	0.8 ± 0	0.8 ± 0

Family count (S), Shannon-Wiener diversity index (H') and Inverse of Simpson as an evenness index (1-λ), family richness was rounded up to the nearest integer and indices to one decimal place

5.3.2. Influence of environmental factors on the functional feeding guilds associated with *Cyclopia* species

The generalized mixed-effects models indicated that several of the environmental factors had a significant influence on either increasing or decreasing the family abundance and richness of functional feeding guilds collected on *Cyclopia* by d-vac sampling from April 2014 to April 2015 (Table 5.2). The various functional feeding guilds each responded differently to the range of environmental factors assessed. On several occasions the impacts of the daily weather conditions were more influential in determining the abundance and richness of arthropods sampled than the respective disturbance levels at the study areas (Table 5.2).

The predators responded favorably toward the increased disturbance, with significantly higher family richness being recorded within the 'high' disturbance study areas (Table 5.2). Predators were significantly more abundant and rich under moderate temperatures and partly cloudy conditions. While increasing levels of cloud cover and temperatures resulted in a significant decline in abundance and richness. Predator abundance and richness also significantly decreased with an increase in windiness. Parasitoid abundance and richness were significantly higher when weather conditions were at their hottest, while they declined under 'rain cloud' conditions (Table 5.2). At moderate wind conditions the abundance and richness of parasitoids was also significantly higher, while very strong winds had the opposite effect.

The abundance and richness of external feeders were affected significantly by both disturbance and weather conditions (Table 5.2). The 'low' disturbance study area was significantly lower with respects to abundance and richness of external feeders in comparison to the moderately disturbed study area. Overcast weather conditions significantly increased the abundance and richness of the external feeders, while warmer temperatures generally resulted in a similar trend. Increasing levels of windiness causes significantly lower abundance and richness of external feeders. Internal feeders were also significantly impacted by disturbance (Table 5.2), and were more abundant and diverse at the 'high' disturbance level in comparison to the moderately disturbance study area. Sap feeders where not significantly affected by the disturbance level at the study areas, but an increase in wind, and overcast skies, caused a significant increase in the abundance and richness of this feeding guild (Table 5.2).

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Table 5.2. Generalized mixed-effects model of the impact disturbance and environmental variables has on the functional feeding guild composition of insects associated with *Cyclopia* spp. Sampling periods were nested as random effects along with sampling plots at each study area.

Functional feeding guild		Disturbance level [a]	Temperature [b]			Cloud cover [c]			Wind condition [d]		
			Moderate	Warm	Hot	Partly cloudy	Overcast	Rain clouds	Breeze	Moderate	Strong wind
Predators	N	L < M < H	(+) ***	ns	(-) *	(+) **	(-) **	ns	(-) ***	(-) ***	(-) ***
	# families	L < M <* H	(+) ***	ns	(-) *	(+) **	(-) **	ns	(-) ***	(-) ***	(-) ***
Parasitoids	N	L > M > H	ns	ns	(+) ***	ns	ns	(-) *	ns	(+) ***	(-) *
	# families	L > M > H	ns	ns	(+) ***	ns	ns	(-) *	ns	(+) ***	(-) *
External feeders	N	L *< M > H	(+) ***	ns	(+) ***	(+) ***	(+) ***	(+) *	(-) ***	(-) ***	(-) ***
	# families	L *< M > H	ns	(+) ***	(+) ***	(+) ***	(+) ***	(+) *	(-) ***	(-) ***	(-) ***
Internal feeders	N	L > M <** H	(-) *	ns	ns	ns	ns	ns	(-) ***	(-) ***	(-) ***
	# families	L > M <** H	(-) *	ns	ns	ns	ns	ns	ns	ns	ns
Sap feeders	N	L > M > H	ns	ns	ns	ns	(+) ***	ns	(+) ***	(+) ***	(+) ***
	# families	L > M > H	ns	ns	ns	ns	(+) ***	ns	(+) ***	(+) ***	(+) ***

Environmental factors

Disturbance level: Low (L), Moderate (M) and High (H).

Reference levels per factor: (a) moderate (M), (b) temperature, 'cool', (c) cloud cover, 'clear sky', (d) wind condition, 'wind still'.

Positive (+) or negative (-) impact per variable, with significance level: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$; ns, not significant.

Impact of disturbance on the arthropod assemblage within Honeybush stands

Family abundance and richness of zoophagous wasps was consistently higher within the honeybush stands in comparison to adjacent Fynbos habitats. This was so across all three disturbance levels for the pan trap data from April 2014 to April 2015. Overall the abundance ($F_{(2,203)} = 0.67$, $p>0.05$) and richness ($F_{(2,203)} = 0.91$, $p>0.05$) of zoophagous wasps were, however, not significantly different between the two habitat types. There was, however, a decline in both wasp abundance and richness with an increase in disturbance within the honeybush stands. The study area with the 'low' and 'moderate' disturbance level had a significantly higher abundance of zoophagous wasps than the 'high' disturbance study area.

Zoophagous wasps from the delta trap data for July 2014 to April 2015 showed similar results, but indicated a significant decrease by up to 50% for both family abundance ($F_{(2,150)} = 3.15$, $p<0.05$) and richness ($F_{(2,150)} = 3.86$, $p<0.05$) between the least and most disturbed study areas (Figure 5.3 a and b). Family richness of zoophagous wasps was significantly lower ($p<0.05$) between the honeybush and Fynbos habitat at the most disturbed site. Abundance and richness of zoophagous wasps was significantly higher within the honeybush stands with the lowest level of disturbance in comparison to the 'high' disturbance study area. The moderately disturbed study area is an intermediate between the other two levels of disturbance (Figure 5.3 a and b).
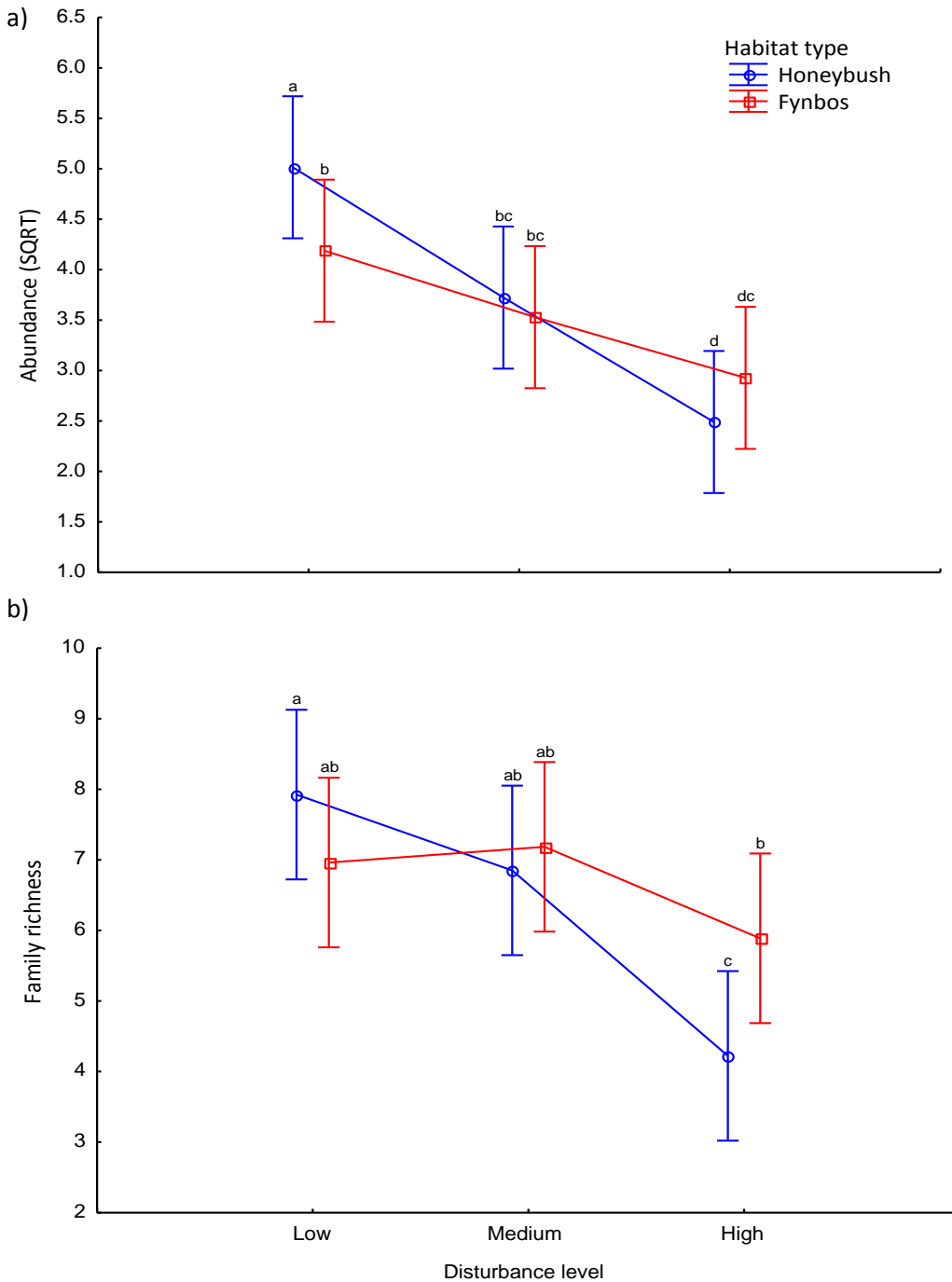
Figure 5.3. (a) Family abundance (square-root transformed) and (b) richness of zoophagous wasps between degrees of disturbance (low, moderate and high) within honeybush stands and the adjacent Fynbos (as reference habitat). Letters indicate significance (p<0.05) between and within study areas and habitat types (REML, with post hoc LSD and 95% confidence intervals).
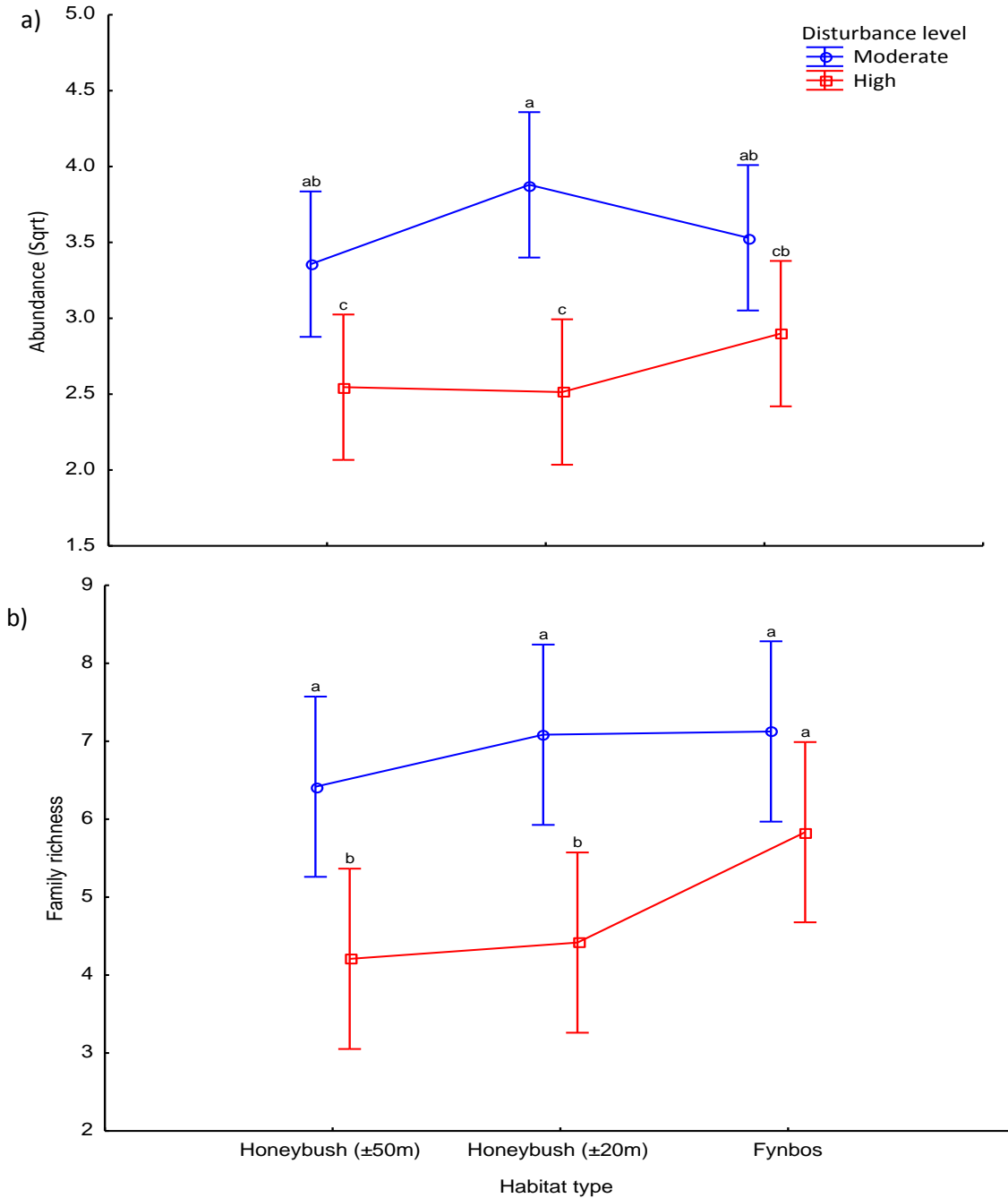
Figure 5.4. Abundance (square-root transformed) and richness of zoophagous wasps at decreasing distances from the Fynbos habitat for two levels of disturbance within cultivated stands of *C. genistoides*. Letters indicate significance differences (p<0.05) between and within study areas (REML, with post hoc LSD and 95% confidence intervals).

