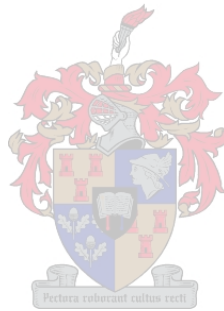


**The conservation value of habitat remnants for
flower visiting insects in the lowlands of the
Cape Floristic Region**

by

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*Dissertation presented for the degree of Doctor of
Agriculture at the University of Stellenbosch*



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Declaration

By submitting this thesis/dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Sven Michael Vrdoljak

December 2010

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General summary

Conservation in biodiversity hotspots is an important challenge facing conservation scientists and practitioners. By definition, hotspots are areas with high biodiversity, that have undergone severe transformation and habitat loss. The existing coverage of protected natural areas is unlikely to meet conservation targets, particularly in bio-diverse regions with high levels of species turnover and endemism. Options for expanding the coverage of protected areas are generally limited, due to the limited extent of remaining natural habitat and the fact that much of what does remain exists as scattered fragments, many of which are situated on privately owned land. However the retention of a significant portion of biodiversity within agricultural landscapes prevents us with a valuable opportunity to address these challenges. To do so, we need to be able to integrate biodiversity and agricultural production to create multi-use, ecoagricultural landscapes. This outlook encompasses not only the biodiversity value of protected areas, but also a range of natural and semi-natural habitat remnants that exist within the transformed matrix.

The broad objective of this dissertation is to determine whether or not insect diversity can be linked to plant diversity not only reserve areas, but also remnants of natural habitats within agricultural land. The aim is also to assess the diversity of plants and insects within these remnants and value of remnants for achieving biodiversity conservation. This study focuses on flower visiting insects (anthophiles), a group that includes insect pollinators and play a keystone role in many terrestrial ecosystems. The study was conducted in floristically diverse, but highly threatened lowland habitats in the Cape Floristic Region (CFR). The CFR is a biodiversity hotspot renowned for its high floral diversity, yet relatively little is known about the insect diversity of the region. The work covers four main topics: the relevance of particular techniques used to survey anthophiles (Chapter 2), species turnover and the relationships between plant and anthophile diversity (Chapter 3), the importance of habitat remnants in farmland for biodiversity conservation (Chapter 4), and plant-insect interactions (Chapters 5 & 6). Ultimately these topics follow the common theme of contributing relevant ecological knowledge towards insect conservation in the CFR, while drawing firm conclusions about the value of remnants of natural habitat for both plant and anthophile conservation in the region.

The study was conducted in habitats below 400 m a.s.l., as these are some of the most threatened in the region. The research area extended from 18° 44' E 33° 24' S to 19° 07' E, 34° 08' S, with sites separated into three distinct regions: the Elandskloofberge, encompassing Elandsberg Nature Reserve and the surrounding Bartholomeus Klip farm; Somerset West, encompassing Helderberg Nature Reserve, Vergelegen Estate and Cordoba Estate; and Groenlandberg Conservancy, encompassing Klipfontein (part of the Hottentots-Holland Nature Reserve), and the Diepkloof Private Nature Reserve. Within each of these regions a reserve area and several satellite sites in remnant, natural/semi-natural habitat were selected. Anthophile assemblages were surveyed across the study area during the spring flowering period (September-December) in 2004 and 2005. Anthophiles were sampled using coloured pan traps. In 2005 flowering plant assemblages were surveyed using detailed line transects at all pan trapping sites. A flower-visitation

survey using observation plots was conducted at Elandsberg Nature Reserve in early October 2007.

Overall, pan traps were an effective method for sampling the major groups of anthophiles in the region (Coleoptera, Diptera and Hymenoptera), but butterflies (Lepidoptera) were strongly underrepresented. Colour played an important role in determining the species-richnesses and composition of those pan trap catches. For monitoring and comparative studies, the use of at least three colours – yellow or white, combined with a short wavelength colour (e.g. blue) and a long wavelength colour (e.g. red) is recommended. For census and inventory studies it is recommended that pan trap surveys be augmented excluded by pan traps.

The pan trap surveys showed species richness and turnover of anthophiles to be similar to that of plants for most sites. While there was some congruence between species turnover and the assemblage similarity of sites based on the two groups, plant diversity was overall a poor indicator of insect diversity. These patterns were consistent across spatial scales ranging from 0.5 – 80 km. While patterns of plant diversity and distribution play a role in shaping anthophile assemblages, they are not reliable predictors and plant species richness has limited applicability as a surrogate for anthophile species richness.

Anthophile species richness for sites outside reserves was found to be similar to those within reserves for anthophiles. Species richness was more variable for plants, although sites outside reserves often retained a high diversity of flowering plants. Comparison of assemblage structure among sites found that sites shared 20-38% of their insect species and 12-28% of plants species, while each category of sites (transformed, heavily disturbed, natural remnants and reserves) retained species that were not found elsewhere in the landscape. The complementarity of sites in different habitats means that species retained in areas outside of reserves make a major contribution to the overall biodiversity of the region. Successful biodiversity conservation in the Cape Floristic Region should follow a more integrative approach, considering the entire landscape as a heterogeneous, ecoagricultural system, rather than considering reserves as islands of diversity within an inhospitable agricultural matrix

At the scale of floral patches, visitation surveys showed a strong positive relationship between visitation frequency and total area, and number of visual displays. Categorical floral traits (e.g. colour), affected visitation less consistently than did continuous traits (e.g. visual display area). There was a positive relationship between visitation frequency and measures of floral similarity for all traits combined, and for continuous traits alone, but not for categorical traits alone. At the community level, visitation frequency was influenced more by the density and abundance of floral resources than by traits specific to individual flowers, making these continuous floral traits more reliable predictors of visitation frequency. Interactions in this highly endemic, southern hemisphere community mirrored those in a northern temperate grassland community, although composition of the visitor pool differed markedly. Anthophile visitation was positively affected by density and diversity of flowers in plots, but was also influenced by floral species composition. Responses to these variables also differed between the various anthophile groups observed. These results show that anthophile activity is affected by very localised, small-scale factors, in particular those related to the abundance and diversity of floral resources

Pollinator conservation needs to consider small scale, localised effects of the surrounding community on plant-pollinator interactions, which can affect the activity and abundance of anthophiles in remnant of natural habitats across the landscape.

Algemene opsomming

Bewaring in biodiversiteit gevaarpunte ('hot spots') is 'n belangrike uitdaging wat deur bewaringswetenskaplikes en praktykbeoefenaars in ag geneem moet word. Volgens definisie is gevaarpunte gebiede met 'n hoë biodiversiteit, maar wat desnieteenstaande, ook ernstige transformasie en habitatverlies ondergaan het. Dit beteken dat bewaringsdoelwitte onwaarskynlik deur die bestaande dekking van natuurgebiede, veral in streke met hoë vlakke van endemisme, bereik kan word. Keuses om die dekking uit te brei, is in die algemeen beperk. Om die uitdagings aan te spreek, is dit nodig dat ons in staat moet wees om biodiversiteit en landbouproduksie deur die skepping van veelvuldige gebruik van ekolandboukundige landskappe te integreer. Hierdie siening behels nie net die biodiversiteitswaarde van beskermde gebiede nie, maar ook 'n reeks van natuurlike en half-natuurlike habitat oorblyfsels wat binne omgeskakelde matrysse bestaan.

Die breë doelwit van hierdie proefskrif is om te bepaal of die insekdiversiteit wel of nie aan plantdiversiteit in reservaatgebiede en oorblyfsel habitatte in die laelande van die Kaapse Floristiese Gebied (KFG) gekoppel kan word. Die doel is ook om die waarde van hierdie oorblyfsels te bepaal om bewaringsdoelwitte in die streek te bereik. Hierdie studie bepaal hom by blombesoekende insekte (BBI), 'n groep wat insekbestuiers wat 'n sleutelrol in hierdie floristies-diverse streek speel. Hierdie werk dek vier hoof aspekte: die toepaslikheid van ekologiese opname tegnieke (Hoofstuk 2), spesies omkering en die verwantskappe tussen plant en BBI diversiteit (Hoofstuk 3), die belang van habitat oorblyfsels in landboulande vir biodiversiteit bewaring (Hoofstuk 4), en plant-insek interaksies (Hoofstukke 5 & 6). Uiteindelik dra hierdie aspekte by tot die gemeenskaplike tema van bydraende toepaslike ekologiese kennis tot insekbewaring in die KFG.

Die studie is in laaglande (onder 400 m b.s.v.) uitgevoer aangesien hierdie van die mees bedreigde habitatte in die streek vorm. Die ondersoekgebied het gestrek van 18° 44' O 33° 24' S tot 19° 07' O 34° 08' S, met areas verdeel in drie aparte streke: die Elandskloofberge, wat die Elandsberg Natuurreservaat en die omliggende plaas Bartholomeus Klip insluit; Somerset-Wes, wat die Helderberg Natuurreservaat, Vergelegen Landgoed en Cordoba Landgoed insluit; en Groenlandberg Bewaringsgebied, wat Klipfontein (deel van die Hottentots-Holland Natuurreservaat) en die Diepklowe Privaat Natuurreservaat insluit. In elk van hierdie streke is 'n reservaatgebied en verskeie satalietareas in oorblyfsel, natuurlik/half-natuurlike habitat gekies. BBI samestellings is regdeur die studiegebied gedurende die lente blomperiode (September-Desember) in 2004 en 2005 bepaal. BBIs is deur middel van gekleurde panvalle gemonster. In 2005 is plantstrookopnames gebruik om blomplant samestellings vir alle panval plotte te bepaal. 'n Blombesoekende opname, deur gebruik van waarnemingplotte, is gedurende vroeg Oktober 2007 in die Elandsberg Natuurreservaat uitgevoer.

In die algemeen was panvalle doeltreffend vir monsterring van die hoofgroepe BBIs in die streek (Coleoptera, Diptera en Hymenoptera), maar skoelappers (Lepidoptera) was grootliks ondervteenwoordig. Kleur speel 'n belangrike rol in die bepaling van spesiesrykheid en samestelling van panvalvangste. Vir monitering en vergelykende studies word die gebruik van ten minste drie kleure

– geel of wit, in kombinasie met 'n kort golflengte kleur (byvoorbeeld blou) en 'n lang golflengte kleur (byvoorbeeld rooi) aanbeveel. Vir sensus en inventaris studies word aanbeveel dat panvalvangste deur aktiewe versameling en ander tegnieke om skaarser taksa en die wat andersins uitgesluit word deur panvalle, aangevul word.

Die panval opnames het aangetoon dat spesiesrykheid en omset van BBIs vergelykbaar is met plante vir die meeste gebiede. Alhoewel daar 'n mate van ooreenstemming tussen spesies omsetting en die soortgelykheid van plekke, gebasseer op die twee groepe, was, was plantdiversiteit oor die algemeen 'n swak aanduiding van insekdiversiteit. Hierdie patrone was standhoudend en in ooreenstemming oor ruimtelike skale wat gewissel het van 0.5 – 80 km. Terwyl patrone van plantdiversiteit en verspreiding 'n rol speel by die vorming van BBI groeperings, is hulle geen betroubare voorspellers en moet alleen met voorbehoud gebruik word.

Spesies rykheid van BBIs in gebiede buite die reservate was soortgelyk aan dié in reservate self. Spesies rykheid was meer veranderlik vir plante, alhoewel gebiede buite die reservate dikwels 'n hoë diversiteit van blomplante behou het. Vergelykings van groeperings tussen gebiede het getoon dat gebiede 20-38% van hulle insekspesies en 12-28% van plantspesies gedeel het, terwyl elke kategorie van gebied (omgeskakel, ernstig versteur, natuurlike oorblyfsels en reservate) spesies behou het wat elders in die landskap afwesig was. Dit beteken dat habitate buite reservate 'n groot

bydrae maak tot die oorhoofse biodiversiteit van die streek. Suksesvolle biodiversiteit bewaring in die Kaapse Floristiese Gebied behoort die hele landskap as 'n heterogene, ekolandbou sisteem te oorweeg, eerder as om 'n "reservaat teenoor landbou" benadering te volg.

Op die skaal van plantgebiede het besoekende opnames 'n sterk positiewe verwantskap tussen besoekfrekwensie en totale gebied en getal visuele vertonings getoon. Uitdruklike blomeienskappe (byvoorbeeld kleur) het blombesoeke minder in ooreenstemming geraak as aanhoudende eienskappe (byvoorbeeld visuele vertoon gebied). Daar was 'n positiewe verwantskap tussen besoekers-frekwensie en maatstawwe van plantgelykheid vir alle eienskappe saam, en vir aanhoudende eienskappe op hulleself, maar nie vir uitdruklike eienskappe op sigself nie. Op die gemeenskapsvlak was besoekfrekwensie meer beïnvloed deur plantdigtheid eerder as deur spesifieke eienskappe van individuele blomme, wat aanhoudende planteienskappe meer betroubaar as voorspellers van besoekersfrekwensie maak. Interaksies in hierdie hoogs endemiese, suidelike hemisfeer gemeenskap word weerspieël in dié van die noordelike gematigde grasveld gemeenskap, alhoewel samestelling van die besoekerspoel duidelik verskil het. BBI besoeke was positief beïnvloed deur digtheid en verskeidenheid van blomme in die plotte, maar was ook beïnvloed deur die samestelling van plantspesies. Reaksie tot hierdie veranderlikes het ook tussen die verskillende groepe BBIs waargeneem, verskil. Die huidige resultate toon dat BBI aktiwiteit beïnvloed word deur veral gelokaliseerde, kleinskaal faktore. Bestuwigsbewaring moet hierdie kleinskaal, gelokaliseerde effekte van die omliggende gemeenskap op plant-bestuier interaksies, veral vir aanhoudende eienskappe oor geheel gemeenskappe in ag neem.

Flowers are essentially tarts. Prostitutes for the bees

. - Uncle Monty, in *Withmail and I* (Bruce Robinson)

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The world on a flowerhead. A pollen covered halictid bee is captured by a crab spider while foraging, as a tephritid fly looks on. Meanwhile, unseen on the top of the flower two male hopliine monkey beetles battle over mating rights to a female.

Sven Vrdoljak, 2004

1

General introduction

"Only by understanding the environment and how it works can we make the necessary decisions to protect it" Kofi Annan, Secretary General, United Nations

"Hope is the only bee that makes honey without flowers." Robert C. Ingersoll

Biodiversity in agricultural landscapes

There is general consensus that the world is currently undergoing a massive extinction event, with species numbers declining at a rate that far exceeds background extinction levels (Lawton & May 1995; Pimm et al. 1995; Vié et al. 2009). This “Sixth Extinction” (Leakey & Lewin 1996) is driven largely by human-induced change to world ecosystems, brought about by an expanding human population and its increasing utilisation of space and natural resources. The most important mode of human-driven extinction is the destruction and fragmentation of natural habitat (Leakey & Lewin 1996; Laurance & Cochrane 2001; Tscharntke et al. 2002). These two, correlated processes leave behind a mosaic of habitat patches of varying size, shape, isolation and quality (Saunders et al. 1991; Banks 2000). Species become isolated in these patches and experience varying degrees of extinction risk depending upon their mobility, degree of specialisation (Krauss et al. 2003; Pauw 2007) and other ecological attributes (Tscharntke et al. 2002). Habitat loss is a pernicious threat to biodiversity in that its effects are often synergistic with other threats such as global climate change, genetic and environmental contamination, and invasive alien organisms (Samways 2007).

The evolutionary biologist Niles Eldredge referred to agriculture as “the single most profound ecological change in the entire 3.5 billion-year history of life” (Eldredge 2001), with Tilman et al. (2001) predicting that another 10^9 ha of natural ecosystems will be converted to agriculture by the year 2050. This massive expansion of agriculture, coupled with the realisation that protected areas alone will not prevent global biodiversity loss (Rodrigues et al. 2004), has led to a shift in the focus of conservation towards including areas outside of protected areas (Norton 2000; Solomon et al. 2003; Goodman 2003; Dudley et al. 2005).

Although reserves currently protect over 18.3 million km² of land worldwide (Chape et al. 2005), their configuration is often sub-optimal in terms of the size required to maintain viable populations, adequately representing habitat and species diversity, resilience to global climate change and compatibility with adjacent land use (Brooks et al. 2004; Rodrigues et al. 2004). The increasing demand for more land by a growing human population, and limits on available funds, precludes large scale expansion of protected area networks in many regions (Perrings et al. 2006), so we need to turn to the ‘next best’ option, integrating conservation into agricultural practice. This is not unrealistic given that agricultural land already holds much of the world’s biodiversity (Pimentel et al. 1992). Studies have already empirically shown the benefits that integrating habitat remnants and human-influenced areas, such as field margins into conservation plans, can have for biodiversity (Kromp &

Steinberger 1992; Lagerlöf et al. 1992; Feber et al. 1996; Dover 1997; Thomas & Marshall 1999; Pryke & Samways 2003; Benton et al. 2003; Duelli & Obrist 2003; Carvell et al. 2004; Woodcock et al. 2005; Pywell et al. 2005; Pywell et al. 2006; Dauber et al. 2006; Öckinger & Smith 2007; Field et al. 2007). However, although many common species can benefit from relatively simple modifications to farming practice, rare and endangered species may still need elaborate conservation measures (Kleijn et al. 2006).

The concept of conservation within agriculture is often promoted on a more utilitarian basis, i.e. the value of conservation in human-influenced areas to human well being, through the provision of ecosystem services (Daily 1997; Jarvis et al. 2007). These benefits are manifested through a variety of ecosystem services, such as pollination, suppression of pest species by parasitoids and predators, and improved hydrology, all of which contribute towards more stable and sustainable agriculture.

Properly managed remnants in the rural, and even urban matrix, can provide essential links between existing reserves, increasing the probability of long-term conservation success (Goodman 2003; Dudley et al. 2005). To do so however, requires a sound knowledge of the ecological functioning and processes affecting biodiversity in human-influenced landscapes (Parker & MacNally 2002). The factors that negatively affect biodiversity in human-influenced landscapes are diverse, and apart from the issue of actual habitat loss and fragmentation, include those impacts which are more insidious and harder to measure, such as disturbance by altered grazing and fire regimes (Potts et al. 2003; Vulliamy et al. 2006), the context and contrast of natural remnants with adjacent transformed land (Tscharntke et al. 2002; Steffan-Dewenter et al. 2002), edge effects (Dauber & Wolters 2004; Chacoff & Aizen 2006) and pollution, to name just a few. Very often these factors are synergistic and highly correlated, making ultimate causation very hard to separate from proximate effects, a problem that has dogged many fragmentation studies (Fahrig 2003). Furthermore, the persistence of species in transformed landscapes may not necessarily indicate their resilience to change but could, in fact, be an artefact brought about by the extinction time lag, what Janzen (1986) called “blurry catastrophes” or through “extinction debt” (Tilman et al. 1994). If environmental conditions deteriorate beyond certain thresholds, a “debt” may be incurred which may not immediately cause the decline of a species, but will eventually need to be “paid”, either by the improvement of conditions or by the extinction of that species (Hanski & Ovaskainen 2002). Maintaining natural habitats within a heterogenous landscape may help buffer the effects of extinction debt in the long term.

The basic principles of maintaining heterogeneity and connectivity within agricultural landscapes form the framework for effective and adaptive

management plans for biodiversity at the landscape level (Samways 2007). In practice however, ecological processes and functioning within these remnants and the magnitude of their contribution to biodiversity conservation at the regional or landscape level are largely unknown and often difficult to assess (Tscharntke et al. 2005). Although a network of extensively dispersed small fragments may seem logical, metapopulation theory also suggests that larger patches are also needed to support more resilient populations (Harrison & Fahrig 1995; Hanski & Ovaskainen 2000). In theory, larger areas hold diverse assemblages (MacArthur & Wilson 1967; Simberloff & Wilson 1969) and are better able to provide important ecosystem services such as pollination (Memmott 1999; Memmott et al. 2004). The optimal configuration of natural remnants and their connectedness to maintain diversity, function and the provisioning of ecosystem services is an important area for further research. The broad objective in this dissertation is to evaluate the importance of small natural and semi-transformed remnants to conservation, and their potential to complement larger protected areas in a human-influenced landscape.

Biotic pollination

Biotic pollination is a mutually beneficial relationship between plants and animals whereby a variety of animals actively or passively facilitate the transfer of pollen between conspecific plants, usually receiving some kind of energetic reward (Faegri & van der Pijl 1979). It is an essential ecosystem service. Sixty to eighty percent of the world's 250 000 flowering plants depend on animals, mostly insects, for pollination (Kremen et al. 2007), while an even larger number may benefit from insect visitation (Husband & Schemske 1996). In some communities, as much as 93 percent of flowering plants are insect pollinated (Bawa 1974; Bawa 1990). Insect pollinators are a diverse group including, tens of thousands of species of beetles (Coleoptera), butterflies and moths (Lepidoptera), wasps and bees (Hymenoptera), and flies (Diptera) worldwide. The most important orders of flower visiting insects are discussed extensively in Procter et al. (1996) and Kevan & Baker (1999). The bees alone account for more than 20 000 species of the world's pollinating insects (Michener 2000).

There is also tremendous diversity in pollination systems, with associated differences in the degree of specialisation of plants to certain pollinators and pollinators to certain plants (Figure 1.1).

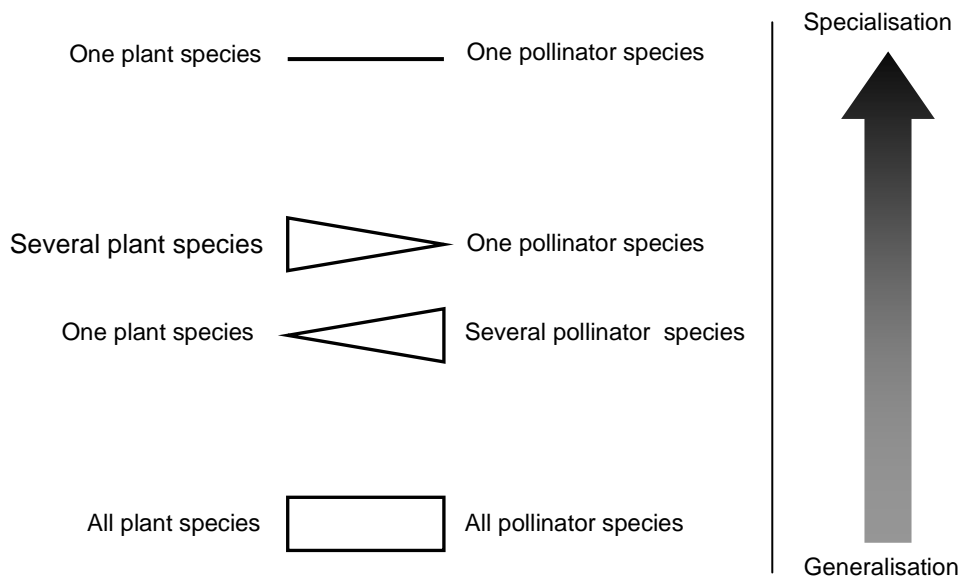


Figure 1.1 - Four scenarios of plant pollinator interactions (Reproduced from Steffan-Dewenter et al. 2006). In reality, there is a continuum from generalisation to specialisation for both plants and pollinating insects.

Flowers may be simple and accessible to many flower visitors, or very complicated and accessible to only very few specialised visitors. Traditionally, pollination systems have been studied within the well established paradigm of pollination syndromes (Procter 1978; Faegri & van der Pijl 1979; Fenster et al. 2004). These syndromes are groupings of plant species that with functionally similar flowers and similar guilds of pollinators. Biotic pollination is dominated by insects, and at least 70 percent of all flowering plants are insect-pollinated (Kearns & Inouye 1997). The relative importance of specialisation versus generalisation in pollination syndromes has recently been the subject of vigorous debate (Ollerton 1996; Waser et al. 1996; Johnson & Steiner 2000; Ollerton & Cranmer 2002; Johnson & Steiner 2003; Waser & Ollerton 2006; Ollerton et al. 2006).

This debate highlights several important conceptual points with respect to the utility of the pollination syndrome concept. Firstly, it is important to consider that the degree of specialisation can be regarded as either evolutionary or ecological. Being ecologically specialised is a state, i.e. being pollinated by visitors in a single functional group compared to other plant species (Armbruster et al. 2000). Evolutionary specialisation on the other hand is a process of evolution towards pollination by fewer functional groups (Fenster et al. 2004). Secondly, specialisation and generalisation should not be regarded as a dichotomy, but rather a continuum (Waser et al. 1996; Johnson & Steiner 2000) (Figure 1.1). Thirdly, interactions between plants and flower visitors are highly asymmetrical (Jordano 1987; Dupont et al. 2003; Vazquez &

Aizen 2004). Specialist plants may also be visited by generalist visitors. Likewise, specialist insects may also visit plants that receive visits from a great numbers of generalist visitors. This may lead to the perceived paradox that plants with specialist traits are also visited by many species of insect (Ollerton 1996; Waser et al. 1996). The paradox may be resolved to some degree by considering the effectiveness of flower visitors as pollinators (Schemske & Horvitz 1984) – not all of the visitors can act as a selective force (Johnson & Steiner 2000; Ollerton & Watts 2000). Furthermore, plants may still display adaptations to relatively uncommon or ineffective visitors, provided that there is no sacrifice in the ability to use more common or effective ones (Aigner 2006). These factors add a great degree of complexity to plant-insect visitation webs, but importantly this may impart a degree of resilience to these interaction webs (Memmott et al. 2004; Fontaine et al. 2006; Gibson et al. 2006).