Within the cultivated stands of *C. genistoides* the 'moderate' level of disturbance is seen to be consistently higher in abundance and richness of zoophagous wasps (Figures 5.4 a and b). For both levels of disturbance the abundance of wasps is comparable (p>0.05) across the step-wise increase in isolation from the Fynbos habitat within the respective study areas. Family richness is, however, significantly lower within the honeybush stands at the 'high' disturbance level (p>0.05) approximately 50 m into the center of the honeybush stand (Figure 5.4 b). The overall trend within the cultivated study areas indicates a decline in zoophagous wasp abundance and richness with an increase in distance from the natural vegetation (Figures 5.4 a and b).

5.3.3. Composition of the functional feeding guilds across a disturbance gradient

Composition of the ant (Formicidae) assemblage

Abundance of ants sampled by pan traps from April 2014 to April 2015 was significantly (2.5 times) higher ($F_{(1,239)}$= 13.25; p<0.001) within the Fynbos habitat than within the honeybush stands (Chapter 4, section 4.3.2, Table 2). Species accumulation curves (Appendix A, Figure A.3.) for ants collected per study area indicated species richness to potentially be higher than what is represented by the current sampling effort. Cluster analyses (with SIMPROF test) of the ant morphospecies indicated no significant (p>0.05) clustering between habitat types (Honeybush versus Fynbos) or disturbance levels ('low', 'moderate' and 'high'). The SIMPER analysis confirmed these results indicating a low level of similarity (20 – 27%) among the Formicidae composition within the study areas and a high dissimilarity (81.43%) between habitat types. Similarity within study areas ranged from 12 - 46%, indicating a high level of ant diversity per study area (SIMPER analysis).

Ant species richness between the honeybush stands and their adjacent Fynbos habitats, and between the 'low' and 'moderate' disturbance levels was similar (Table 5.3). The 'high' disturbance study area varied the most with respect to the species richness and abundance of ants within the honeybush stands. Ant abundance and species richness at the 'high' disturbance study area was 82% and 31% higher within the Fynbos habitat than within the honeybush stand (Table 5.3). Abundance at the "low" disturbance site was 56% higher in the adjacent Fynbos habitat.

Table 5.3. Genus and morphospecies richness and abundance of Formicidae with three levels of disturbance (low, moderate and high) within honeybush (HB) and in adjacent Fynbos (FB) habitats.

| | Disturbance level and habitat type | | | | | |
| Measure | **Low** | | **Moderate** | | **High** | |
	HB	FB	HB	FB	HB	FB
# genus	6	5	8	6	7	7
# morpho spp.	10	11	13	12	11	16
Total abundance	39	88	58	60	49	282

Ant species richness within the honeybush stands was similar across the three disturbance levels; the moderately disturbed site, however, had 1 to 2 additional genus groups present within the honeybush stand (Table 5.3). There were five dominant species at the 'low' disturbance study area of which two were invasive species, namely *Linepithema humule* (Argentine ant) and *Technomyrmex pallipes* (Pallid-footed ant), both in the family Dolichoderinae. The moderate and high disturbance study areas had only three dominant species (SIMPER analysis) (Table 5.4).

Table 5.4. Dominant Formicidae species within *Cyclopia* stands across varying levels of disturbance.

Disturbance level	Species	Subfamily	Av. Abund.	Av. Sim.	Sim/ SD	% Contrib.	Cum.%
Low	*Crematogaster* (cf) *peringueyi*	Myrmicinae	1.5	4.44	0.41	44.01	44.01
	Monomorium sp. 7b	Myrmicinae	0.5	2.22	0.41	22	66.01
	Monomorium sp. 9	Myrmicinae	1	1.28	0.41	12.69	78.71
	Linepithema humile	Dolichoderinae	4	1.08	0.41	10.65	89.35
	Technomyrmex pallipes	Dolichoderinae	1	1.08	0.41	10.65	100
Moderate	*Lepisiota* sp. 1	Formicinae	9	12.12	1.77	42.87	42.87
	Lepisiota sp. 1b	Formicinae	3.67	8.67	2.21	30.68	73.55
	Camponotus irridux	Formicinae	1.67	6.06	1.77	21.43	94.98
High	*Meranoplus* (cf) *peringeuyi*	Myrmicinae	8.75	8.12	0.85	51.7	51.7
	Lepisiota sp. 1b	Formicinae	6	6.2	0.57	39.46	91.16

SIMPER similarity output of the average abundance per sampling period (Av.Abund.), average similarity (Av.Sim.) between site replicates and similarity standard deviation (Sim/SD) and % contribution and cumulative % contribution per family to the overall similarity between samples per habitat. Species numbering as recorded in the CIB ant collection.

The composition of dominant ant species within the honeybush stands varied considerably between the disturbance levels, with only the 'moderate' and 'high' disturbance study areas having *Lepisiota* sp. 1b (Formicinae) in common (Table 5.4). The Argentine ant was especially abundant at one of the "low" disturbance study sites that was located within a highly transformed landscape (e.g. a river bank highly invaded with Port Jackson and a commercial apple orchard). *Crematogaster* (cf) *peringueyi* (Black cocktail ant). The native Cocktail ant (*Crematogaster* (cf) *peringueyi*) was the most prominent species in the 'low' abundance study area and was often found in arboreal nests inside of *C. maculata*. Several of these arboreal ant nests were observed

to harbour colonies of mealybugs (Pseudococcide), especially at sites near cultivated lands (e.g. apple orchards).

The comparison of the ant assemblage composition between the habitat types per study area revealed high levels of dissimilarity across all three study areas (SIMPER analysis) The 'low' disturbance study area had the highest dissimilarity at 92.54%, while the 'moderate' and 'high' disturbance study areas were equally high in dissimilarity (74.34% and 82.25%, respectively). Several ant species were only present in the two habitat types (Table 5.5).

Table 5.5. Comparison of the ant assemblage within various levels of disturbance of honeybush (HB) stands, with adjacent Fynbos as the reference habitat per study area.

Disturbance level	Species	Subfamily	Fynbos Av.Abund	Honeybush Av.Abund	Av. Diss	Diss/SD	%Contrib	Cum.%
Low	*Oligomyrmex* sp. 1	Myrmicinae	15.25	0	19.33	0.56	20.69	20.69
	Linepithema humile	Dolichoderinae	1	4	18.43	0.79	19.72	40.41
	Crematogaster (cf) *peringueyi*	Myrmicinae	0.25	1.5	11.08	0.86	11.85	52.26
	Monomorium sp. 8	Myrmicinae	1	0	8.64	0.8	9.25	61.51
	Lepisiota sp. 1b	Formicinae	0.5	0.5	8.5	0.45	9.09	70.61
	Lepisiota sp. 1	Formicinae	1.25	0.25	8.39	0.6	8.98	79.59
	Monomorium sp. 9	Myrmicinae	0.25	1	4.99	0.81	5.34	84.92
	Technomyrmex pallipes	Dolichoderinae	0	1	4.04	0.79	4.32	89.24
	Monomorium sp. 9	Myrmicinae	0	0.5	3.95	0.74	4.23	93.48
Moderate	*Pachycondyla peringueyi*	Ponerinae	8	0.67	20.52	2.49	27.6	27.6
	Lepsiota sp. 1	Formicinae	2.33	9	15.34	0.95	20.63	48.23
	Lepsiota sp. 1b	Formicinae	1.33	3.67	7.98	1.83	10.73	58.96
	Camponotus irridux	Formicinae	3.67	1.67	7.65	1.19	10.29	69.25
	Myrmicinae sp. (a)	Myrmicinae	1.33	0.33	3.29	0.92	4.42	73.68
	Pheidole sp.	Myrmicinae	1.33	0.67	3.21	0.84	4.32	78
	Monomorium sp. 15	Myrmicinae	0	0.67	2.54	0.63	3.42	81.42
	Tetramorium sp. 1	Myrmicinae	0	0.67	1.84	1.03	2.48	83.89
	Monomorium sp. 9	Myrmicinae	0.33	0.33	1.4	0.72	1.88	85.78
	Crematogaster (cf) *peringueyi*	Myrmicinae	0.33	0	1.24	0.61	1.66	87.44

Table 5.5 cont. Comparison of the ant assemblage within various levels of disturbance of honeybush (HB) stands, with adjacent Fynbos as the reference habitat per study area.

Disturbance level	Species	Subfamily	Fynbos Av.Abund	Honeybush Av.Abund	Av. Diss	Diss/SD	%Contrib	Cum.%
Moderate	*Monomorium* sp. 7b	Myrmicinae	0.33	0.33	1.2	0.75	1.61	89.06
	Meranoplus (cf) *peringeuyi*	Myrmicinae	0	0.67	1.14	0.66	1.54	90.59
High	*Crematogaster* (cf) *peringueyi*	Myrmicinae	48.5	0	33.25	1.08	40.43	40.43
	Meranoplus (cf) *peringeuyi*	Myrmicinae	7.25	8.75	12.72	0.95	15.46	55.89
	Lepsiota sp. 1b	Formicinae	5.5	6	12.52	0.82	15.23	71.12
	Pachycondyla peringueyi	Ponerinae	6.75	1	10.34	0.97	12.57	83.69
	Camponotus irridux	Formicinae	2.25	0	2.34	1.09	2.84	86.53
	Camponotus sp. (a)	Formicinae	0.75	1	2.28	0.67	2.78	89.3
	Lepsiota sp. 1	Formicinae	0.75	1	1.43	0.69	1.73	91.04

SIMPER dissimilarity output of average abundance per sampling period (Av.Abund), average dissimilarity (Av.Diss) between habitat types and dissimilarity standard deviation (Diss/SD) and % contribution and cumulative % contribution per family to the overall dissimilarity between samples. Species numbering as recorded in the CIB ant collection, expect for those letters in parenthesis.