Theoretical concerns aside, pollinators and other insect visitors to plants form an integral part of most terrestrial ecosystems by virtue of the “small world” properties of pollination interaction webs where almost all species may exert direct or strong indirect influences on each other (Olesen et al. 2006). This gives pollinating insects the ability to affect, and be affected by, both structure and functioning of ecosystems (Figure 1.2). The keystone role of pollinators in terrestrial systems and their sensitivity to various environmental stressors makes pollinators good bioindicators that can be used to diagnose ecosystem health, even when the nature of environmental stressors are unknown or only partially understood (Kevan et al. 1997; Kevan 1999). As such, they are an ideal group of organisms to study when assessing the effects of landscape transformation.

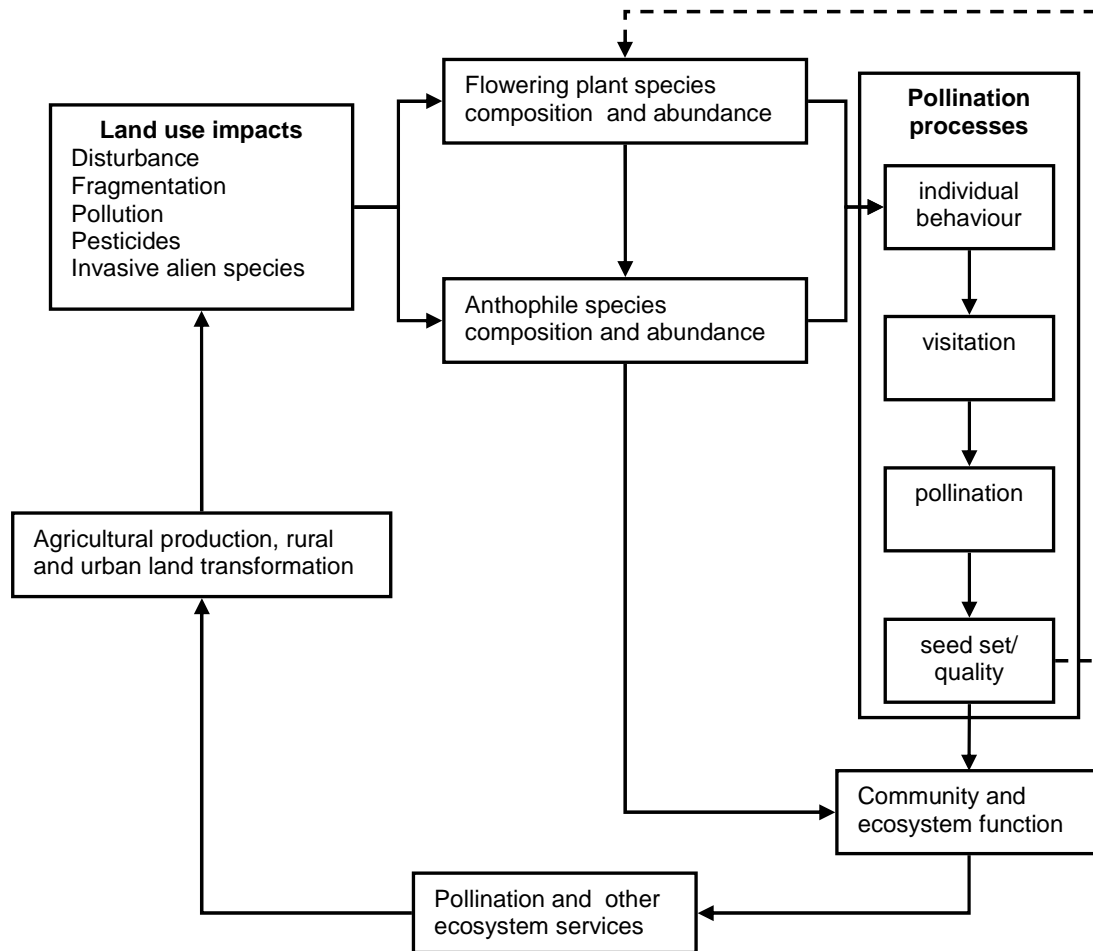


Figure 1.2 - Plant-pollinator interaction at the landscape and community level, showing the inter-relatedness between the two communities and the effect of land-use impacts on these interactions. Feedback between pollination influenced seed set affects both flowering plant and anthophile diversity (adapted from Donaldson 2002).

Pollinators and landscape change

Pollinators are important for maintaining the diversity and abundance of flowering plants (Figure 1.2) and consequently a myriad of other organisms that depend on these plants for food and shelter. Although they may not directly affect ecosystem processes, they can still have indirect effects on ecosystem properties through their potential to change the structure and diversity of plant communities (Lundberg & Moberg 2003). This makes them a keystone group in many terrestrial systems, providing a range of ecosystem services, facilitating plant reproduction and providing the basis of an energy-rich food web (Kearns et al. 1998). Altering pollinator communities could affect pollen delivery, thus altering plant communities and the ecosystem services that they provide (Ashman et al. 2004; Knight et al. 2005). Humans

also depend heavily upon ecosystem services provided by pollinators for agricultural production (Figure 1.2). Of the 124 most commonly planted crops in the world, 87 are animal pollinated. About 35% of global crop production depends upon biotic pollination (Klein et al. 2007). Estimates of the annual economic value of pollination services vary widely and generally under, or overestimate the value of pollination services depending upon the methodology used (Allsopp et al. 2008). Costanza et al. (1997) estimated global pollination services to be worth US\$ 117 billion per year. Using specific national estimates for the role of pollination in the United States, Canada, Europe, New Zealand and Australia an FAO report (FAO 2008) estimated the value of more than US\$ 50 billion per year to global agriculture alone. Estimating the true value of pollinators to include pollination in natural ecosystems is far more difficult given the many pollinator species (globally more than 400 000) and interactions involved, the paucity of detailed information on many of these species, as well as the many ecosystem services provided by natural plant communities dependent upon pollination. Whatever the total economic value of pollinators, their intrinsic and ecological worth is beyond dispute.

Despite their importance, there has been a worldwide decline in pollinators (Buchmann & Nabhan 1996). This has led to concern over the negative effects that pollinator declines may have on the reproduction of both wild plants and planted crops (Kevan 1974; Kevan 1975a; Kevan 1975b; Parker et al. 1987; Torchio 1990; Kevan et al. 1990a; Kevan et al. 1990b; Osborne et al. 1991; Ellis & Ellis-Adam 1993; Watanabe 1994; Buchmann & Nabhan 1996; Matheson et al. 1996; Kearns & Inouye 1997; Fisher 1998; Allen-Wardell et al. 1998; Kearns et al. 1998; Kremen & Ricketts 2000; Cane & Tepedino 2001; Richards 2001; Kremen et al. 2002; Steffan-Dewenter et al. 2005; Tscharrntke et al. 2005; Kremen et al. 2007; Steffan-Dewenter & Westphal 2008). It is feared that we are on the brink of a global “pollination crisis” (Buchmann & Nabhan 1996; Kearns et al. 1998). Although some have questioned this verdict (Cane 2001; Ghazoul 2005), there is substantial evidence decline in pollinator populations around the world (Allen-Wardell et al. 1998; Kearns et al. 1998; Donaldson 2002; de Ruijter 2002; Biesmeijer et al. 2006; Oldroyd & Wongsiri 2006)

Pollinators face many threats associated with anthropogenic changes caused through agriculture. Habitat destruction, pesticide use, the spread of diseases and competition from introduced flower visitors are the major contributing factors (Kevan 1974; Kevan 1975b; Johansen 1977; Rathcke & Jules 1993; Kearns et al. 1998; Kevan 1999; Kremen & Ricketts 2000; Kevan 2001; Morandin & Winston 2005). Of these, the most important cause of pollinator decline is habitat destruction (Kevan 2003). Habitat destruction

through land clearing, overgrazing, monoculture row-cropping and irrigation destroys essential resources for pollinators such as food sources, nesting or oviposition sites, and resting or mating sites (Kevan & Wojcik 2007). The effects of habitat destruction on pollinators have been documented from around the world (e.g. Stephen 1955; Winder 1977; Gess & Gess 1993; Kevan 1999; Kevan 2001; Rasmont et al. 2005; Goulson et al. 2005). Pollinator declines through habitat loss lead to further problems by initiating a vicious cycle of declining pollinator populations, reduced pollination service and reduced seed set and reproduction by plants, resulting in a diminishing capacity for natural habitats to recover from disturbance (Janzen 1974).

Plant-pollinator mutualisms may, however, be more resilient than originally thought (Cane 2001; Memmott et al. 2004). The age and complexity of pollination add a degree of buffering and flexibility to the system in most terrestrial ecosystems (Kevan 2003). Some plant-animal mutualisms can remain intact in transformed landscapes (Klemm 1996; Edwards 1996), and the effects of landscape fragmentation and landuse intensity may not always be negative (Klein et al. 2002). Bees and other pollinators may survive, even in urban or suburban settings if there are appropriate nesting sites and diverse floral resources to meet their needs (Frankie et al. 2005; Cane et al. 2006). Nonetheless, given the importance of pollinators in both natural and altered landscapes, the further monitoring of pollinators is well founded (Ghazoul 2005), considering the degree of uncertainty surrounding the resilience of pollination interactions. Indeed, there are documented cases where pollination systems break down when pollinators of wild plants, but also cultivated crops are lost (Kevan & Opperman 1980; Kevan et al. 1997; Fleishman et al. 1999; Sessions 2000; Kremen et al. 2002; Ricketts 2004; Kremen et al. 2004; Pauw 2007).

Although concern over the effects of pollinator declines dates back to at least the 1970s (e.g. Kevan 1974; Janzen 1974; Kevan 1975b), the publication of Buchmann and Nabhan's book *The Forgotten Pollinators* (1996) and subsequent emphasis of pollination as a vital ecosystem service (Daily 1997) elevated pollinator decline to an issue of global concern. Since then, there have been a number of national and international initiatives to investigate, and address the status of pollinators worldwide. These include, the International Pollinator Initiative¹ (IPI) originating from the "São Paulo Declaration on Pollinators" (1999) which was formally established at the Fifth Conference of the Parties (COP 5) to the Convention on Biodiversity (CBD) in 2002. Several international, regional and national initiatives supporting the IPI

¹ CBD website with details of IPI <http://www.cbd.int/agro/pollinator.shtml>

have been created including the African Pollinator Initiative² (API), Brazilian Pollinator Initiative³ (BPI), European Pollinator Initiative⁴ (EPI) and North American Pollinator Protection Campaign⁵ (NAPPC). A recurrent theme of the various meetings and publications emanating from them (e.g. Matheson et al. 1996; São Paulo Declaration on Pollinators 1999; Stubbs & Drummond 2001; Kevan & Imperatriz-Fonseca 2002; Strickler & Cane 2003; Freitas & Pereira 2004; Eardley et al. 2006; Committee on the Status of Pollinators in North America 2007; FAO 2008) is the conservation, restoration and sustainable use of pollinator diversity in agricultural ecosystems.

The Cape Floristic Region - threats to biodiversity in a global hotspot

The Cape Floristic Region (CFR) is a biodiversity hotspot of global importance (van Wyk & Smith 2001; Cowling et al. 2003; Mittermeier et al. 2004). It is listed as one of the 34 Global Biodiversity Hotspots, a Global 200 Ecoregion (Cowling et al. 2003), a Centre of Plant Diversity, and was added to UNESCO's World Heritage List in 2004 (UNESCO World Heritage Centre 2004). Covering 90 000 km² of the southern tip of Africa, the CFR is noted for its exceptionally high levels of plant diversity and endemism, with over 9000 recorded species of vascular plants, 70% of which are endemics (van Wyk & Smith 2001; Goldblatt & Manning 2002). The CFR is also a centre of diversity and endemism for vertebrates (Branch 1988; Stattersfield et al. 1998; Brooks et al. 2001; Kerley et al. 2003; Skelton et al. 2005) and many invertebrate groups (Stuckenberg 1962; Picker & Samways 1996).