Abundance of the predatory beetles associated with *Cyclopia* species

Abundance of Anthicidae (ant beetles) were significantly higher ($H_{(2,103)}$= 20.17, p<0.001) at the 'high' disturbance study area in comparison to the 'low' and 'moderately' disturbed study areas. The other three predatory beetle groups were similar (p>0.05) across the three disturbance levels. The abundance of predatory beetles within the study areas only differed significantly at the 'high' disturbance study area (Figure 5.5). With Anthicidae again being the most prominent family, they were significantly higher (p<0.05) in abundance in comparison to the joint abundance of Staphylinidae and Cleridae ('other' category) (Figure 5.5). Coccinellidae were one of the more abundant predatory beetles within all three disturbance levels.
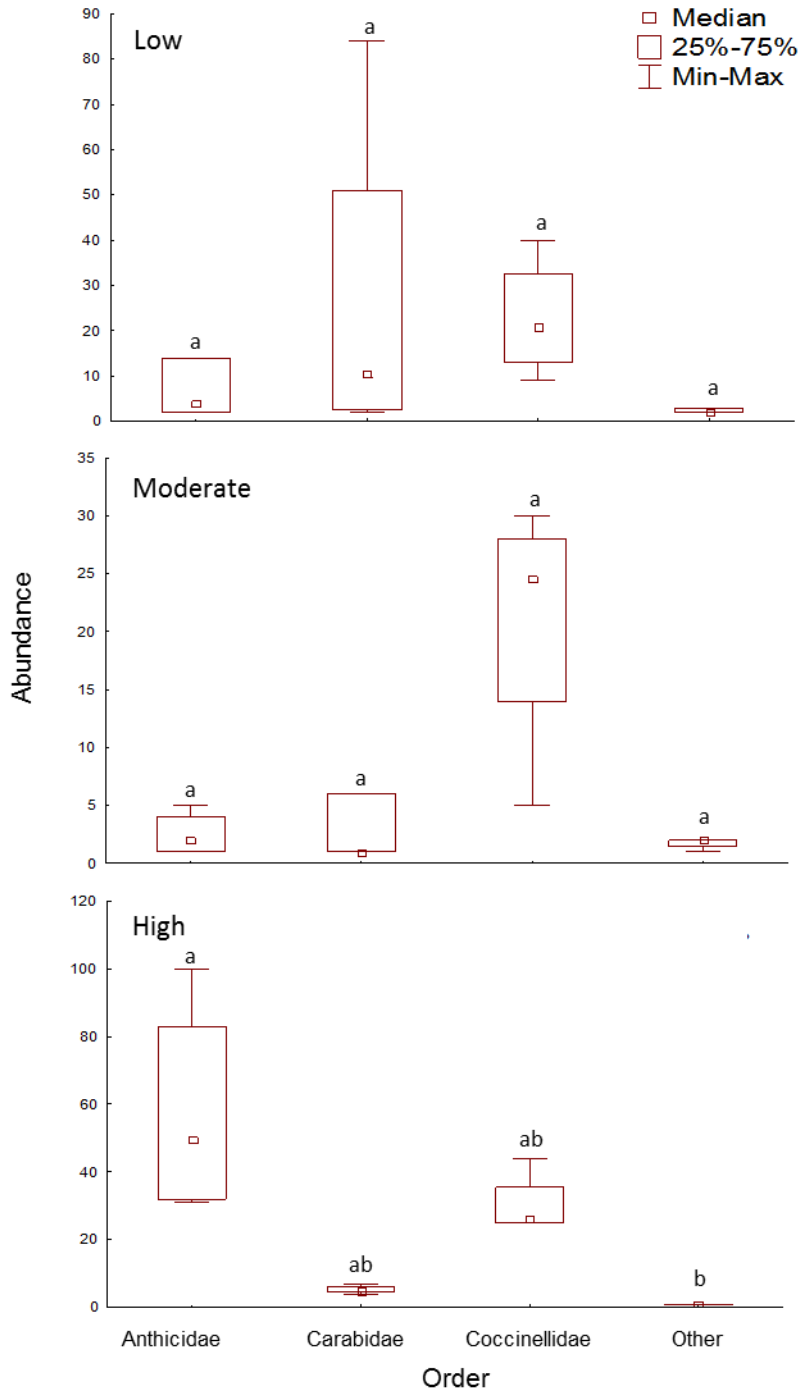
Figure 5.5. Abundance of the predatory Coleoptera associated with *Cyclopia* under various levels of disturbance (low, moderate and high). The category 'other' includes Staphylinidae and Cleridae. Letters indicate significant differences (Kruskal-Wallis ANOVA, 2-tailed multiple comparison) with the median and upper and lower quartiles.

5.4. Discussion

Disturbance within the wild and cultivated honeybush stands altered the composition of the associated arthropod assemblage. The phytophagous taxa were distinctly different between the three levels of disturbance and the diversity of the zoophagous arthropods proportionally lower within the highest disturbed study area. These results suggest that the balance between phytophagous and zoophagous functional groups was altered (Altieri & Nicholls 1999; Krüger & McGavin 2001; Manisegaran *et al.* 2006) within cultivated stands of honeybush with moderate to high levels of disturbance.

5.4.1. Impact of environmental factors on arthropods

Potential influence of plant host identity on the arthropod assemblage

The difference in the natural enemy complex associated with the *C. maculata* and *C. genistoides*, with regard to dominance of various predatory and parasitoid wasps (Chapter 4, section 4.3.2) and predatory beetles (Figure 5.5), suggests either a compositional difference caused by the host species and/or the impact of habitat disturbance within the cultivated honeybush stands. The phenology, growth habit and surface structures (e.g. trichome (leaf hair) density) of plant hosts, such as *Cyclopia*, also play a role in determining the species identity and composition of the associated natural enemy complex (Martin & Sauerborn 2013). *Cyclopia maculata,* being a much taller tree-like shrub would naturally harbor a different cohort of natural enemies than the low growth form of *C. genistoides*. Disturbance within the cultivated stands of *C. genistoides* seems to promote the dominance of Anthicidae. These are generally ground dwelling and predators of insect eggs or scavengers (Scholtz & Holm 1985). The low re-growth leaf canopies of *C. genistoides*, at the 'high' disturbance study area, seem to provide a favourable foraging niche for these generalist feeders.

Impact of land management practices on the functional assemblage of arthropods

Habitat disturbance, within the honeybush stands significantly altered the abundance and richness of defoliators (external feeders) and internal feeders at the low and high disturbance study areas, respectively. The impact of disturbance on these herbivorous groups is of relevance to honeybush production as several of the abundant families are potential pests, for example Curculionidae and Apionidae (as noted in Chapter 4, section 4.3.2). The altered abundance and richness of these phytophagous groups could be attributed to a range of factors potentially with synergistic effects. The habitat disturbance and unnatural density of honeybush due to cultivation could either dilute the regulatory role of natural biological control agents and/or promote the expansion and dispersal of herbivorous insect populations (Altieri & Letourneau 1982) that utilize

Cyclopia species as a host. The altered habitat conditions within the cultivated stands of honeybush could also have resulted in the loss of key natural predators and parasitoids for several of the abundant phytophagous families (Chapter 4, section 4.3.2). This is potentially the case at the 'high' disturbance study area with respect to the natural enemy complex associated with internal coleopteran feeders (e.g. Curculionidae and Apionidae). The diversity of external feeders at the 'moderately' disturbed study area was possibly due to favourable conditions created within the cultivated area (e.g. increased access to resources of both the *Cyclopia* and other early succession plants) (Altieri & Letourneau 1982; Tscharntke *et al.* 2005). The high plant diversity (personal observation) maintained within these cultivated fields would have promoted the abundance and diversity of natural enemies (Gaigher *et al.* 2015; Letourneau *et al.* 2011) thus promoting natural biological control (Kean *et al.* 2003; Nicholls *et al.* 2001) within honeybush stands. Recent work by Gaigher *et al.* (2015) found a positive relationship between the diversity of parasitoids and plant species richness within cover crops in vineyards and Fynbos fragments. While Nicholls and colleagues (2001) present evidence of the significant pest regulation exerted by natural enemies present within commercial crop plantations.

Impact of weather conditions on the arthropod assemblage

Wind specifically altered the abundance and richness of several feeding guilds by potentially either favouring or disrupting effective dispersal and/or foraging activity by arthropods within honeybush stands. The increased abundance and richness of feeding guilds; such as predator and parasitoid wasps and external feeders (Chrysomelidae), under windy conditions is presumably linked to the use of honeybush as sheltering sites during windy conditions. This was noted during windy sampling periods where low insect activity was often linked with high abundance of arthropods by d-vac sampling. The influence of wind could also be closely linked to the study areas and their respective management practices. The 'low' disturbance site generally had less frequent wind in comparison to the other two study areas. The altered ground cover at the 'high' disturbance study area further enhanced the impact wind would have on the movement of arthropods. The reduced alternative shelters and 'wind-breaks' provided by ground cover vegetation would have increased the level of dustiness within honeybush stands. Dusty conditions, resulting from exposed sandy soil and windiness, would have a negative effect on small insects, such as parasitoids, due to the dehydration caused by dust abrasion of their protective waxy lipid layers (Busvine 2013; Subramanyam & Hagstrum 2012). Ground cover plants within honeybush plantations would thus be beneficial for protecting natural enemies from dehydration caused by dusty conditions (Pettigrew 1998 in Addison 2004) and by providing additional refugia and foraging sites.

5.4.2. Consequences of disturbance on the natural enemy complex associated with *Cyclopia*

Ants (Hymenoptera: Formicidae)

The altered species composition and significant difference in abundance of ants between the honeybush and Fynbos habitats indicated a distinct change in the ant assemblage between the habitat types. The low level of similarity with respect to species composition between the habitat types suggests that the natural and cultivated stands of *Cyclopia* contain a distinctly different ant assemblage than the surrounding Fynbos vegetation. The sharp decrease of dominant ant species within the cultivated stands suggests that the complexity of the ant assemblage is altered such that less resilient, and potentially rare species, are lost within the system (Bihn *et al.* 2010; Tscharntke *et al.* 2002). Ants form an important function in the ecosystem with a wide range of feeding requirements; several polyphagous predators are important natural enemies while others have more diverse diets, including honeydew (e.g. *Camponotus* and *Technomyrmex*).The altered composition of ants, as important polyphagous predators (Aliniazee & Croft 1999; Philpott & Armbrecht 2006), could result in an altered ecosystem functioning within the honeybush stands. Bihn *et al.* (2010), for example, found that even a small change in species diversity of an ant assemblage to significantly decrease the ecological functioning within an ecosystem. The dominance of only a few common species, such as *Camponotus* and *Lepisiota,* within the cultivated honeybush stands in comparison with the higher diversity of species present within the Fynbos habitat suggests potential species loss under both 'moderate' and 'high' disturbance levels. The dominance of ants that include honeydew as part of their diet (e.g. *Campomotus*) could have a negative outcome by promoting infestations of other insects, such as aphids, as ant have a symbiotic relationship with these potnetail pests (protecting them from parasitoids in return for the honeydew they feed on).

The loss of ecosystem complexity, which is closely linked to species diversity, consequently could lead to a decrease in reliability of ecosystem functioning (Naeem 1998) within cultivated honeybush stands. More extensive sampling is recommended to determine the extent to which the ant assemblage has changed and how this has impacted on ecological functioning with regards to population regulation of potential pest organisms. Ants, as effective biological indicators (Andersen *et al.* 2002; Verdú *et al.* 2011), can also further be used to monitor the ecosystem integrity of honeybush plantations.

Parasitoid and predatory wasps (Hymenoptera)

The combination of isolation from natural vegetation and disturbance of non-crop vegetation within cultivated stands of *Cyclopia* had an antagonistic effect on the diversity and movement of

parasitoid and predatory wasps within honeybush stands. The high abundance and richness of zoophagous wasps (at increasing distances into the cultivated stands) at the moderately disturbed study area suggests that these sites harboured more natural enemies that could serve as natural biological control agents. The decrease in abundance and family richness of zoophagous wasps, as caused by isolation from natural vegetation (Chapter 4, section 4.3.2), was seen to be amplified by habitat disturbance (Figure 5.4). This synergistic outcome could be attributed to dispersal limitations created within cultivated landscapes (Henri *et al.* 2015; Tscharntke *et al.* 2005). Similar to the altered composition of ants within the honeybush stands, the confounding effect of disturbance and isolation could be attributed to the lower level of ground cover at the 'high' disturbance study area.

5.4.3. Concluding remarks

In conclusion, this study set out to determine the impact of disturbance, as created by land management practises within honeybush stands, on the functional composition of arthropods associated with *Cyclopia* species. The results indicated that the composition and functioning of the arthropod assemblage changed with an increased level of disturbance and isolation from the adjacent natural habitat. Results also suggested that the negative impact of isolation can be countered by use of land management practises that allow for moderate levels of disturbance which promote within field diversity of native plants (i.e. effective field-scale habitat management).

The species diversity of natural enemy complexes associated with *Cyclopia* species need to be conserved in order to ensure high functional diversity for the regulation of potential pest populations. Additional research is needed to determine the factors that will ensure ecological functioning within cultivated stands of honeybush. These would include the critical size of cultivated fields to maintain sufficient levels of movement of natural enemies between natural vegetation and cultivated stands, and the size and quality of refugia habitat required to maintain substantial populations of diverse natural enemies (i.e. effective landscape-level habitat management). Research within commercial South African crops, such as mango plantations (Henri *et al.* 2015) and vineyards (Gaigher *et al.* 2015), suggest distances ranging from 100 – 200 m for effective circulation of parasitoids and sufficient rates of parasitism within agroecosystems. The current study provides a preliminary guideline for field widths of approximately 100 m where natural vegetation is present adjacent to the cultivated area. More detailed and specialized studies are required to confirm optimal field widths and dispersal patterns of key natural enemies. If natural biological agents are not sufficiently conserved within honeybush plantations the resulting predation release of phytophagous arthropods could result in pest outbreaks. Should natural

biological control be maintained within *Cyclopia* plantations the industry would require minimal, if any, external chemical pest control measures. Given that the honeybush industry has the economic development of margainlised land-users as one of its goals (Du Toit *et al.* 1998), the reduced input costs associated with suggested land-use practices would be especially welcomed amongst these resource-poor producers. This combination of coarse- and fine-scale habitat management (Samways 2007) will promote sustainable, ecologically-friendly production. This holistic approach is suitable for the growing markets for ecologically and socially responsible produce.