Biodiversity conservation in the CFR faces significant challenges. Threats include global climate change, transformation by urban and agricultural expansion, and the invasion by alien species. About 30% of the region has already been transformed or invaded by alien shrubs and trees (Rouget et al. 2003b). Twenty percent of the CFR lies in formally protected areas but this coverage is biased towards areas topographically and climatically unsuitable for agriculture, resulting in inadequate representation of many biodiversity patterns and processes (Rouget et al. 2003a). Particularly affected by this bias are lowland habitats. In some cases, protected areas make up less than 5% of the habitat and more than 80% of the natural vegetation has already been lost (Rouget et al. 2003a; Rouget et al. 2003b). Further agricultural expansion is most likely to affect lowland habitats (Fairbanks et al. 2004), which are the most poorly protected. Considering that 75% of the

² On ARC (South Africa) website with details of API <http://www.arc.agric.za/home.asp?pid=3493>

³ Online document by Imperatriz-Fonseca & Dias http://eco.ib.usp.br/beelab/bpi_ceara.pdf

⁴ EPI homepage <http://www.europeanpollinatorinitiative.org/>

⁵ NAPPC homepage <http://www.napcc.org/>

CFR lies on privately owned land, high land values and the high degree of fragmentation preclude the expansion of existing, formally protected areas (Fairbanks et al. 2004). Alternative conservation measures need to be sought. Involving landowners, particularly farmers, to manage and protect remnants of natural vegetation and semi-natural vegetation outside of reserve areas has been widely proposed as an important, if not the only available option, for achieving conservation targets in the lowlands of the CFR (Kemper et al. 1999; Cowling et al. 2003; Fairbanks et al. 2004)

These challenges are being addressed, at a national, for example the clearing of alien vegetation by Working for Water Programme a highly successful project operating in all nine of South Africa's provinces (van Wilgen et al. 1998; Turpie et al. 2008), as well as at a provincial level where various initiatives are aimed at integrating biodiversity conservation into agricultural practice. In the Western Cape, programmes include the Cape Action Plan for People and the Environment (CAPE) (Younge & Fowkes 2003), the Western Cape Nature Stewardship Programme (Winter 2004a) and the Biodiversity and Wine Initiative (BWI) (Winter 2004b). Collectively, these programmes aim to promote biodiversity conservation on private lands and create incentives for landowners to conserve natural remnants on their land. The concept of integrating conservation into agriculture is well established worldwide and is based upon sound principles of landscape ecology – promoting sustained biodiversity by maintaining connectivity and a heterogeneous landscape mosaic within an agricultural matrix (Samways 2007). Although initiatives like the Cape Nature Stewardship Programme and BWI have a sound theoretical basis, assessment of the biodiversity within the natural remnants on private lands is important to establish whether or not they actually make a difference. Part of this dissertation attempts to determine whether biodiversity conservation within reserves is complemented by the remnants outside of these reserves.

Insect visitors to the Cape flora

The floral diversity of the CFR has been well studied, yet relatively little is known about its insect assemblages (Johnson 1992; Picker & Samways 1996; Giliomee 2003). The relative diversity of insects and plants in the CFR has been debated and has been found to be high for certain groups such as gall forming insects (Wright & Samways 1998), although Giliomee (2003) suggested that insect diversity in the CFR is relatively low. This assessment, may however, not have been particularly well founded, given the relative paucity of information on invertebrates in the CFR at the time, and may simply reflect a lack of sampling effort for many groups (Slotow & Hamer 2000) rather than a lack of diversity. More recently neighbouring biomes to

the CFR, arboreal insects have been found to be no less diverse than plants and are comparable to what may be expected at similar latitudes (Proches & Cowling 2006). The CFR is also an important centre of endemism for several groups of insects including the leafhoppers (Cicadellidae) (Stiller 2002) and dung beetles (Scarabaeidae: Scarabaeinae) (Davis 2002). The CFR is also important for rare and threatened insects. Thirty eight percent of southern Africa's Red Listed butterflies occur here (Rebelo 1992), along with 10 out of the 40 threatened or near-threatened Odonata in South Africa, of which six are endemic (Samways 2006).

Arthropods, many of them insects, form an integral part of most ecosystems, dominating abundance and biomass of biodiversity worldwide (Major et al. 2003). They are also responsible for the provision of many ecosystem services such as nutrient cycling, controlling the population of other animals through predation, maintaining plant populations, seed dispersal and pollination, thus playing a keystone role in many ecosystems (Samways 2005). Insects are sensitive to disturbance at a number of spatial and temporal scales (Samways 2005), yet relatively little is known about the effects of disturbance on insect assemblages in the CFR (Picker & Samways 1996; Donaldson et al. 2002).

One group of insects in the CFR that has attracted the interest of biologists are the insect pollinators. The earliest work on the relationship between certain Cape flora and their insect pollinators dates back to the 1800s (Trimen 1864; Marloth 1896). The initial development of pollination biology studies in the CFR was slow. Even by the late 1980s, knowledge of insect pollination in the Cape floral species was limited to mainly anecdotal accounts of flower visitors rather than more detailed studies of pollination biology (Whitehead et al. 1987), although Vogel's (1954) extensive survey of potential pollinators already recognised a number of distinct categories of pollinators. More recently however, there has been a great deal of renewed interest in the pollination biology of the region (see references in Johnson & Steiner 2003 for an extensive list of South African pollination studies). Much of the contemporary work has focused on what seems to be a remarkable specialisation of pollination systems in the region compared to other parts of the world (Johnson & Steiner 2000; Ollerton et al. 2006). Examples of some of specialised pollination systems in the CFR include dull-coloured, yeasty-odoured Proteaceae that are pollinated by rodents (Wiens et al. 1983; Johnson et al. 2001), members of the milkweed family (Asclepiadaceae) with pollinaria adapted for transfer on the the tongues of nectivorous birds (Pauw 1998), long-tubed flowers pollinated by large, hovering, long-tongued flies, (Nemestrinidae and Tabanidae) (Goldblatt & Manning 2000; Manning & Goldblatt 1997; Manning et al. 1999), red-flowers pollinated exclusively by the

satyriine butterfly *Melenis tulbaghia* (L.) (Johnson & Bond 1994) and flowers adapted for pollination by oil-collecting bees (Melittidae) (Vogel 1974; Vogel 1984; Pauw 2006). Other pollinators such as the monkey beetles (Scarabaeidae: Rutelinae: Hopliini) (Picker & Midgley 1996; Goldblatt et al. 1998; Steiner 1998; Mayer et al. 2006), and other anthophilous beetles, flies and bees (Rebelo 1987; Whitehead et al. 1987; Hepburn & Radloff 1998; Goldblatt et al. 2009) may be more generalised in their interactions, but are still important pollinators of many different Cape flora.

The disruption of these mutualisms by changes in land use, agricultural and urban expansion, and invasion of alien plants, are of particular concern as the consequences of such disruptions are largely unknown (Johnson 2004). This concern is well founded, especially given the recent and rather startling suggestion by Vamosi et al. (2006) that due to the increased magnitude of pollen limitation in species rich communities, plants in diversity hotspots may be more prone to pollination limitation and face higher extinction risks in the face of habitat destruction than in less diverse areas.

There is still a paucity of data on the effects of habitat change on pollinators in the CFR. Pollinator assemblages and seed set showed variable responses to habitat fragmentation in a renosterveld study by Donaldson et al. (2002). In the Namaqualand succulent Karoo region Colville et al. (2002) found that overgrazing disrupted monkey beetle (Rutelinae: Hopliini) assemblages, most likely due to changes in vegetation caused by the overgrazing. However, another study in the same area (Mayer et al. 2006) found that annual variation had a greater effect on monkey beetle diversity than grazing regime, although some species were still affected. Pauw (2007) found that the loss of a generalist pollinator, an oil collecting bee (Redividae) had cascading effects on the seed set of specialist oil producing plants, but not on generalist plants. Furthermore, these effects were more severe in natural remnants in an urban matrix than in a rural matrix. These few examples illustrate that the effects of habitat destruction and fragmentation in the CFR are complex and not easily predictable, making the task of effectively conserving these interactions a rather daunting prospect.

Aims and outline of this dissertation

Sound ecological principles and knowledge of the interactions between organisms and the biotic and abiotic components of their environment can provide a solid basis for the effective management and conservation of biodiversity in human-influenced landscapes. The broad objective of this dissertation is to determine whether or not insect diversity can be linked to plant diversity in reserve areas and remnant habitats in the lowlands of the

CFR, and to assess the value of these habitats towards achieving conservation objectives for the region. The study focuses on flower visiting insects (anthophiles) as a functional group, given their keystone role in this floristically-diverse region. It is reasonable to expect that insect diversity will track plant diversity (Wright & Samways 1998; Haddad et al. 2001; Proches & Cowling 2006) even though it has been speculated that this may not be the case in the CFR (Cottrell 1985; Johnson 1992; Giliomee 2003). Given the close relationship and many mutualisms between the flowering plants and anthophiles we can expect that in this case, insect diversity and abundance would track plant diversity in natural remnants. This concept is used as a working hypothesis, which is tested in the study.

In Chapter 2, the effects of anthophile colour preferences on the efficacy of coloured pan traps are tested, as such effects can have important implications for the design of and interpretation of results from pan trap surveys.

Chapter 3 considers the species turnover of plants and insects across the study area, and whether or not there is any congruence in the two groups, using survey data collected on plants and insects in the three sample areas of study sites. In Chapter 4 the complementarity between species richness and abundance in reserve areas versus remnants in each of the three sample areas is tested, and the potential value of remnants for biodiversity conservation in the CFR is discussed.

In the latter chapters (Chapters 5 and 6), some aspects of the behaviour of anthophiles that may affect the activity and abundance of these insects at a local scale are explored at one of the study localities (Elandskloofberge). Chapter 5 tests the effect of floral traits and the density of floral displays on flower visitation within patches of flowering plants. In Chapter 6 these local-scale effects are examined further as the effect of biotic variables such as floral density versus floral diversity and the 'magnet species effect' on flower visitation frequency are investigated.

It is important to note here that although this dissertation uses insect pollinators as a focal group, it is not a pollination study *per se*. The term 'anthophile' is used in a broad sense to refer to the flower visiting-insects that includes species known to pollinate flowering plants and makes no claims to the effectiveness of those species for pollinating certain species of plants. To do so would require a narrower focus on issues such as pollen transfer and seed set that fall outside the scope of the study given its broader ecological focus and the wide range of plants and insects considered.

Chapters 2-6 were written as individual manuscripts for publication, which does necessitate some repetition. Finally, Chapter 7 provides a brief

summation of the overall findings and places these in the broader arena of ecological and conservation theory.

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Visual signals play an important role in attracting potential pollinators to flowering plants in the Cape Floristic Region. Here, *Peritrichia* monkey beetles cram tightly into the brightly coloured flower-head of *Phaenocoma prolifera*, in the Hottentots-Holland Nature Reserve.

Sven Vrdoljak, 2005

2

Colour matters: assessing diversity of flower-visiting insects using coloured pan traps in the Cape Floristic Region

SUMMARY

Colour is an important attractant for many flower-visiting insects (anthophiles). Consequently, coloured pan trapping is an efficient technique that can be easily and cost-effectively used to quantitatively sample assemblages of anthophiles. Colour preferences of anthophile is an important source of bias that needs to be considered in pan trap surveys. Using data from pan trap surveys in the lowlands of the Cape Floristic Region, I examine the effects of colour on pan trap catches and discuss the efficacy of this technique for sampling anthophiles among the Cape flora. Pan traps were found to be an effective means of sampling the major groups of anthophiles in the region (Coleoptera, Diptera and Hymenoptera), but butterflies (Lepidoptera) were severely underrepresented. Colour played an important role in determining the species-richness and composition of pan trap catches. Although coloured pan traps captured a diverse range of flower-visiting insects, for monitoring and comparative studies, the use of at least three colours – yellow or white, combined with a short wavelength colour (e.g. blue) and a long wavelength colour (e.g. red) is recommended. For census and inventory studies it would be wise to augment pan traps with active collecting and other techniques to include rarer taxa and those which may be otherwise excluded by pan traps.

Introduction

Many flowering plants rely on insects for pollination and use flowers of different colours, shapes, sizes, fragrances and rewards (pollen/nectar/oils) to attract pollinators (Niesenbaum et al. 1999). Colour is a particularly important attractant (Kevan & Backhaus 1998), and colour traps can be used to survey and monitor pollinator diversity and abundance (Westphal et al. 2008).

Coloured pan trapping is a passive sampling method that requires no specialised equipment, with no collector/observer effect (Leong & Thorp 1999). This makes pan traps an efficient, cost-effective method for sampling flower-visiting insects (anthophiles) and they are widely used in pollinator assemblage studies. In principle, pan trap samples can yield estimates of the relative abundances of certain insect taxa (Southwood & Henderson 2000) and potentially estimates of richness and diversity as well. To obtain the latter however, requires that the sampling method is representative of the target taxa (Southwood & Henderson 2000). As with most trapping methods, characteristics of the trap itself can influence its effectiveness and, subsequently, ecological measures calculated from the samples.

For pan traps, these characteristics may include trap size (Boiteau 1990), scent (Laubertie et al. 2006), trap placement (Pucci 2008; Tuell & Isaacs 2009), surrounding vegetation (Wilson et al. 2008) or habitat (Missa et al. 2009) and weather conditions (McCall & Primack 1992). Trap colour is particularly important, and the degree of attraction of anthophiles to a particular colour or set of colours determines pan trap effectiveness (Dafni et al. 2005). Such preferences may cause catches to vary between species (e.g. Picker & Midgley 1996) and even sexes within a species (e.g. Leong & Thorp 1999), depending on the colour of the trap. This can result in significant bias that should be considered when using coloured pan traps to survey anthophiles.

Later chapters in this dissertation examine distribution of anthophiles across natural and semi-transformed habitats in the lowlands the Cape Floristic Region (CFR). The CFR is well known for its particularly high plant diversity (Goldblatt & Manning 2002) as well as high prevalence of specialised pollination syndromes (Johnson & Steiner 2003; Ollerton et al. 2006). Pan trapping was extensively used to assess the distribution and abundance of anthophiles in these habitats. Here, I examine differences in the richness and diversity of anthophiles caught in different coloured pan traps and discuss the effectiveness of sampling with different trap sets comprising different colour combinations to adequately represent the anthophile diversity of the region.

Methods

Study area

The study was conducted in the lowlands (below 400 m a.s.l.) in the Cape Floristic Region (CFR). The research area extended from 18° 44' E 33° 24' S to 19° 07' E, 34° 8' S, with sites separated into three distinct regions: the Elandskloofberge, encompassing Elansdberg Nature Reserve and the surrounding Bartholomeus Klip farm; Somerset West, encompassing Helderberg Nature Reserve, Vergelegen Estate and Cordoba Estate; and Groenlandberg Conservancy, encompassing Klipfontein (part of the HottentotsHolland Nature Reserve), and the Diepklowe Private Nature Reserve. Within each of these regions a reserve area and several satellite sites in remnant, natural/semi-natural habitat were selected.

The lowlands of the CFR are generally highly transformed (Rouget et al. 2003), and the three localities represent a range of natural and semi-transformed areas of vegetation within the predominately agricultural matrix. Further description of the study sites can be found in Appendix 1.

Anthophile sampling

Insects were sampled using coloured pan traps. Flower visitors in the Western Cape (Picker & Midgley 1996) and elsewhere (Leong & Thorp 1999; Campbell & Hanula 2007) have been found to show differential colour preferences to pan traps, so a range of colours were used, namely red, orange, yellow, blue, violet, and white. Reflectance spectra were measured using an Ocean Optics (Dunedin, Florida, USA) USB 4000 photo spectrometer with a Mikropack (Ostfildern, Germany) DH-2000-BAL UV-VIS-NIR light source and are given in (Figure 2.1). All colours used had low reflectance in the UV range (wavelength <400 nm). However, this was unlikely to affect the results of a comparative study of this nature, given that UV is just another primary colour in bi-, tri- and tetra chromatic vision and is no more or less important than any other primary (Kevan et al. 2001). Polypropylene tubs (RL350, Marco Plastics, Alberton South Africa), 115 mm diameter by 50 mm deep (350 ml volume), were painted with gloss enamel paint (Dulux SA, Alberton, South Africa). For each site, three arrays of six coloured pan traps were used, arranged in a — | — configuration of three 50 m lines in each site, with the six colours arranged randomly at 10 m intervals on each line. Pans were elevated and set at the level of flowers in the surrounding vegetation (Figure 2.2) and half filled with water, with a little detergent added to reduce surface tension. Elevating pan traps to the level of the canopy where insects are actively foraging has been shown to significantly increase catches (Tuell & Isaacs 2009). Trapping took place only on sunny days, from 08h00 until 17h00. At the

end of each day, trapped insects were removed from the water and preserved in 80% ethanol for later identification. Whenever possible, trapping occurred on two consecutive days per site, although as the weather at this time of year is highly variable, often the next suitable day was used. Anthophiles were sampled in the spring (August-December), in 2004 and 2005 to coincide with times of peak flowering at each site.

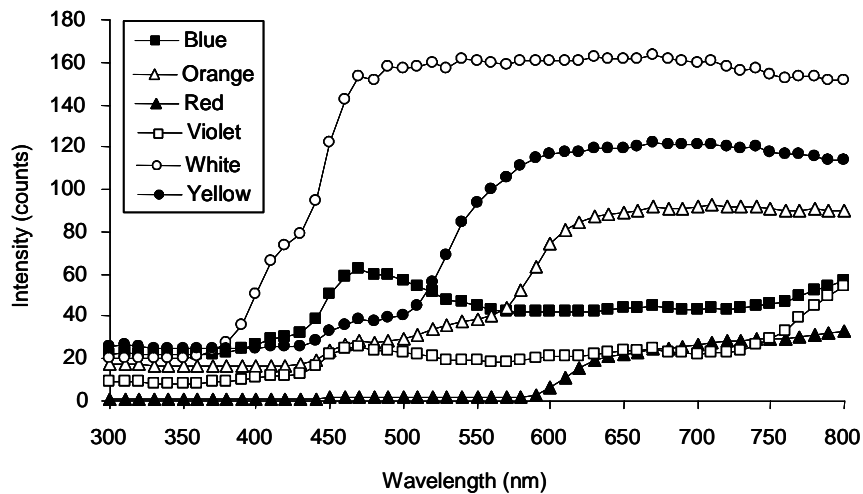


Figure 2.1 – Reflectance spectra for coloured pan traps used to sample flower visiting insects in the lowlands of the Cape Floristic Region.



Figure 2.2 – Example of a coloured pan trap used to sample flower visiting insects in lowlands of the Cape Floristic Region. Pan traps were elevated to the height of flowers in the vegetation (left) and half filled with water with a few drops of detergent added (right).

Upon completion of sampling, anthophiles were counted and identified. Initial identifications were to morphospecies or recognisable taxonomic units (RTUs), with later identification using the entomology collection at the Iziko South African Museum in Cape Town and consultation

with experts on certain groups. All insects were identified to at least family level, and to genus and species where possible. Morphospecies are widely used in ecological studies and can act as good surrogates for formal species (Oliver & Beattie 1996). A voucher collection is kept in the Entomology museum at the Department of Conservation Ecology and Entomology, Stellenbosch University. For convenience, RTUs are referred to as 'species' hereafter.

Dataset

In total, 997 coloured pan traps, around 163 of each of six colours, were included in the dataset. Some trap losses in the field meant that the final numbers of each of the six colours was not quite even, but these differences were not significant (T-value = -0.164; $p = 0.876$). These data were stored in a relational database in Microsoft Access. The database included count data for species caught in each pan trap as well as the colour, locality and date of sampling for each trap. Analyses were performed on the entire dataset as a whole, as well as random subsamples of the dataset according to certain criteria.

Relative abundance and diversity

Reported richness and abundance figures were calculated from the entire pooled dataset. To determine the adequacy of sampling effort, a sample-based rarefaction curve, which plots species richness against the number of individuals for the entire area sampled (Gotelli & Colwell 2001) was calculated using the software package EstimateS Version 8.0 (Colwell 2006). Species richness estimators were also calculated using EstimateS (with replacement) to determine the predicted species richness of the region. To estimate species diversity I used Incidence-based Coverage Estimator (ICE) (Chazdon et al. 1998) which uses presence/absence incidence data, as the abundance of species in the pan traps often varied by one or two orders of magnitude. Species richness estimators are numerous and vary in their accuracy, i.e. combination of precision and bias (Walther & Moore 2005), but they nonetheless provide useful information and at least a minimum estimate of true species richness in areas that lack complete inventories (Hortal et al. 2006).

Catch composition

To compare taxa caught in different coloured pan traps, the catch data were pooled by trap colour. Cluster analysis of the aggregated dataset using Bray-Curtis similarity was performed using the software package, PRIMER 5, Version 5.2.9 (Primer-E Ltd 2002). From the cluster analysis, the six pan trap

colours were split into three categories namely 'short wavelength' (blue and violet), 'long wavelength' (red, orange and yellow) and white. Numbers of unique and shared species for each category were calculated from the aggregated dataset and their degree of similarity measured using Jaccard's Index of similarity based on presence/absence of shared species, calculated from the formula $C_j = j/(a+b-j)$, where j = number of species in both categories, a = number of species in category A and b = number of species in category B (Magurran 1988).

Assessment relative to colour

For each colour the number of individuals (by order and family), species, singletons (species represented by a single individual) and uniques (species represented by more than one individual from that particular colour) were enumerated. There are 63 possible combinations for six colours, ranging from single colours through 2, 3, 4, 5 to all six colours and all species were counted in one of these categories depending on which colour pans they occurred in.

Species richness estimates from sub samples

The 63 colour combinations were used to define sub samples of 150 randomly selected pans from the entire dataset. The size was determined by the largest round number of any single colour of pans that could be drawn from the dataset without replacement. Each sub sample comprised a unique colour set of between one and six colours, with the colours drawn in equal proportions when more than one colour was used. Species composition of colour sets were compared by non metric Multi-dimensional Scaling (MDS) using Bray-Curtis similarity for the square-root transformed data using PRIMER. The significance between colour groupings shown on the MDS was tested using the ANOSIM (analysis of similarity) procedure using PRIMER (Clarke & Warwick 2001).

To assess how well colour sets were able to predict actual diversity, EstimateS was used to calculate ICE from the sub samples which were then compared to the known diversity of the entire dataset (254 species). To simplify comparisons between ICE values, colour sets were placed into seven categories depending on whether they contained long wavelength (red, orange); short wavelength (blue, violet); or 'high reflectance' (white, yellow) colours. Differences between categories were tested using a one-way ANOVA in Statistica, Version 8.0 (StatSoft Inc. 2007).

Results

Relative abundance and diversity

In the pooled dataset there were 34 219 individuals, representing, 254 observed species in 64 families (Table 2.1). A complete list of species is given in Appendix 2.

Table 2.1 – Summary of total pan catches of anthophiles from the Cape Floristic Region lowlands. Singleton = species represented by a single individual, Unique = species recorded from a single colour only.

	Coleoptera	Diptera	Hymenoptera	Hemiptera	Other taxa	All taxa
Families	14	14	25	5	4	64
Species	115	46	81	10	2	254
Singletons	13	7	28	3	3	54
Uniques						
Red	1	0	5	2	0	8
Orange	3	1	5	1	1	11
Yellow	7	1	10	1	0	19
White	6	2	3	0	0	11
Blue	3	1	1	1	0	6
Violet	2	2	8	1	0	13

Coleoptera were by far the most abundant group, followed by Diptera, Hymenoptera and Thysanoptera (Figure 2.3). Lepidoptera occurred very rarely in the traps, with only three individuals recorded in total.

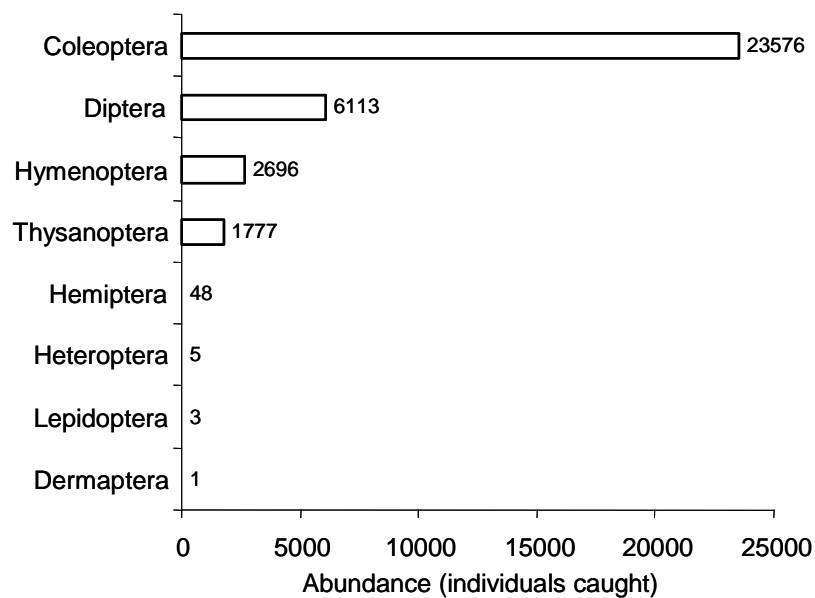


Figure 2.3 – Relative abundance of eight orders of insects captured in 997 coloured pan traps in the lowlands of the Cape Floristic Region.