5.5. References

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CHAPTER 6.

GENERAL DISCUSSION AND CONCLUSION

As an indigenous crop *Cyclopia* (Honeybush) species have the potential for ecologically sound commercial production through the endorsement of agroecosystem principles. As part of this commercialization approach it is important to understand the ecological framework within which honeybush cultivation and associated ecological interactions are taking place (Altieri & Letourneau 1982; Wilby & Thomas 2007). Understanding the interaction between plants and insects, with specific reference to insect herbivory, and the various factors that influence the ecological functioning becomes increasingly important in landscapes aimed at plant biomass production. The aim of the current study was to address the knowledge gap regarding the arthropod ecology of *Cyclopia* species as an upcoming indigenous South African crop. Identification of arthropod taxa relevant to honeybush production is important for establishing the potential arthropod-mediated ecosystem services and disservices associated with *Cyclopia* species. In order to do this the ecological framework of these interactions was investigated, firstly, by describing and analysing the phenology of the host plants and the abundance and richness of the associated arthropod assemblage (Chapter 3). From here the potential arthropod-mediated ecosystem services (AMES) and disservices associated with *Cyclopia* species were identified (Chapter 4). Lastly the impact that land management practices have on the functional composition of arthropod assemblages associated with *Cyclopia* species was assessed (Chapter 5). Identification of these AMES and disservices and their role in honeybush plantations are the first step toward valuing the economic contribution of these ecosystem services. Research findings will aid in establishing suitable agroecosystem guidelines for the expanding industry, as discussed in this final chapter. A synopsis of the main research findings and land management recommendations are outlined below.

6.1. Significant research outcomes and implications

Honeybush phenology and arthropod diversity

Qualitative phenology observations of wild *C. maculata* and cultivated *C. genistoides* indicated a high level of resemblance in seasonality of phenophase stages. Specific duration and timing of transitions between phenophases of the two honeybush species varied only with several days or one to two weeks. Flowering for both species peaked during October 2015. Transition between

phenophases was considered to be influenced by weather conditions and potentially also internal cues. The arthropod monitoring within honeybush stands revealed a high abundance and diversity of arthropods. The highest arthropod abundance corresponded with the spring time flowering period from September to October 2015. Harvesting of plant biomass during the flowering period could interfere with plant-insect interactions, such as pollination. The arthropod assemblage contained a diversity of families per functional feeding group relevant to biomass production, namely phytophagous, zoophagous and omnivorous taxa. These results revealed an existing level of ecological functioning in wild and cultivated stands of honeybush.

 As with other commercial crops, *Cyclopia* phenology and weather conditions (both seasonal and daily trends) can be useful in predicting insect development, foraging activity and migration between host plants in an agroecosystem (Ascerno 1991; Forrest & James 2011). These indicators would be useful for monitoring and estimating insect activity, especially insect herbivory and for informing pest management programmes for honeybush cultivation.

Arthropod-mediated ecosystem services and disservices associated with *Cyclopia* species

Several potential arthropod pests, similar to those found on rooibos (Hatting 2009, Hatting 2015), were found to be associated with *Cyclopia* species. In addition, a diverse collection of natural enemies, including parasitoids and predators from several Coleoptera and Hymenoptera families, were also recorded in wild and cultivated honeybush stands. Of the families recorded, several are known to be effective natural biological control agents in agroecosystems (Aliniazee & Croft 1999; Stevens *et al.* 2007). Several of the parasitoids were reared from Lepidoptera and scale insects collected on *Cyclopia* species, indicating that existing ecological interactions regulating potential agricultural pests are present.

The high abundance and richness of zoophagous wasps (i.e. parasitoids and predators) collected in *Cyclopia* stands in comparison to the adjacent Fynbos habitat suggest a high level of foraging activity in honeybush stands. The natural vegetation adjacent to cultivated *Cyclopia*, however, fulfills an important role in maintaining a high diversity of zoophagous wasps in central regions (approximately 50 meters from the field edge) of cultivated stands. Natural vegetation adjacent to cultivated fields provides essential refugia containing necessary resources and source populations of parasitoids and predators (Landis *et al.* 2000; Letourreau & Goldstein 2001). Increased isolation from natural vegetation through extensive cultivation could thus jeopardize the efficiency of the parasitoid or predation pressure by natural parasitoids and predators in

honeybush plantations. These ecological disruptions within cultivated honeybush fields could result in pest outbreaks.

The impact of land management practices of honeybush associated arthropods

The range of functional feeding guilds relevant to honeybush biomass production responded differently to disturbance, caused by land management practices, and prevailing weather conditions. External and internal phytophagous feeders were generally more abundant within the cultivated stands of honeybush with moderate to high levels of disturbance. Natural enemies (parasitoid and predatory wasps) were the most abundant within the low disturbance study area. Family richness of zoophagous wasps decreased significantly with increased isolation from the natural vegetation and habitat disturbance of the non-crop vegetation within the cultivated fields. The composition of the ant assemblage within the honeybush stands also differed from that of the adjacent Fynbos habitat and was accentuated by habitat disturbance brought about by land management practices. These changes in species composition of arthropods altered the functional composition of the assemblage (Bihn *et al.* 2010; Kruess & Tscharntke 1994) and could result in the loss of ecological functioning within cultivated honeybush stands.

These findings support the trend seen in species loss of different functional guilds as a consequence of habitat loss, isolation and varying levels of habitat degradation (Golden & Crist 1999; Holzschuh *et al.* 2010). Higher trophic levels (and especially specialist feeders), such as natural enemies within an arthropod assemblage, are more sensitive to habitat transformation (at field- and landscape scale) than lower trophic levels (Chaplin-Kramer *et al.* 2011; Holzschuh *et al.* 2010). The potential decrease in functional guild diversity of natural enemies in cultivated honeybush stands would have negative, cascading effects on trophic level interactions (e.g. complementary of natural enemy complexes) and efficiency of natural biological control (Kruess & Tscharntke 1994; O'Connor *et al.* 2013; Wilby & Thomas 2002). The altered ecosystem functioning and the loss of AMES could have negative implications for honeybush biomass production as is evident in the rooibos industry (e.g. see Hatting *et al.* 2011). The extensive commercial plantations of rooibos use a traditional 'weed-free' monoculture approach. This approach disregards the potential of natural biological control by not incorporation landscape elements and land management practices that create a suitable agricultural matrix for natural enemies to survive and forage in rooibos plantations. Consequently many farmers suffer high production losses under heavy pest infestation (Hatting *et al.* 2011).

6.2. Honeybush cultivation: challenges, opportunities and future research

The commercialization of *Cyclopia* species as an indigenous crop has created rising tension between the value of biodiversity and the market value (Wiens 2009) of honeybush. Since biodiversity is often side lined or even disregarded in favour of increased production (Altieri & Nicholls 1999; Naeem *et al.* 1999), the current challenge for the honeybush industry is whether there is common ground. Although many studies have shown that maintaining biodiversity within agricultural landscapes has benefits for production (e.g. enhanced pest control) (Bianchi & Wopke 2003; Thies *et al.* 2011), there are, however, also a few studies with ambiguous results *(*Bell *et al.* 2006; Long & Finke 2014).

Although the presence of natural enemies within an agroecosystem does not necessarily relate to effective biological control (Chaplin-Kramer *et al.* 2011) its value is often under estimated as the dependence of producers on natural biodiversity is greater than realized. The extent and value of the 'service', such as natural biological control, is only appreciated once the organisms are no longer present or in high enough population numbers to make a significant contribution (Altieri & Nicholls 1999). Considering the potential pest complex and diverse natural enemy complex identified in this study, taking on a "precautionary approach" (Freestone & Hey 1996; Vandermeer 2011) in avoidance of future pest outbreaks is recommended. The alternative economic expense, should pesticides be required, is an additional external input that is not feasible for the current size of the industry (Joubert *et al.* 2011). It would also add to the financial burden of resource-poor small-scale land-users for whom honeybush is a potential means of livelihood sustenance.

Existing research suggests that to maintain a high level of ecosystem function, and reap the benefits of the associated AMES, that the complexity of agroecosystems needs to be conserved (Altieri & Nicholls 1999; Holzschuh *et al.* 2010; Isaacs *et al.* 2009). The potential for natural biological control to be maintained within commercial honeybush plantations thus depends on several factors pertaining to habitat management pre- and after a harvest event, as well as the conservation of adequate portions of natural vegetation adjacent to cultivated stands. The main goal of these habitat management strategies should be to maintain or enhance the habitat complexity within and near to agricultural land.

For example, habitat management techniques of crop fields and non-crop vegetation include, among others, planting suitable cover-crops; use of ground-cover mulch; polycultures; inter-cropping, companion planting; push-pull technology (e.g. see Khan *et al.* 2008); crop rotation;

weed manipulation; various tillage practices (e.g. no-tillage practices or seasonal tillage of crop residue) and manipulation of field margins or other landscape features (e.g. windbreaks or hedge rows) (Altieri & Letourneau 1982). The push-pull technology, for example, is a fairly advanced IPM strategy that has shown promise for control of *Eldana saccharina* (Walker) (Lepidoptera: Pyralidae) in KwaZulu-Natal sugar cane fields (Cockburn 2013). It is, however, recommended that this system be used as part of an Integrated Pest Management (IPM) program together with appropriate land management practises. Many of these techniques have been developed for high intensity, monoculture agroecosystems where extensive habitat transformation has already taken place across the biogeographical region. Several of these techniques could be applicable for honeybush cultivation depending on the state of the surrounding landscape.

Habitat management strategies for promoting natural biological control, however, use a fine- and coarse-scale approach for conserving the 'ecological infrastructure' natural enemies require for survival and effective foraging in agroecosystems (Landis *et al.* 2000). These habitat management practices, of which several are very similar to those listed above, additionally focus on the importance of natural vegetation for maintaining the natural enemy complex in agricultural landscapes. Henri *et al.* (2015), for example, found that the intact natural vegetation surrounding mango plantations in the north-eastern part of South Africa serve as refugia for a diverse natural enemy complex that provides effective natural biological control of three key mango pests. The rate of successful predation and parasitism was jeopardized by increased isolation from the natural vegetation. This ecologically based approach also places emphasis on maintaining functional connectivity within the agricultural landscape, for example, movement of arthropods between remnant patches of natural vegetation and into agricultural fields. This requires that land management strategies provide natural enemies alternative or additional food and shelter resources within and adjacent to cultivated areas. Field level (fine-scale) strategies include, among others, retaining habitat corridors into cultivated fields, or establishing floral insectary strips (pollen and nectar resources) or beetle banks (alternative shelter and prey) were natural vegetation has already been removed. The rooibos industry has recently set up biodiversity guidelines that promote similar, among other, best practice ideals (Pretorius 2009; Pretorius *et al.* 2011). These include farm planning that maintains habitat corridors that are 10 – 20 meters wide and within 500 m of other natural habitat, or restoration vegetation corridors of ±10 meters in areas already under extensive rooibos cultivation. The optimal width of plantations are set at a maximum of 30 meters (Pretorius 2009). Although, the adoption and implementation of these strategies on cultivated rooibos plantations are still premature and many experience severe pest

infestations, strategies such as these are suitable for the implementation in the honeybush industry. The current research findings (this thesis) could be used to develop similar ecology-based sustainability guidelines for the honeybush industry.

The additional coarse-scale approach of habitat management strategies aimed at conserving natural biological control is relevant for maintaining structural and/or functional connectivity across the agricultural landscape. This is achieved through effective landscape planning. Farmland layout is strategic, using conservation principles (Samways 2007), to ensure that a sufficient amount of high quality natural habitat is retained and connectivity between these are maintained (e.g. via corridors between remnants of natural vegetation) (Landis *et al.* 2000). These landscape features enhance ecological interaction between crop and non-crop habitat and promote natural biological control. Holzschuh *et al.* (2010), for example, noted the impact habitat fragmentation and the agricultural matrix had on the beneficial ecological interactions in the wheat production region of Germany. Their comparison of commercial versus low-intensity (organic farming) land management practices revealed the latter to maintain a significantly higher rate of predation by predatory wasps. Low-intensity farming practices (including setting aside non-crop habitat) created a favourable habitat network within cultivated areas and housed a population of predatory wasps comparable to that of adjacent non-crop habitat.

Recommendations from the current study underscore the importance of a combined fine- (field level) and coarse-scale (landscape) approach for conserving the diverse natural enemy complex associated with *Cyclopia.* This will promote efficiency of natural biological control among other unaccounted AMES (e.g. pollination and nutrient-cycling) within cultivated honeybush plantations. The negative impact of isolation, resulting from cultivation of extensive areas, can be countered by use of land management practices that promote high native plant diversity within the cultivated area, for example, the low-intensity cultivation practices used for wildflower propagation. Intermediate-intensity cultivation practices used for wildflower propagation has been found to be a biodiversity-friendly land-use practice for the Agulhas plain (Joubert *et al.* 2009). Joubert *et al.* (2009) found that shallow-plough treatments, preceding augmentation of a low growing protea species, to increase native plant diversity of understory vegetation. This was presumably due to the delay of natural veld succession, thus favouring the diversity of native weedy and pioneer plants within cultivated fields. This approach would also be beneficial to honeybush farmers as ground cover of native plants is superior to other cover crops in promoting natural biological control in agroecosystems (Isaacs *et al.* 2009). Relying on natural succession of native Fynbos plants would also be more cost effective requiring minimal external input.

129

Low-intensity land management practices are becoming more widely used in European countries, as well as South Africa. Research by Nicholls *et al*. (2001) in European vineyards found that organic field management should be combined with habitat corridors to promote effective biological control in vineyards. A recent study in South African vineyards by Gaigher *et al*. (2015), had similar recommendations of combining conservation of natural vegetation remnants and low-intensity land management to create a more 'arthropod-friendly agricultural matrix. The combined approach would conserve natural enemy populations and facilitate movement and foraging of potential biological control agents into commercially cultivated areas. Similar land management practices are already successfully implemented by some honeybush farmers, as was the case at the moderately disturbed study area. This low-intensity approach is especially relevant for agricultural activity within a biodiversity rich matrix (Perfecto & Vandermeer 2008), and is suitable across the full spectrum of potential honeybush production (small- and large-scale farmers). Recommended land management practices would also be in line with legislature and land management regulations for agricultural activity in biodiversity rich areas (e.g. Environmental Management: Biodiversity Act, among other). These habitat management practices would additionally render Honeybush cultivation as a potential alternative for restoring fallow lands to productive landscapes that also have conservation value.

The opportunity of ecological and social sustainability holds great potential to become part of the honeybush trademark. The mechanisms by which this is possible already exist in the persuence of the industry in such initiviates as application for Geographic Indication statis for honeybush (Anonymous n.d.; Troskie & Biénabe 2013), fairtrade labels and other market-oriented assurance schemes. These schemes are well established in the rooibos sector, and, by implication, may be somewhat less onourous for the honeybush industry to embark upon. Whichever land management approach is used it should be effective in maintaining the functional diversity of natural enemies and the ecological interactions of honeybush-associated arthropod assemblages, at field- and landscape level. This will allow for the continued regulation of undesired organisms in commercial honeybush stands.

Several aspects related to the efficiency and seasonality of arthropod-mediated ecosystem services associated with *Cyclopia* species could be further investigated, as discussed in the conclusion of each data chapter. One of the most important aspects would, however, be to quantify the contribution of the AMES and estimate its economic value for Honeybush cultivation. Establishing economic thresholds of potentential pests would be part of the research steps toward developing sound intergrated pest management strategies for the honeybush industry.

Quantifying the contributuion of natural biological pest control for the industry would also be relevant for influencing current and future policy frameworks aimed at sustainable honeybush production, especially in light of cultivation and conservation in agricultural landscapes.

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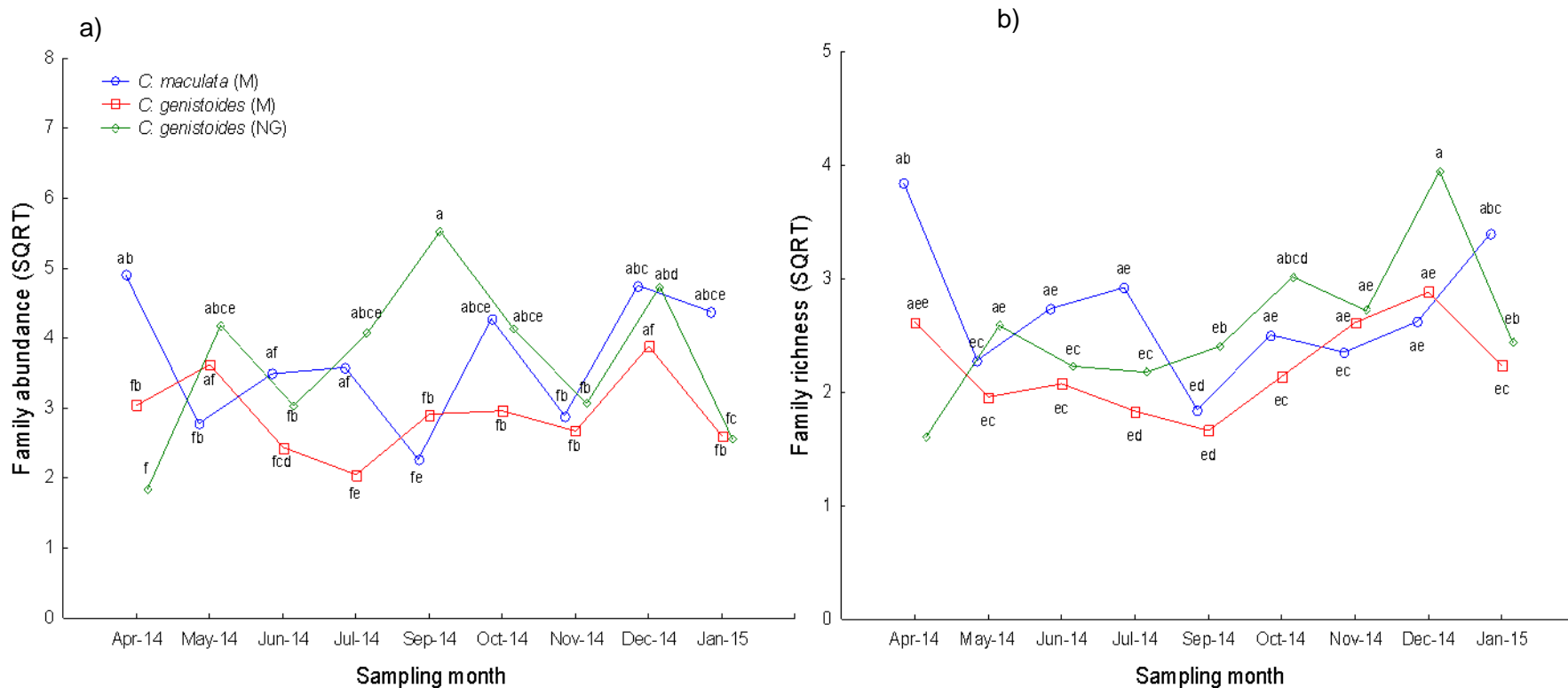
APPENDIX A

Figure A.1 (a) Family abundance and (b) family richness of the zoophagous invertebrate assemblage associated with *Cyclopia* spp. by d-vac sampling from April 2014 to January 2015. Two of the study areas were dominated by mature wild *C. maculata* (M) and cultivated *C. genistoides* (M); the third study area of cultivated *C. genistoides* (NG) was harvested shortly before arthropod monitoring commenced. Different alphabetical letters indicating significant differences within and across months (REML, LSD post hoc). To simplify graph interpretation, 95% confidence intervals have been omitted.

Figure A.2 Family abundanc e of the phytophagous insect assemblage associated with *Cyclopia* spp. by d-vac sampling from April 2014 to January 2015. Two of the study areas were dominated by mature wild *C. maculata* (M) and cultivated *C. genistoides* (M); the third study area of cultivated C. genistoides (NG) was harvested shortly before arthropod monitoring commenced. Different alphabetical letters indicating significant differences within and across months (REML, LSD post hoc). To simplify graph interpretation, 95% confidence intervals have been omitted.
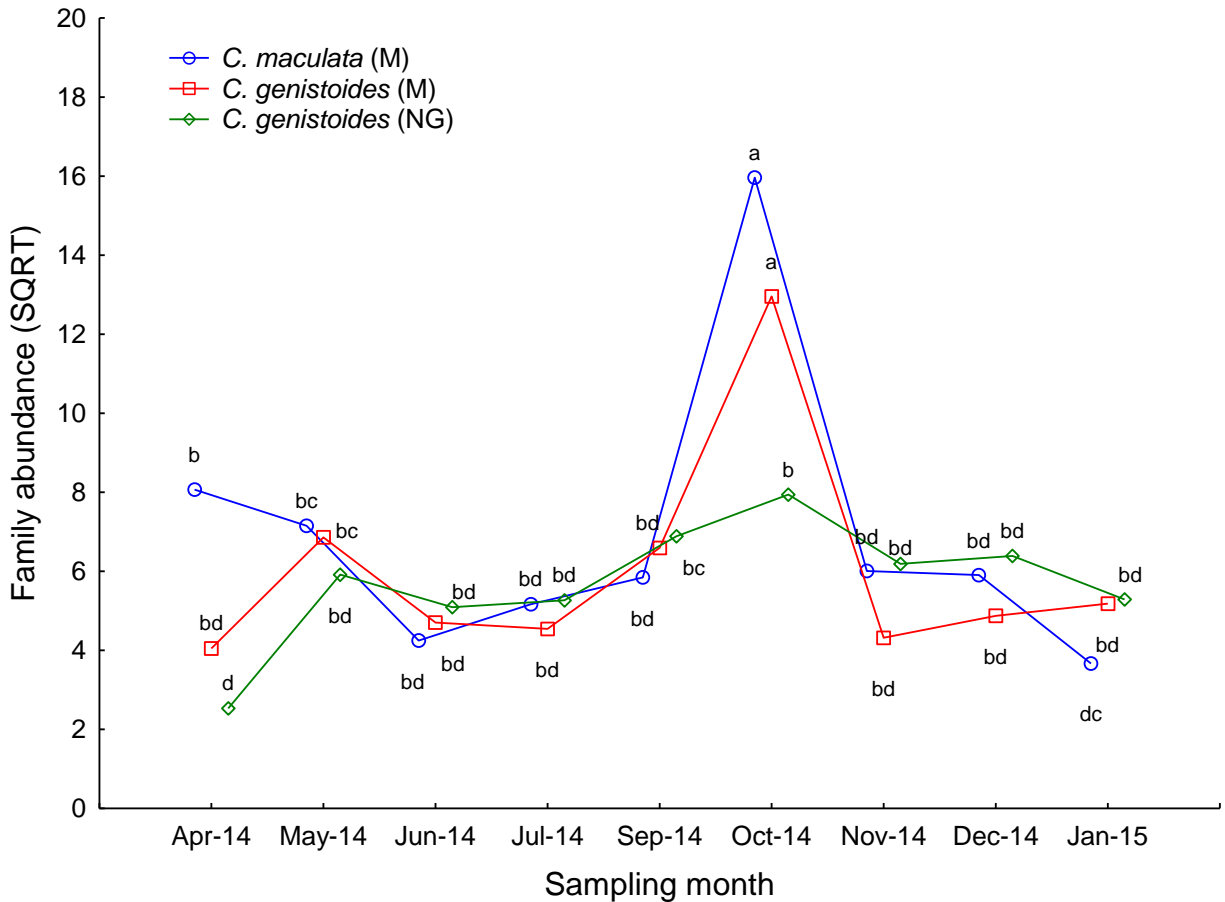
Table A.1. Dominant zoophagous wasps per habitat type (Honeybush and Fynbos) as collected by pan trap sampling from April 2014 to April 2015.

Habitat type	Family	FFG	Av. Abund	Av. Sim	Sim /SD	% Contrib	Cum. %
Fynbos	Pompillidae	Pred	2.04	11.83	1.49	23.07	23.07
	Sphecidae	Pred	2.05	10.23	1.8	19.95	43.02
	Platygastridae	Para	1.77	7.77	1.24	15.15	58.17
	Encyrtidae	Para	0.85	3.72	0.88	7.25	65.42
	Bethylidae	Para	0.77	3.14	0.82	6.12	71.54
	Ichneumonidae	Para	0.68	2.89	0.74	5.63	77.16
	Tiphiidae	Para	0.8	2.59	0.73	5.06	82.22
	Mymaridae	Para	0.82	2.53	0.75	4.94	87.16
	Plumariidae	?Para	0.64	1.85	0.43	3.61	90.78
Honeybush	Platygastridae	Para	2.86	9.51	2.73	17.14	17.14
	Pompillidae	Pred	2.2	8.85	1.62	15.95	33.09
	Encyrtidae	Para	1.44	4.8	1.7	8.65	41.74
	Mymaridae	Para	1.32	4.5	1.24	8.11	49.85
	Sphecidae	Pred	1.16	4.28	1.13	7.72	57.58
	Bethylidae	Para	0.95	2.89	0.97	5.21	62.79
	Eulophidae	Para	1.02	2.8	1.04	5.06	67.85
	Ichneumonidae	Para	1.24	2.71	0.8	4.89	72.73
	Pteromalidae	Para	0.89	2.57	0.9	4.63	77.36
	Braconidae	Para	0.98	2.54	0.74	4.57	81.93
	Plumariidae	?Para	0.87	2.53	0.66	4.56	86.49
	Diapriidae	Para	0.75	2.09	0.61	3.77	90.26

'FFG', Functional feeding guild ('Pred', predator, 'Para', parasitoid); 'Av.Abund', average abundance per sampling period, 'Av.Sim', average similarity and 'Sim/SD' similarity standard deviation and % contribution and cumulative % contribution per family to the overall similarity between samples per habitat.