Chapter 2

The three most abundant orders all tended to be dominated numerically by a few families each (Table 2.2). For Coleoptera, the most abundant family by far was Scarabaeidae, mainly monkey beetles (Ruteliinae, Hopliini). In the Diptera there were particularly high catches of Bibionidae, and the Hymenoptera were dominated to a lesser extent by Halictidae. The Hymenoptera had a particularly diverse array of families, 25 in total, many of which were chalcidoid or ichneumonid parasitoids and rarely occurring species, represented by less than 10 individuals.

Table 2.2 – Total numbers of individuals of anthophiles captured in six colours of pan trap in the lowlands of the Cape Floristic Region.

	Red	Orange	Yellow	White	Violet	Blue	Total
Coleoptera							
Scarabaeidae	4010	7012	7002	1948	955	690	21617
Chrysomelidae	7	62	180	271	39	34	593
Melyridae	4	50	151	183	98	53	539
Buprestidae	79	100	223	84	11	20	517
Byrrhidae	1	22	24	75	2	25	149
Meloidae		6	15	11	15	5	52
Dermestidae	2	3	11	26	5	3	50
Staphylinidae	2	4	1	1	1	4	13
Cleridae	1	1	4	5			11
Curculionidae		1	4	2	2	2	11
Cerambycidae		1	5	1	1	1	9
Carabidae			3		1	2	6
Coccinellidae		1	3	1			5
Elateridae			1				1
Dermaptera							
Labiduridae		1					1
Diptera							
Bibionidae	21	95	199	2517	719	744	4295
Drosophilidae	3	63	354	56	4	3	483
Bombyliidae	39	42	167	109	26	30	413
Muscidae	18	35	39	90	40	53	275
Calliphoridae	5	18	44	36	77	74	254
Tachinidae	4	23	57	15	2	3	104
Tabanidae	3	15	32	6	3	5	64
Scathophagidae	5	8	9	20	8	6	56
Tephritidae	1	3	24	20	2	1	51
Asilidae	4	7	10	12	2	3	38
Heleomyzidae	1	2	8	20	2	3	36
Empididae		3	2	10	4	1	20
Syrphidae		2	7	6	1		16
Dolichopodidae	1	1				1	3
Hemiptera							
Reduviidae	1			3	1		5
Coreidae					1		1
Cydnidae			1				1
Lygaeidae	5	5	7	14	4	6	41

	Red	Orange	Yellow	White	Violet	Blue	Total
Pentatomidae	1	1			1		3
Scutelleridae	1						1
Hymenoptera							
Halictidae	7	63	273	157	181	150	831
Platygastridae	47	101	260	94	26	53	581
Apidae	14	22	24	62	26	23	171
Tiphiidae	3	13	34	25	23		98
Ormyridae	5	13	18	31	6	8	81
Scelionidae	1	7	9	11	3	5	36
Megachilidae		1	4	11	4	6	26
Mellitidae			2	8	7	5	22
Braconidae	1		2	3	4		10
Colletidae		2	2	2	2		8
Pompilidae	2	3	1	1		1	8
Ichneumonidae	2	1	2		1		6
Vespidae		2	3	1			6
Eulophidae	1			2		1	4
Bethylidae			2	1			3
Cercopidae		2			1		3
Eumenidae					2	1	3
Figitidae	1				2		3
Formicidae	2		1				3
Tenthredinidae			2	1			3
Melittidae					2		2
Pteromalidae	1			1			2
Chalcidae			1				1
Encyrtidae		1					1
Megaspilidae					1		1
Thysanoptera							
Phlaeothripidae	111	140	305	968	145	108	1777

Estimated species richness (ICE) was 295 while the Chao 2 estimate, which provides confidence intervals, ranged between 271 and 351 species (upper and lower 95% confidence intervals). The actual species diversity of the region is probably somewhat higher, as the rate of new species observation had not yet reached an asymptote (Figure 2.4), although the trend to asymptote is as good as could be expected compared to similar studies (Williams et al. 2001).

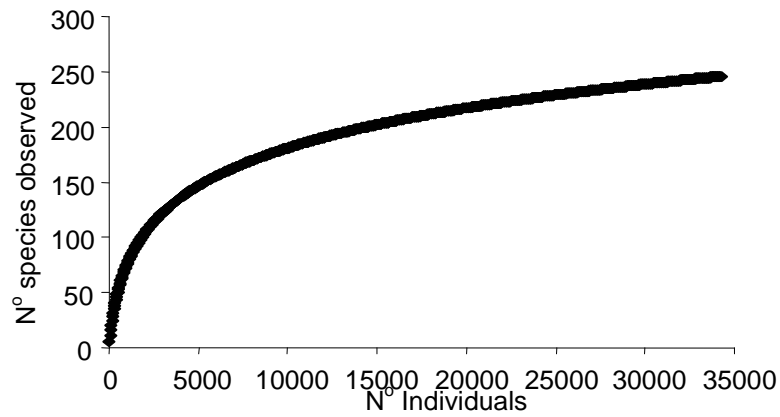


Figure 2.4 – Species accumulation curve for 997 coloured pan trap samples collected in the lowlands of the Cape Floristic Region.

Most taxa were site specific, with more than a third of all taxa found at single sites only, while just 3 percent occurred at all sites (Figure 2.5).

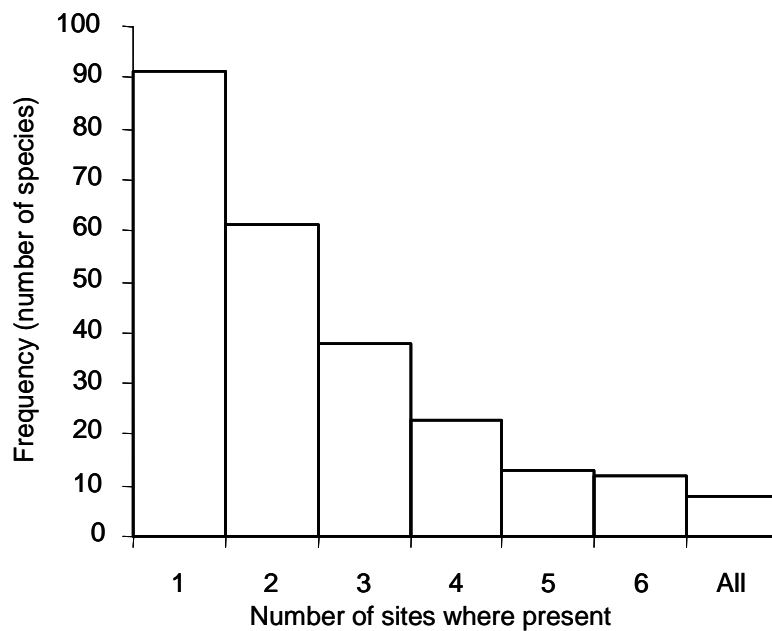


Figure 2.5 – Site specificity of 254 species of anthophiles caught in coloured pan traps in the lowlands of the Cape Floristic Region.

Catch composition

The cluster analysis of all pans, aggregated by colour, grouped pans into three categories – long wavelength colours (red, orange, yellow) short wavelength colours (blue, violet) and white which grouped closer to the short wavelength colours (Figure 2.6).

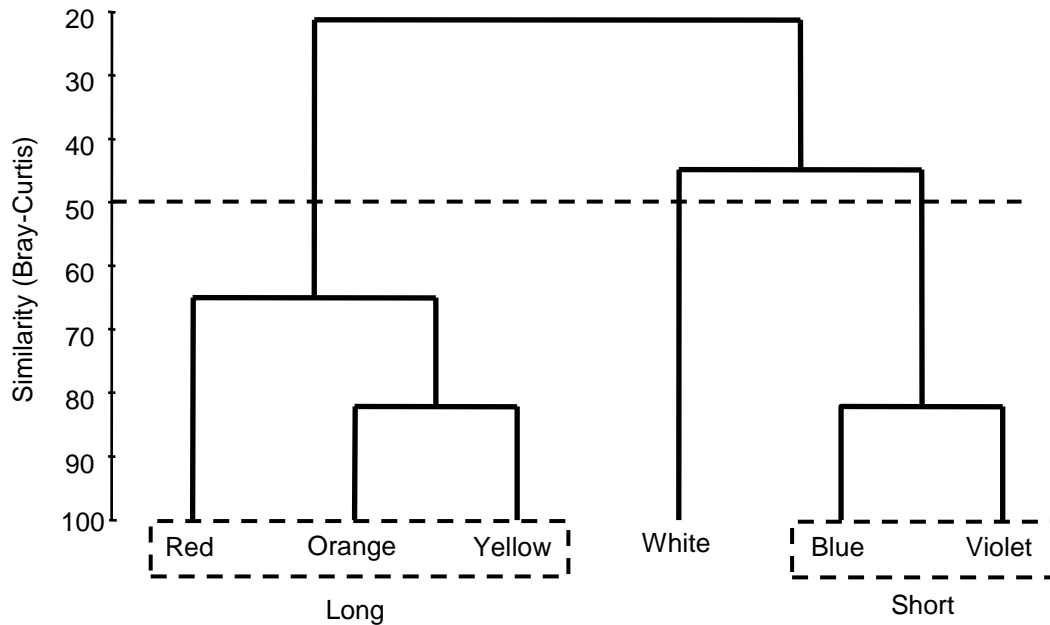


Figure 2.6 – Classification of 997 coloured pan traps from the lowlands of the Cape Floristic Region. The vertical axis represents Bray-Curtis similarity, based on catch composition of each trap. The dashed horizontal line represents 50% similarity.

There was a high degree of overlap between the species composition of the three colour groupings resolved in Figure 2.6, which is reflected in the high degree of similarity (C_j = Jaccard's Index) between the three groups in Figure 2.7, with the majority of taxa occurring in all three colour groups. However, each group still contained a number of unique species that did not occur in the other groups.

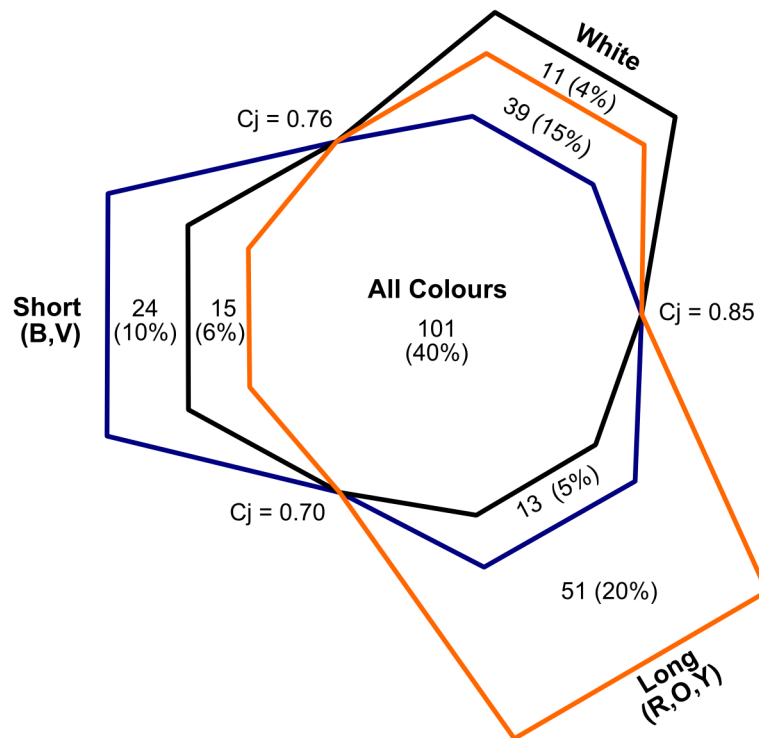


Figure 2.7 – Area proportional Venn diagram showing overlap in coloured pan trap catch-composition and numbers of shared and unique species per category for long-wavelength, short-wavelength and white coloured pan traps from the lowlands of the Cape Floristic Region. The area of each region on the diagram is scaled according to the number of species in that category. Similarities between pairs of colour groups are indicated by Jaccard's Index (C_j).

Influence of colour

Proportions of total number of individuals caught per colour varied among orders of anthophiles (Figure 2.8). More than 80% of Coleoptera were caught in long wavelength coloured traps, whereas for the Diptera, 78% of individuals were caught in white or short wavelength colours. Hymenoptera were more evenly distributed across the colours with 42% in long wavelength, 26% in white 32% in short wavelength traps. Thysanoptera were most prevalent in white traps, with 54% caught in this colour alone.