Table A.2. Comparison of the zoophagous wasp composition between honeybush and Fynbos habitat.

| Family | Habitat type | | | | | |
| | Fynbos | Honeybush | | | | |
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	% Contrib	Cum.%
Platygastridae	1.77	2.86	4.69	1.13	9.07	9.07
Tiphiidae	0.8	0.7	3.11	1.03	6.03	15.1
Mymaridae	0.82	1.32	3.07	1.46	5.94	21.05
Sphecidae	2.05	1.16	2.99	1.33	5.79	26.84
Eulophidae	0.49	1.02	2.88	1.23	5.57	32.41
Pompillidae	2.04	2.2	2.59	1.13	5.02	37.43
Diapriidae	0.4	0.75	2.59	0.96	5.01	42.44
Braconidae	0.31	0.98	2.41	1.08	4.66	47.1
Encyrtidae	0.85	1.44	2.39	1.04	4.64	51.73
Ichneumonidae	0.68	1.24	2.38	1.03	4.61	56.35
Eupelmidae	0.51	0.55	2.25	1.01	4.36	60.71
Bethylidae	0.77	0.95	2.18	0.98	4.23	64.93
Pteromalidae	0.31	0.89	2.03	0.96	3.94	68.87
Eurytomidae	0.08	0.65	1.79	0.89	3.47	72.34
Plumariidae	0.64	0.87	1.79	0.72	3.46	75.8
Proctotrupidae	0.08	0.57	1.59	0.87	3.07	78.87
Torymidae	0.2	0.45	1.43	0.86	2.76	81.63
Chrysididae	0.37	0.17	1.19	0.76	2.31	83.94
Chalcididae	0.08	0.45	1.16	0.8	2.25	86.19
Eumenidae	0.28	0.08	0.95	0.63	1.83	88.03
Aphelinidae	0.08	0.28	0.87	0.62	1.69	89.71
Scoliidae	0.28	0	0.83	0.55	1.6	91.31

Average abundance per sampling period (Av.Abund), average dissimilarity (Av.Diss) and dissimilarity standard deviation (Diss/SD) and % contribution and cumulative % contribution per family to the overall dissimilarity between samples.

Table A.3. Composition of Coccinellidae within the three honeybush stands of either mature (M) or new growth (NG) *C. maculata* and *C. genistoides*. (Waiting on species identifications)

Study area	Species	Av.Abund	Av.Sim	Sim/SD	% Contrib	Cum. %
C. maculata (M)	Coccinellidae sp. 1	1.92	15.92	2.79	42.43	42.43
	Exochomus flavipes	1.37	6.78	0.85	18.08	60.51
	Coccinellidae sp. 4	1	5.57	0.89	14.85	75.36
	Hippodamna variegata	0.71	2.24	0.41	5.96	81.32
	Coccinellidae sp. 5	0.71	1.98	0.41	5.29	86.61
	?Epilachna infirma	0.75	1.76	0.41	4.69	91.3
C. genistoides (M)	Coccinellidae sp. 2	1.85	16.46	4.55	36.8	36.8
	Coccinellidae sp. 1	1.75	10.24	0.91	22.9	59.7
	Cheilomenes lunata	1.18	6.39	0.89	14.3	74
	Coccinellidae sp. 3	0.85	6.15	0.88	13.76	87.76
	?Epilachna infirma	0.79	2.14	0.41	4.8	92.55
C. genistoides (NG)	Coccinellidae sp. 2	2	16.5	6.82	30.27	30.27
	Coccinellidae sp. 3	1.93	12.06	7.41	22.12	52.4
	Cheilomenes lunata	1.31	10.02	3.71	18.38	70.78
	Coccinellidae sp. 6	1.79	4.26	0.41	7.82	78.6
	Hippodamia variegata	0.93	3.99	0.9	7.31	85.91
	Coccinellidae sp. 7	1.44	3.7	0.91	6.79	92.7

Average abundance per sampling period (Av.Abund), average dissimilarity (Av.Sim) and similarity standard deviation (Sim/SD) and % contribution and cumulative % contribution per family to the overall similarity between samples per study area.

Table A.4. Dominant hemipteran species associated with *Cyclopia* species; namely *C. maculata* and *C. genistoides*, (M) = mature, unharvested bushes, (NG) = new growth of recently harvested bushes. (Waiting on species identifications)

Study Area	Species	Av.Abund	Av.Sim	Sim/SD	% Contrib	Cum.%
C. maculata (M)	Cicadellidae sp. 1	9.87	41.39	1.53	65.51	65.51
	Aphididae sp. 1	6.44	21.8	3.18	34.49	100
C. genistoides (M)	Cicadellidae sp. 1	10.22	42.62	3.03	76.2	76.2
	?Flatidae sp. 1	1.63	4.98	0.79	8.9	85.09
	Aphididae sp. 1	2.14	4.15	0.83	7.42	92.51
C. genistoides (NG)	Aphididae sp. 1	4.04	18.68	7.32	36.44	36.44
	Cicadellidae sp. 2	3.28	11.98	5.16	23.36	59.8
	Cicadellidae sp. 1	3.04	6.2	0.83	12.1	71.91
	Fulgoridae sp. 1	2.17	5.22	0.81	10.18	82.09
	?Flatidae sp. 1	1.7	3.74	0.81	7.3	89.39
	Cercopidae sp. 1	1.39	2.88	0.88	5.62	95.01

Average abundance per sampling period (Av.Abund), average dissimilarity (Av.Sim) and similarity standard deviation (Sim/SD) and % contribution and cumulative % contribution per family to the overall similarity between samples per habitat.

Table A.5. Dominant Apionidae and Curculionidae associated with *Cyclopia* species, namely *C. maculata* and *C. genistoides*, (M) = mature, unharvested bushes, (NG) = new growth of recently harvested bushes. (Waiting on species identifications)

Study area	Species	Av.Abund	Av.Sim	Sim/SD	% Contrib	Cum.%
C. maculata (M)	Apionidae sp. 1	3.63	30.71	2.48	75.12	75.12
	Baris sp. 1	1.24	7.2	0.85	17.6	92.72
C. genistoides (M)	Curculionidae sp. 1	0.75	6.67	0.41	54.55	54.55
	Apionidae sp. 1	0.5	5.56	0.41	45.45	100
C. genistoides (NG)	Apionidae sp. 1	2.88	10.58	7.4	25.68	25.68
	Apionidae sp. 2	2.24	9.45	6.93	22.93	48.6
	Tanyrrhynchus sp. 1	2.39	6.73	2.8	16.32	64.92
	Curculionidae sp. 2	1.95	3.59	0.73	8.71	73.63
	Curculionidae sp. 3	1.35	2.91	0.9	7.05	80.68
	Curculionidae sp. 4	1.96	2.91	0.9	7.05	87.73
	Curculionidae sp. 5	0.79	1.21	0.41	2.94	90.67

Average abundance per sampling period (Av.Abund), average dissimilarity (Av.Sim) and similarity standard deviation (Sim/SD) and % contribution and cumulative % contribution per family to the overall similarity between samples per habitat.

Table A.6. Comparison of habitat types, honeybush and Fynbos, in terms of Lepidoptera abundance from Delta traps.

| Family | Habitat type | | | | | |
| | Fynbos | Honeybush | | | | |
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	% Contrib	Cum.%
Tortricidae	3.43	2.93	12.02	1.2	31.77	31.77
Noctuidae	1.4	1.62	6.64	0.99	17.56	49.32
Pyralidae	1.34	1.3	6.1	1.08	16.13	65.46
Geometridae	0	0.53	3.39	0.88	8.96	74.42
Syntomidae	0.63	0.65	3.39	0.71	8.95	83.37
Lasiocampidae	0.23	0.31	3.28	0.67	8.66	92.03

Average abundance per sampling period (Av.Abund), average dissimilarity (Av.Diss) and dissimilarity standard deviation (Diss/SD) and % contribution and cumulative % contribution per family to the overall dissimilarity between samples.
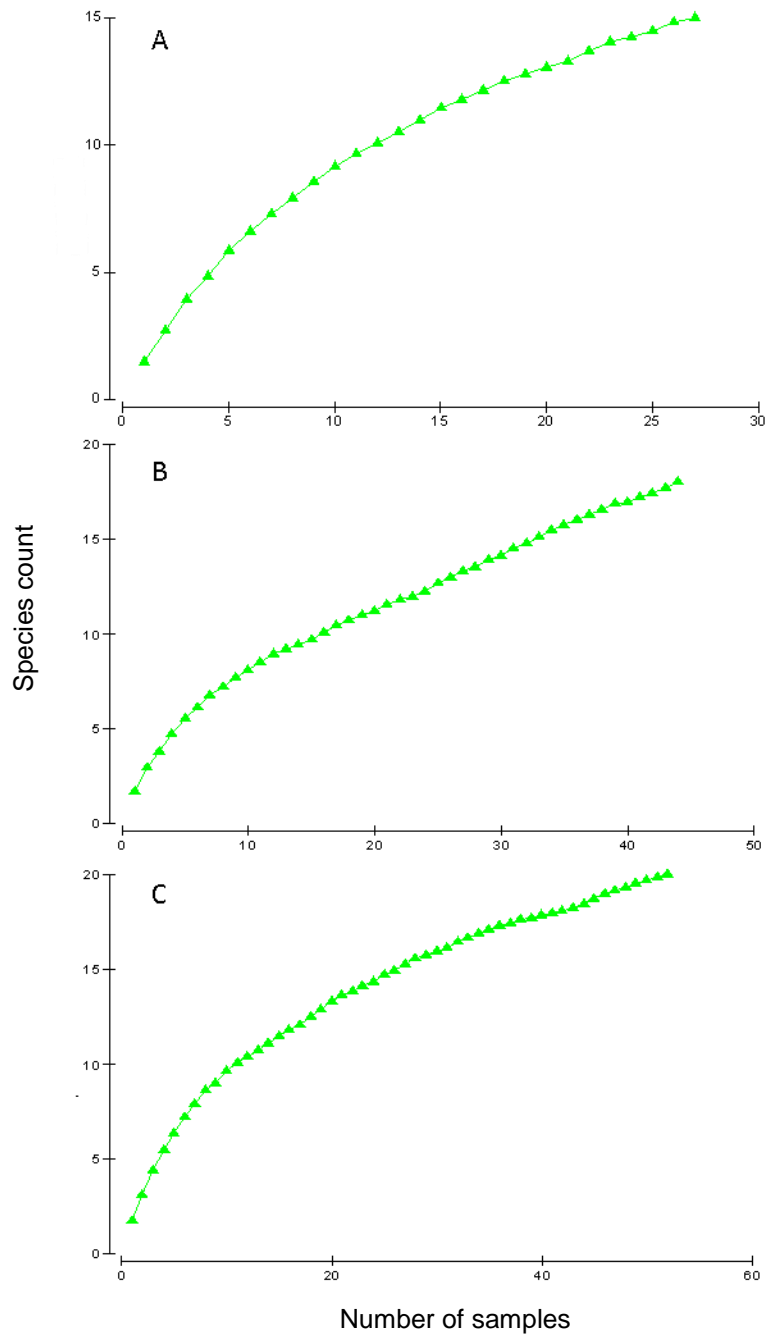
Figure A.3. Species accumulation curves for the Formicidae at the three study areas, namely near Genadendal (A), Bredasdorp (B) and Pearly Beach (C) for pan trap sampling from April 2014 to April 2015.