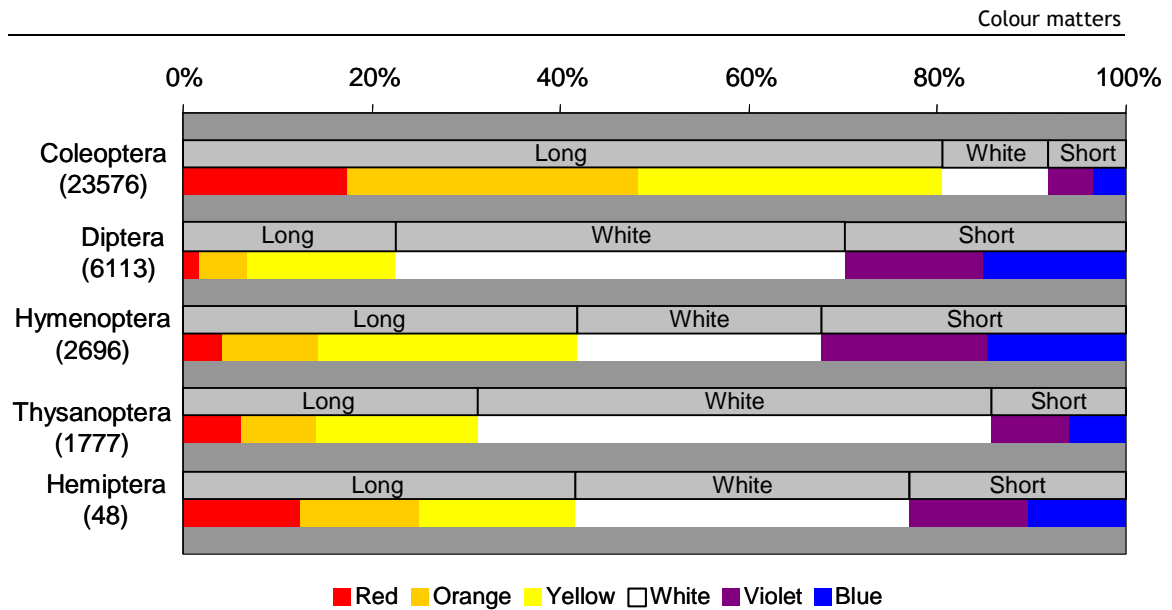


Figure 2.8 – Number of individuals caught per colour for five orders of anthophiles from 997 pan traps in the lowlands of the Cape Floristic Region.

Species richness also varied among colours (Figure 2.9). Yellow and white caught the highest number of species when considering all taxa, and this pattern was consistent across the three main orders of anthophiles (Coleoptera, Diptera and Hymenoptera). Of the 254 observed species, only 48 were attracted to all six colours, while 68 were only encountered in single colours (Figure 2.10). Blue traps had the least diverse catches, containing 45% of the total number of species, compared to 67% in yellow traps.

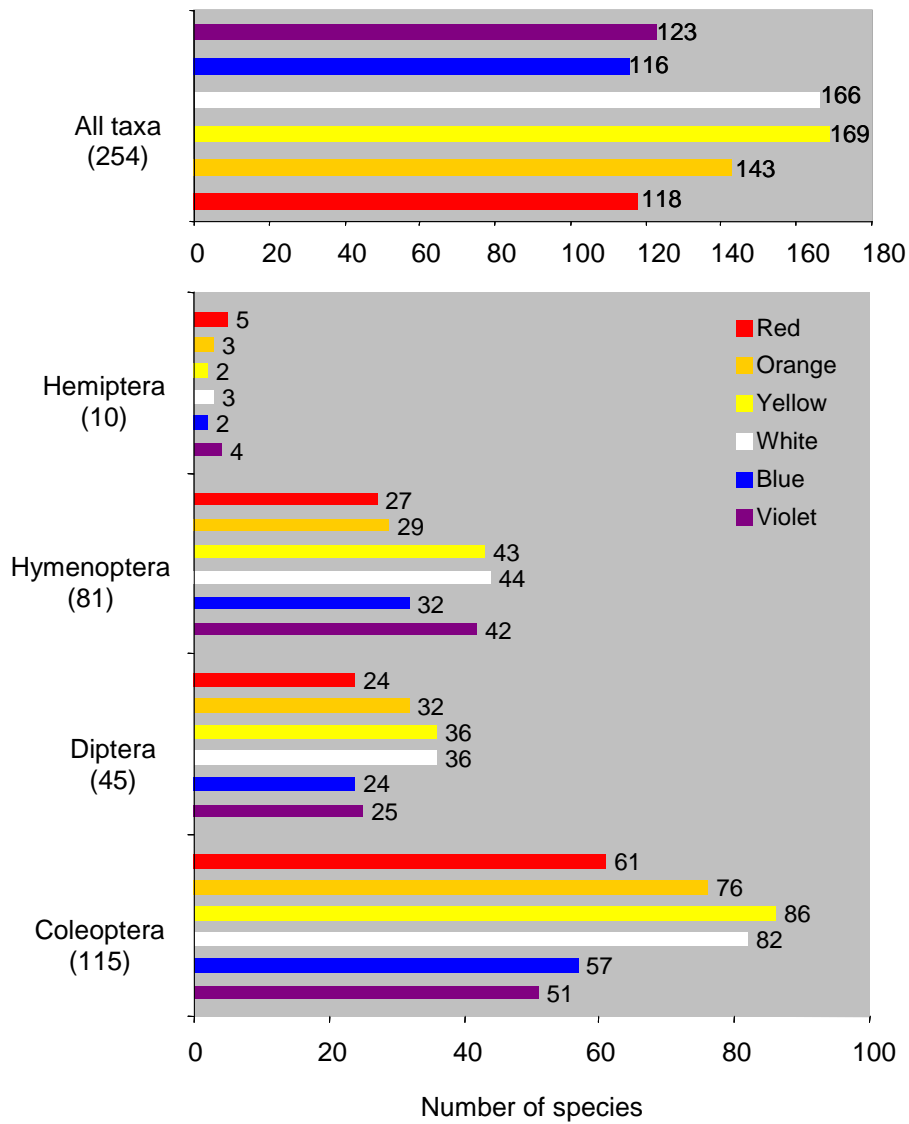


Figure 2.9 – Number of different species caught per colour in 997 pan traps in the lowlands of the Cape Floristic Region. Thysanoptera and Dermaptera were each recorded as single morphospecies and are not shown.

Species richness estimates from sub samples

The species composition of the 63 colour sets showed a similar grouping of colours to the grouping of individual pans in the entire dataset (Figure 2.11) showing a clear separation between long and short wavelength combinations, with two intermediate groups of mixed wavelength combinations. Analysis of similarity (ANOSIM) showed these grouping to be significantly different (Global R = 0.586, P = 0.001).

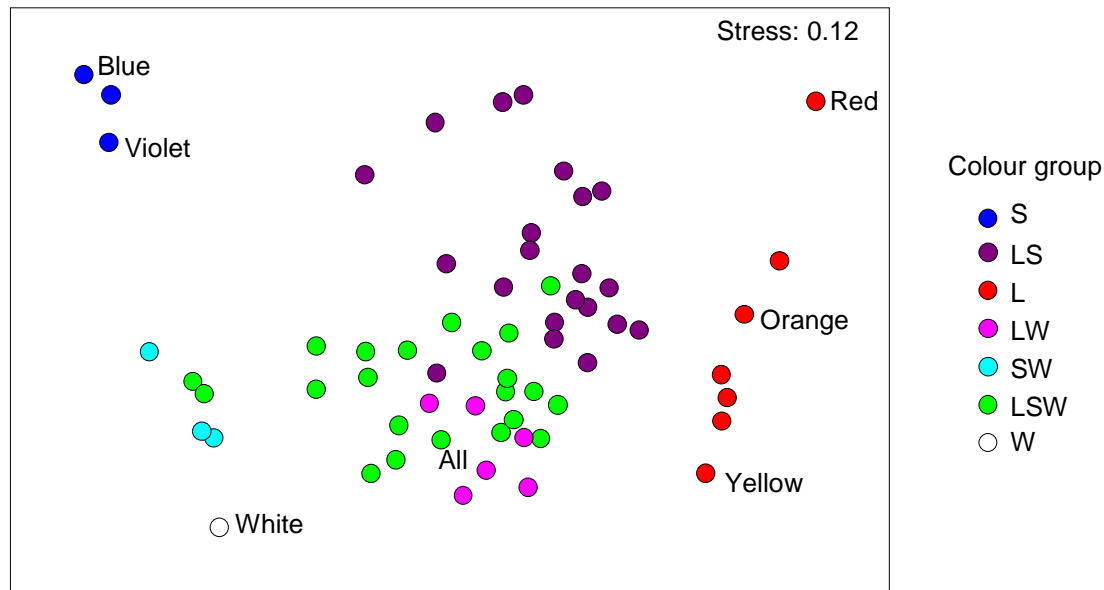


Figure 2.11 – Multi-dimensional scaling plot showing similarity of catch composition between sub samples by 63 different unique colour sets of six colours of pan traps. Each sub sample represents 150 pans drawn from a total pool of 997 coloured pan traps from the lowlands of the Cape Floristic Region. Single coloured samples are labelled for reference. Mixed colour sub samples are grouped by three colour types: S = short wavelength; L = Long wavelength; W = white; and combinations of these.

The species richness estimates based on the 63 colour sets showed significant differences ($F = 5.617$, $P < 0.001$) in terms of how well they estimated the actual species richness of the entire dataset (Figure 2.12). The highest diversity estimates were obtained from colour sets that included all three colour classes - long wavelength (orange; red), short wavelength (blue; violet) and 'high reflectance' (yellow; white) pans. Colour sets that included only long or only short wavelengths provided the lowest estimates while mixtures of long and short wavelength colours gave an intermediate figure. Diversity estimates also increased with the number of colours used, and simple linear regression found a significant, positive relationship ($N = 63$; $r^2 = 0.136$; $P = 0.003$) between

the mean estimated diversity (ICE) and number of colours per sub sample, represented by the equation: $Mean\ ICE = 182.35 + 5.23(number\ of\ colours)$.

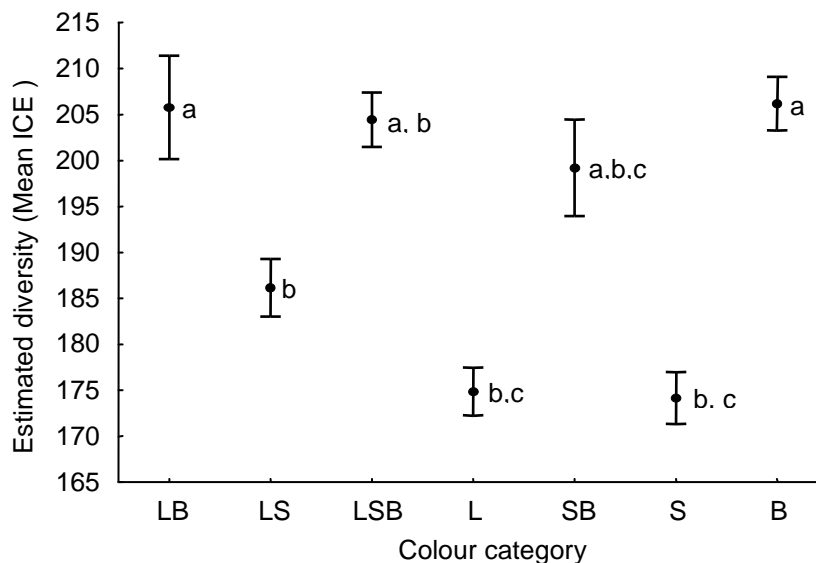


Figure 2.12 – Mean (\pm SE) diversity estimates from 63 sub sampled colour sets drawn from a total pool of 997 coloured pan traps from the lowlands of the Cape Floristic Region. Sub samples represent unique combinations of the six colours used and are grouped into seven categories depending on whether they contain long wavelength colours red and orange (L), short wavelength colours blue and violet (S), and 'high reflectance' colours yellow and white (B), or combinations thereof. Points with different letters are significantly different (Bonferroni test, $P < 0.05$).

Discussion

Suitability of pan traps for sampling insects among the Cape Flora

Pan traps are an effective method for sampling anthophiles in the lowland vegetation in the CFR. They are easily deployed in generally low and scrubby vegetation typical of the region, where sweep netting for insects is often difficult. As with any single trapping method however, they are not without shortcomings. Although I was able to sample a wide variety of anthophiles, in all likelihood this does not fully represent the complete range of anthophiles in the region. One immediately apparent gap is that pan traps perform poorly when sampling Lepidoptera. Although butterflies tend to be underrepresented in the CFR (Cottrell 1985) they were very poorly sampled in this study, represented by only three individuals of a single species, *Colias electo electo* (Lepidoptera: Pieridae), from more than 10 000 trap hours, even though they were abundant at most sampling sites during this period (pers. obs.). Even though colour is an important attractant for butterflies seeking nectar (Goulson & Cory 1993; Weiss 1995; Weiss 1997), the relatively small size of

these traps may not be suitable for catching larger taxa such as butterflies, as was noted by Campbell & Hanula (2007), who observed butterflies which were not captured by pan traps. Such limitations mean that pan trapping may not always represent the true diversity of an area (Cane et al. 2000). If the aim is to inventory all anthophiles in a particular area, then pan traps should be augmented by other trap types. For monitoring or for comparative studies however, such a shortfall would not be as important, as the same bias is across all comparative samples.