APPENDIX B
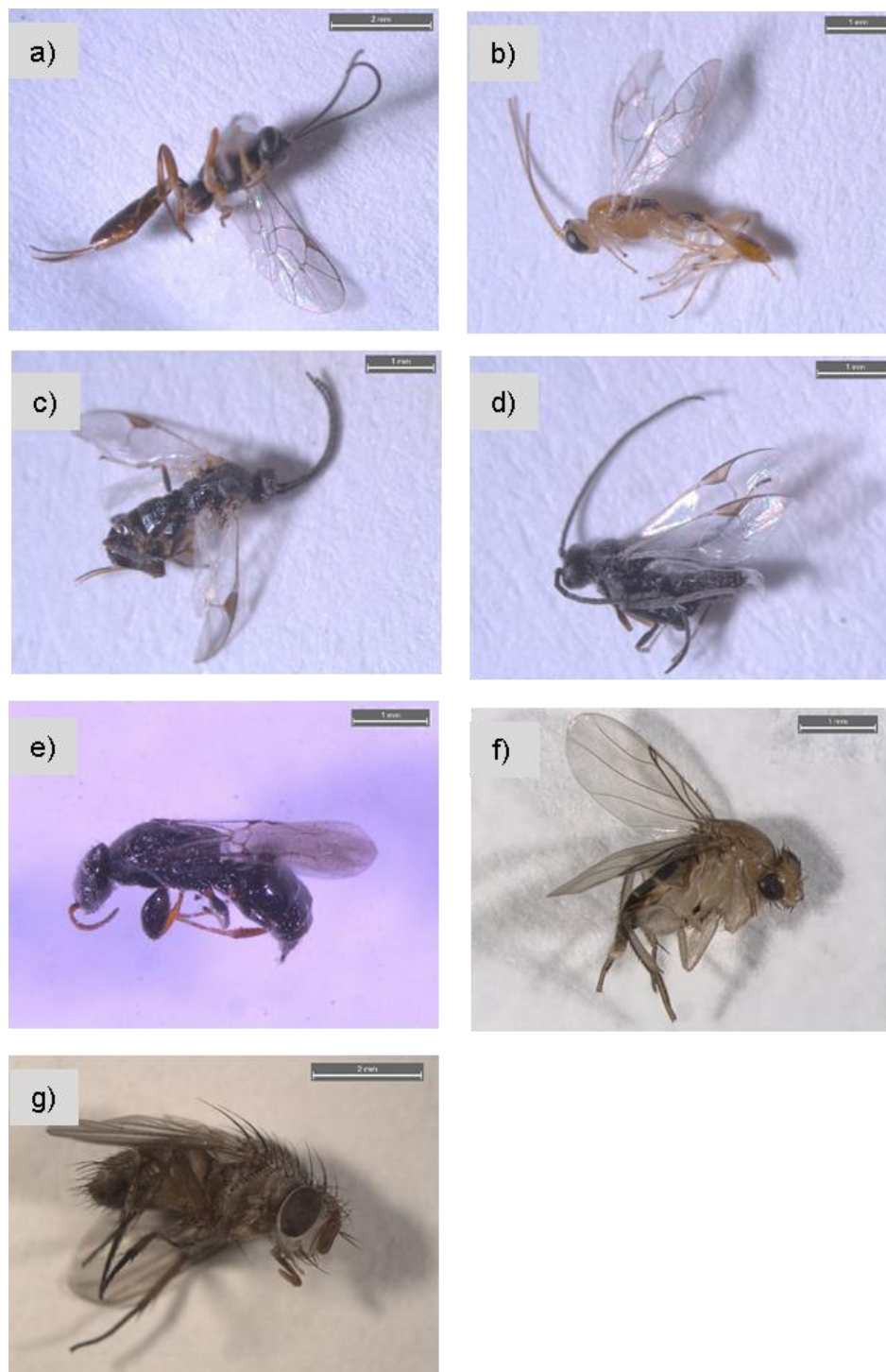
Figure B.1. Parasitoid wasps (Hymenoptera) and flies (Diptera) reared from Lepidoptera larvae: (a) Ichneumonidae sp. 1; (b) Ichneumonidae sp. 2; (c) Proctotrupidae sp. 1; (d) Proctotrupidae sp. 2; (e) Bethylidae sp. 1; (f) Tachinidae sp. 1 and (g) Tachinidae sp. 2.
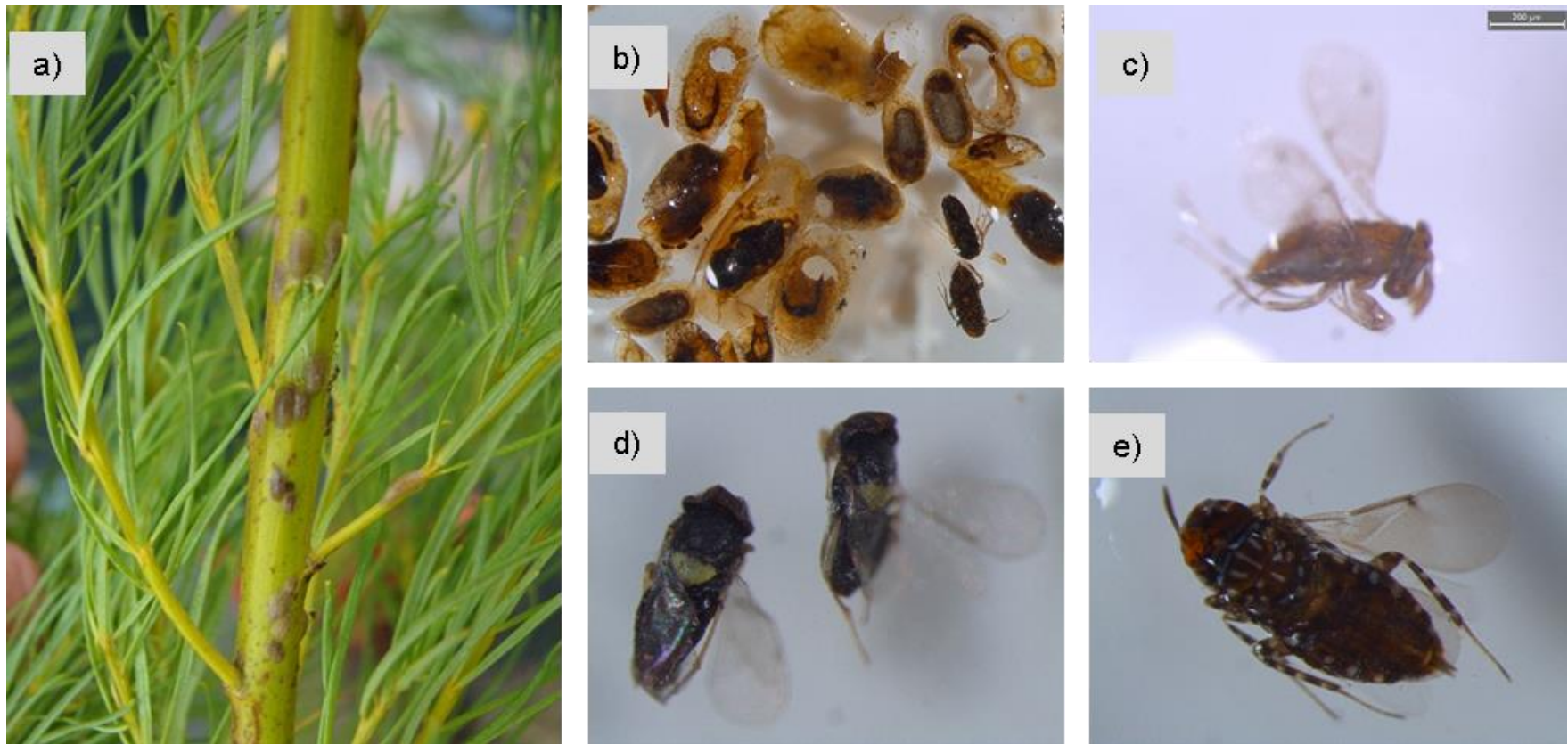
143

Figure B.2. (a) Soft Brown Scales (Cossidae) (on wild *Cyclopia maculata*) and parasitoid wasps reared from an (b) infested colony (on cultivated *C. subternata* in the Genadnedal area), these included three Aphelinidae species, (c) Aphelinidae sp. 1 (<1 mm); (d) Aphelinidae sp. 2 (<1 mm); (e) Aphelinidae sp. 3 (<1 mm).
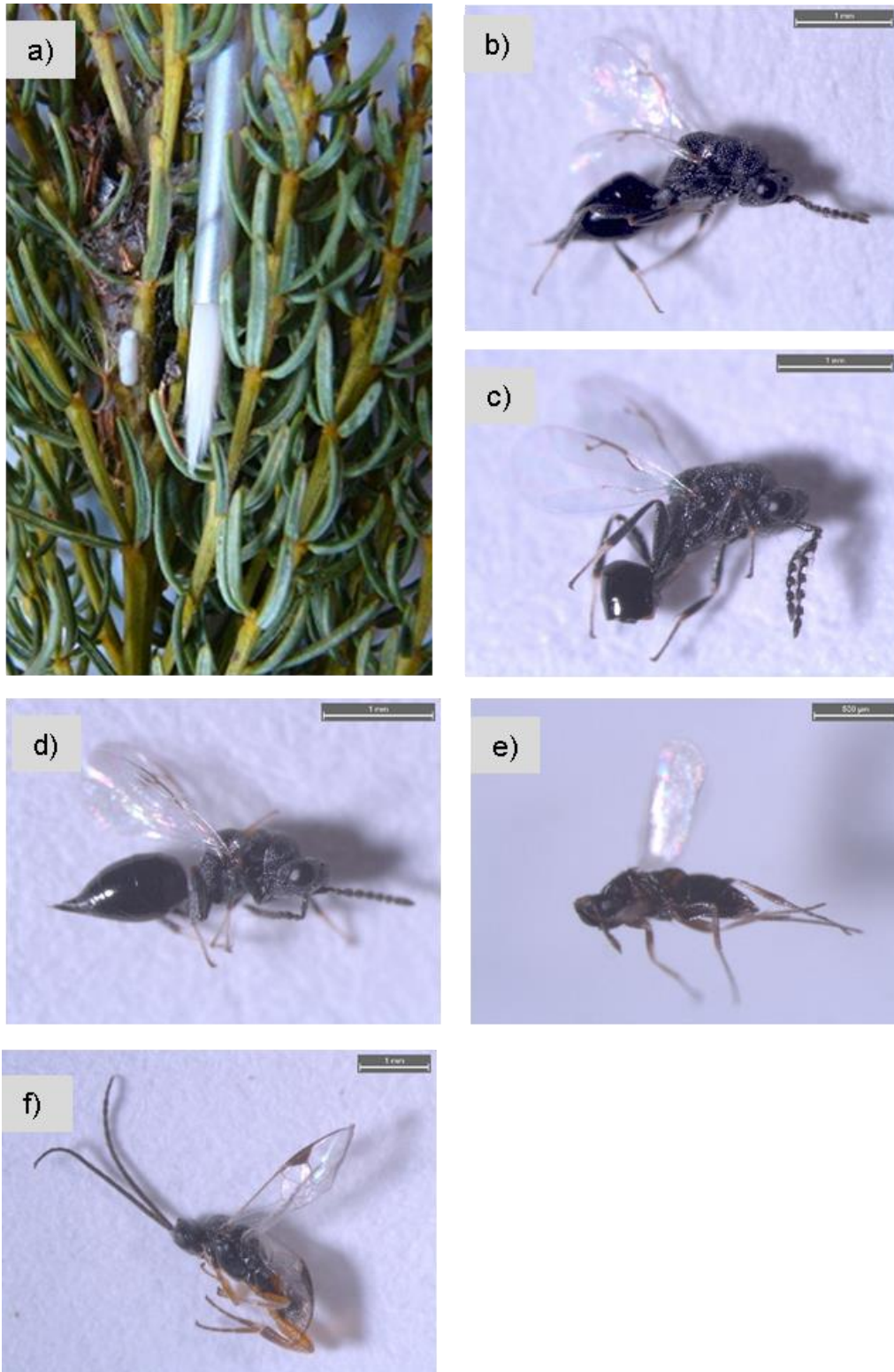
Figure B.3. Hyperparasitoidson braconids, (a) Braconidae cocoon; (b) Eurytomidae sp. 1; (c) Eurytomidae sp. 2; (d) Eupelmidae sp. 1; (e) Eulophidae sp. 1 (<1 mm) and (f) Proctotrupidae sp. 3.
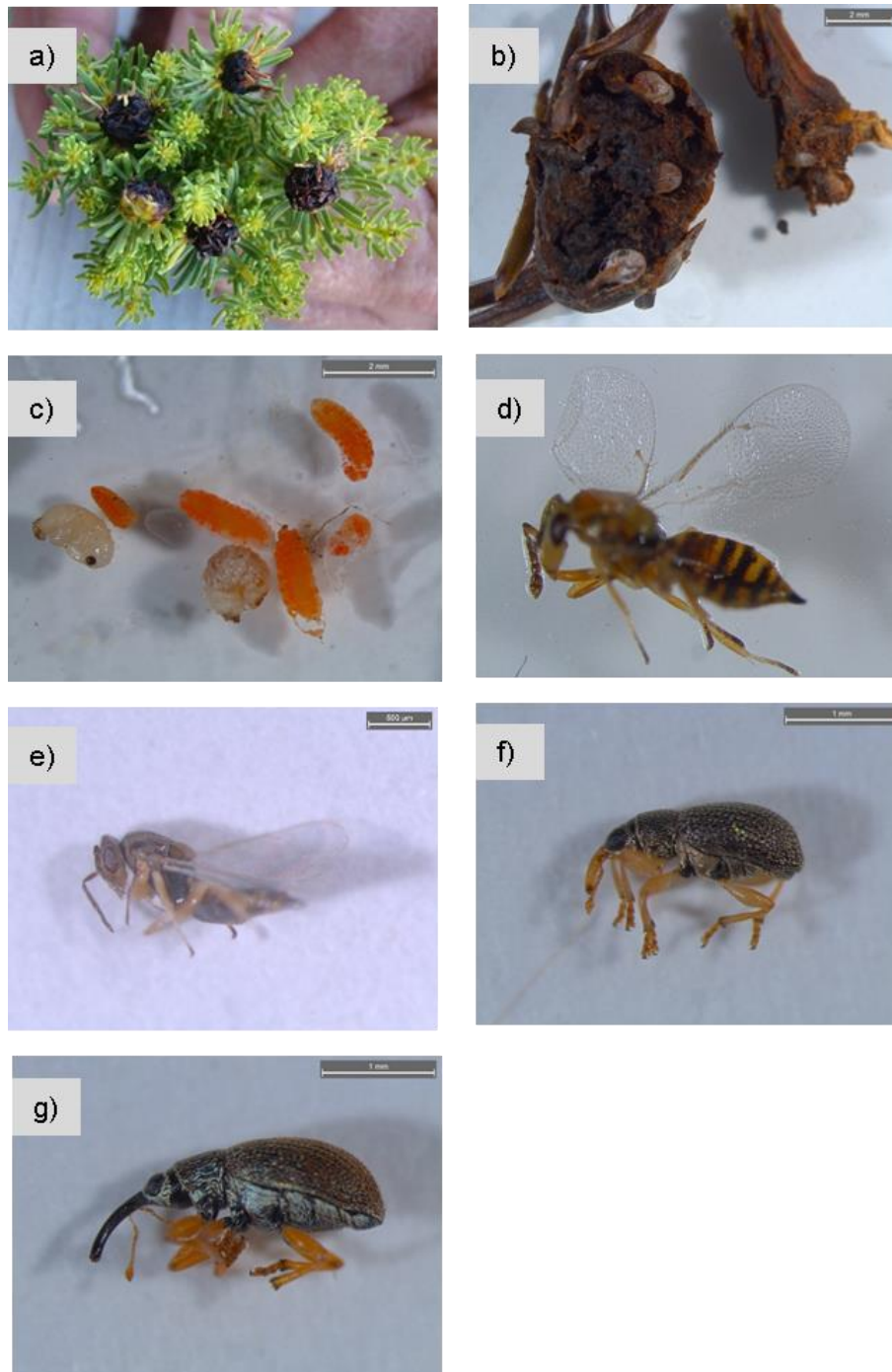
Figure B.4. Green galls on cultivated *Cyclopia genistoides* potentially caused by eriophyt mites with a secondary infestation of (?) phytophagous wasps and apionidae: (a) mature galls that have turned brown; (b and c) larvae of wasps (orange grubs) and apionidae (pale grubs) inside galls; (d) Eulophidae sp. 3 (±0.5 mm); (e) Eupelmidae sp. 2 (<1 mm); (f) Apionidae sp. 1 (±1.5 mm) and (g) Apionidae sp. 2 (±2.5 mm).
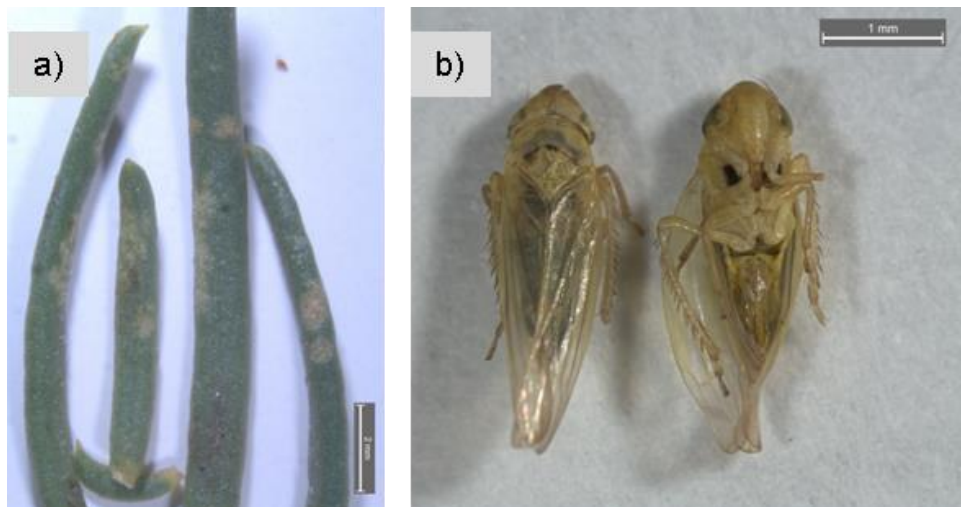
Figure B.5. (a) Plant feeding damage by leafhoppers (b) Cicadellidae sp. 1 (Hemiptera).
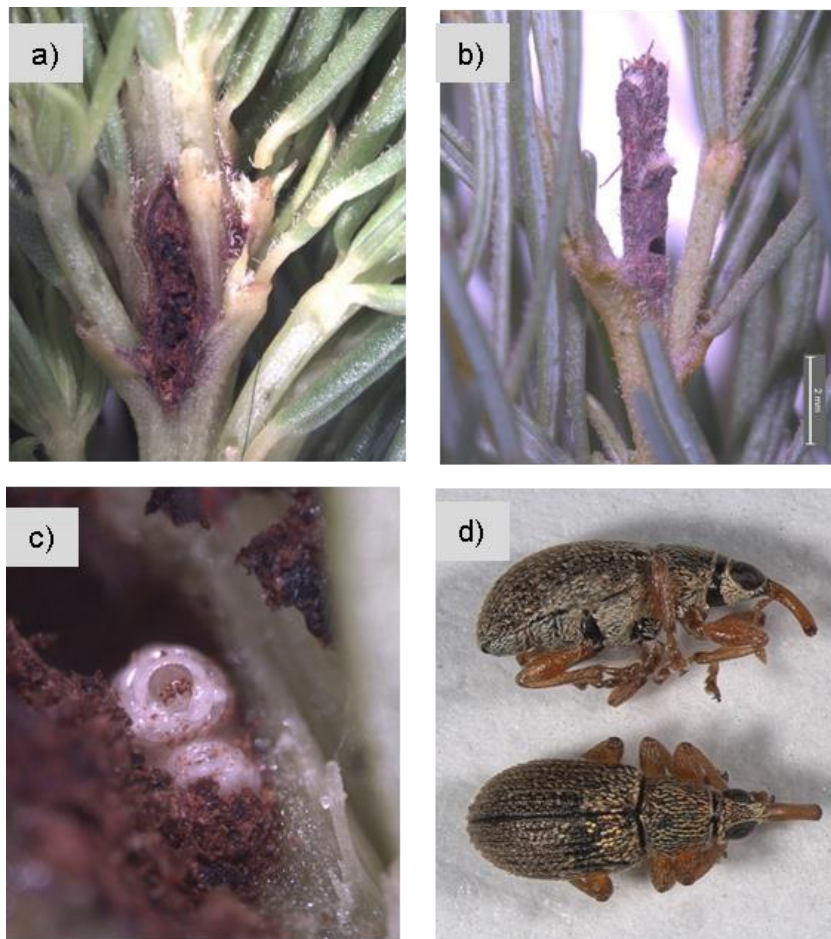
Figure B.6. Internal feeding damage by Apionidae forming (a) galls and (b) shoot damage, (c) pale apionid grub feeding inside gall, these reared into two apionid species (d) Apionidae sp. 1 1 (±1.5 mm) and sp. 2 (±2.5 mm).
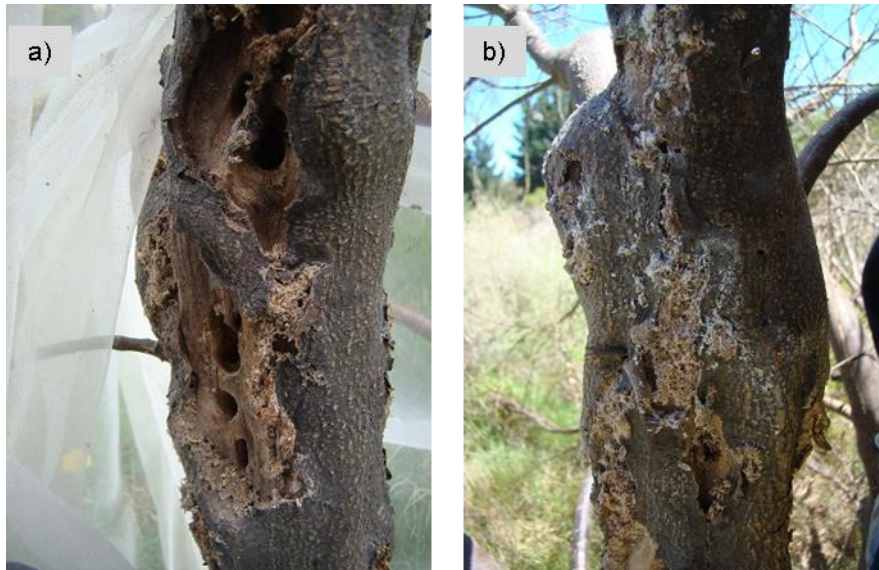

Figure B.7. (a) Internal stem feeding damage by a *Coryphodema tristis* (Quince borer) on wild *Cyclopia maculata,* (b) with a secondary infestation of mealybug (Pseudococcidae) and ants occupying the stem cavities*.*
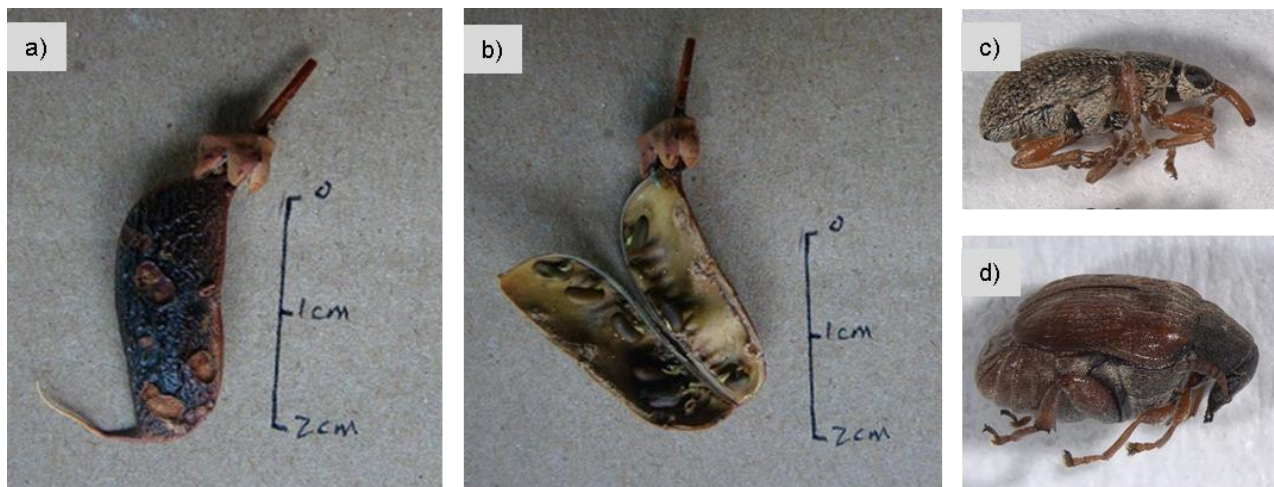

Figure B.8. (a and b) Seed pod feeding damage by (c) Apionidae sp. 1 (±1.5 mm) (reared from wild *Cyclopia maculata* and cultivated *C. genistoides*) and (d) Bruchidae sp. 1 (±2 mm) (reared from cultivated *C. subternata*).

148