Colour preferences affecting pan trapping for anthophiles, particularly bees, have been investigated by several authors (Toler et al. 2005; Laubertie et al. 2006; Wells & Decker 2006; Campbell & Hanula 2007; Wilson et al. 2008; Tuell & Isaacs 2009; Missa et al. 2009). For the CFR, Picker & Midgley (1996) describe distinct colour guilds in monkey beetles (Scarabaeidae: Hopliini), and both Johnson & Midgley (2001) and Van Kleunen et al. (2007) describe the effects of colour affecting alighting behaviour of monkey beetles on model flowers.

In my study, there were marked differences between both the number and diversity of anthophiles caught in different coloured pan traps. Although many species were caught across a range of colours, more than a quarter of the taxa recorded in this study occurred in a single colour trap, indicating the importance using a range of colours rather than relying on a single broad-spectrum colour such as white or yellow, as is often the case.

Richness and diversity estimates from coloured pan traps

Colour selection had a discernable effect on how well the random sub samples drawn from the entire dataset were able to estimate the actual species richness of the entire dataset. Although all of the estimates fell below the actual figure of 254 species, most performed well, with estimates ranging from 170 (69%) to 238 (97%). Estimates could be broadly divided into three groups, a) colour sets that contained yellow or white. These colours represent widely visited flowers with a high reflectance (Kevan 1983) and are often used as 'standards' for pan trapping (e.g. Mattoni et al. 2000; Missa et al. 2009). These provided the highest estimates, followed by b) colour sets containing mixes of long and short wavelength colours which gave intermediate estimates and lastly c) those containing only colours from one end of the spectrum gave the lowest estimates. Similarly colour sets that included more colours tended to give higher estimates of species richness.

The grouping of colour sets based on their species composition, combined with the high proportion of species that were only caught in a single colour also show the importance of using a range of colours to make pan trap samples representative. Yellow traps, for example, may provide a

good species composition of an area by excluding taxa specific to colours other than yellow (Toler et al. 2005). This would be an important consideration for inventory studies, or when the aim is to target certain taxa that display distinct colour preferences (e.g. Leong & Thorp 1999).

Advantages of pan trapping

Pan trapping provides an economical, efficient and quantifiable method for collecting anthophiles, provided that biases such as the effect of colour are considered in both the study design and interpretation of the results. Large amounts of sample material and data can be generated with relatively little effort or specialised expertise in the field. Additionally, the technique is easily replicable and can be deployed simultaneously across several sites. Although it is easy to standardise and compare results within a particular study, comparing results across studies needs to be done with care, given the effects that various trap design variables may have on the efficacy of the traps.

Although collecting many specimens may be desirable for certain studies, large volumes of material collected significantly increases the amount of time spent required to process and identify samples. Because these activities require more specialised skills, this could in the long run, negate the economy and efficiency of deploying pan traps in the field. Pan trapping is a destructive method (i.e. individuals are removed from the population) so care may also need to be exercised when sampling rare species, or when intensively or repeatedly sampling a particular area.

The wide range of taxa captured in pan traps makes it an ideal method for the multi-species approach to monitoring or assessing the effects of disturbance, which may be more sensitive than using indicator species (Kremen et al. 1994; Lawton et al. 1998; Kotze & Samways 1999; Mattoni et al. 2000).

Conclusions

Coloured pan traps capture a diverse range of anthophiles in the CFR. For monitoring and comparative studies, I recommend the use of at least three colours – yellow or white, combined with a short wavelength colour such as blue and a long wavelength colour such as red. Pan traps alone however, are probably not sufficient for complete censuses, where it is necessary to augment this method with active collecting and other trapping methods to include rarer taxa and those which may be excluded by pan traps.

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The landscape mosaic of natural remnants embedded within a matrix of vineyards, farmland and urban development stretches across the lowlands of the Cape Floristic Region, as seen from the flank of the Helderberg between Stellenbosch and Somerset West.

3

Species turnover and relationships between flower visiting insects and plant diversity

SUMMARY

The Cape Floristic Region (CFR) has high plant species richness and endemism. Insects of the region are less well known, although limited information suggests proportionally high levels. Although the CFR has a comprehensive spatial planning and prioritisation framework for conservation, it rests largely on Broad Habitat Units, delineated along topographic, climatic and vegetation data. Knowledge of the congruence between patterns of plant and insect diversity would be useful, in conservation planning, as information on largely unknown groups such as insects often relies strongly on the better known plants as surrogates. Here, I compare species richness, turnover and diversity relationships between two co-occurring groups, flowering plants and flower visiting insects. Species richness and turnover of insects was comparable to that of plants for most sites. Although there was some congruence between species turnover and the similarity of sites based on the two groups, plant diversity was overall, a poor spatial surrogate for insect diversity. These patterns were consistent across spatial scales ranging from 0.5 – 80 km. While patterns of plant diversity and distribution play a role in shaping flower visiting insects assemblages, they are not reliable predictors and should be used with caution.

Introduction

The Cape Floristic Region (CFR) has high levels of plant species richness and endemism (Goldblatt & Manning 2002). Less is known about its invertebrate taxa, although it has been suggested that the diversity of insects in the CFR does not match that of the plants (Giliomee 2003). However, other studies suggest that this is not the case for groups such as plant-boring insects (Wright & Samways 2000). It is more likely that the insects of the CFR are proportionally as diverse as its plants, or at least similar to that of neighbouring biomes (Proches & Cowling 2006).

Conservation planning and priorities are well established in the CFR, with much focus on spatial planning and setting goals for conservation strategies (Pressey et al. 2003; Cowling et al. 2003). The basis of this work rests largely on Broad Habitat Units (BHUs) (Cowling & Heijnis 2001) which were defined using climate, topography, geology and vegetation as well as some ecological processes. More recently, there have been efforts to refine conservation planning using more sophisticated analyses such as phylogenetic diversity (PD) which attempts to include a measure of evolutionary 'value' into conservation planning by maximising 'feature diversity' rather than just species diversity (Forest et al. 2007). Yet these methods are still limited to taxa such as plants for which the necessary, detailed distribution and phylogenetic data are available. We know comparatively little however, about the diversity distribution of insects in the CFR, nor how well they would be protected within these spatial planning frameworks.

The lack of complete biodiversity data means that conservation planning is usually based on surrogates, under the assumption that unknown diversity should also be effectively conserved by plans for more familiar taxa or habitats (Rodrigues & Brooks 2007). Effective surrogacy relies strongly on the degree of congruence between the surrogate or indicator taxa and target groups. Congruence between plant and insect diversity has been widely discussed, with varying results depending on region, taxa and diversity measures used. Although plant diversity has been found to be a good predictor of herbivorous insects (Novotny et al. 2006), the relationship may not necessarily hold for non-herbivorous insects, nor across different spatial scales. Furthermore, tests of taxonomic surrogacy often produce contradictory results (Kremen 1992; Prendergast 1997; Duelli & Obrist 1998; van Jaarsveld et al. 1998; Osborn et al. 1999; Dauber et al. 2003). However, if environmental factors such as climate and topography affect insect diversity in the same way as plant diversity, then similar relationships may hold across a range of functional groups (Hawkins & Porter 2003), although this may only be

apparent at spatial scales large enough to encompass sufficient climatic or topographic variation (Gering & Crist 2002; Finlay et al. 2006).

Here, I compare species turnover of plant assemblages and closely associated assemblages of flower visiting insects (anthophiles) in natural and semi-transformed habitats in the CFR, at a range of spatial scales from 0.5 to 80 km. I address two key questions of relevance to conservation planning in the region: 1) Is turnover of anthophiles comparable to that of plants in the CFR? 2) Is the diversity of anthophiles in an area related to local plant diversity?

Methods

Study sites

This study was conducted in the lowlands of the CFR, as these lowlands are the most highly transformed and threatened habitats in the region (Rouget et al. 2003). Six sites, either in formally protected areas, or on farms, where land had been set aside for conservation purposes were selected. At each of these sites between one and four plots were selected, either in reserve areas, where available, or in remnant patches of natural habitat. In total, sixteen plots were used for analyses. All plots were situated in areas of natural or relatively undisturbed vegetation, below 400 m.a.s.l. and were selected to represent the heterogeneity of lowland habitats in the region.

The most northerly site (33.27°S, 19.03°E) was situated in the Elandsberg Nature Reserve (EL1-EL4). In the south-west (34.06°S, 18.87°E) the municipal Helderberg Nature Reserve (HE1-HE3) lies on the edge of the town of Somerset West. In the immediate surrounds of Helderberg Nature Reserve, sites were at Vergelegen (VG1-VG3) and Cordoba (CO1, CO2) estates in remnants of natural habitat. In the south-east, two more sites were selected, one at Klipfontein (KL1), part of the 42 000 ha HottentotsHolland Nature Reserve (33.98° S, 19.13° E). The last site was situated in the Diepklowe Private Nature Reserve (GB1-GB3) in the Bot River valley about 10 km from the Klipfontein site. Further details of the plots are given in Appendix 1.

Insect sampling

Insects were surveyed using coloured pan traps. Anthophiles in the CFR (Picker & Midgley 1996) and elsewhere (Leong & Thorp 1999; Campbell & Hanula 2007) have been found to show differential colour preferences to pan traps, so a range of colours were used, namely red, orange, yellow, blue, violet, and white. Polypropylene tubs (RL350, Marco Plastics, Alberton South Africa), 115 mm diameter by 50 mm deep (350 ml volume), were painted with gloss enamel paint (Dulux SA, Alberton, South Africa). For each site, three

arrays of six coloured pan traps were used, arranged in a — | — configuration of three 50 m lines in each site, with the six colours arranged randomly at 10 m intervals on each line.

Pans were elevated and set at the level of flowers in the surrounding vegetation, and half filled with water, with a little detergent added to reduce surface tension. Elevating pan traps to the level of the canopy where insects are actively foraging has been shown to significantly increase catches (Tuell & Isaacs 2009). Trapping took place only on sunny days, from 08h00 to 17h00. At the end of each day, trapped insects were removed from the water and preserved in 80% ethanol for later identification. Whenever possible, trapping occurred on two consecutive days per site, although as the weather at this time of year is highly variable often the next suitable day was used. Anthophiles were sampled in the spring (September-November) of 2005 to coincide with times of peak flowering at each site. Further detail of pan trapping and its suitability for sampling anthophile diversity in the CFR are given in Chapter 2 of this dissertation.

Upon completion of sampling, insects were counted and identified using a Leica Microsystems Ltd. (Heerbrugg, Switzerland) M-Series stereomicroscope. Initial identifications were to morphospecies, with later identification using the entomology collection in the Iziko South African Museum in Cape Town and consultation with experts on certain groups. All insects were identified to at least family level or further where possible. Morphospecies are widely used in ecological studies and can act as good surrogates for formal species (Oliver & Beattie 1996). A voucher collection is housed in the Entomology museum at the Department of Conservation Ecology and Entomology, Stellenbosch University.

Vegetation transects

Vegetation was surveyed the day before the first day of pan trapping at each site. Vegetation composition, height and cover were measured over three, 20 m transects per site. The transects overlaid the three pan trap lines used per site. All plants that covered the transect line were measured (height in centimetres, length of transect covered in metres), identified and their flowering status noted (not flowering, flowering, in bud, in seed). For sections of mixed vegetation, where several species formed a uniform ground cover mix, each was recorded separately but the distance covered was divided by the number of species in the mix. Open patches of ground were recorded and classified according to whether they were bare ground, rock, leaf litter or woody debris.

Species richness estimates

For insects, total abundance of each species per site was calculated from the pooled data of six arrays per site (three arrays x two sample days per site). For plants, data from all three transects were pooled for each site, to calculate total distances covered by each plant species and ground cover category. Species richness was estimated using the EstimateS Version 8.0 software package (Colwell 2006), using the pan trap data pooled per array in each plot. Many different species richness estimators are available, each with their own combinations of precision and bias that affect their accuracy (Walther & Moore 2005). Given that certain anthophiles were highly abundant in pan trap samples, an incidence-based estimator, the Incidence Coverage Estimator, ICE (Chao et al. 2000), was calculated for each plot, using 1000 randomisations, with replacement. Although non-parametric species richness estimators do have drawbacks and potential inaccuracies they can still provide useful information and at least minimum estimates of species richness for areas and taxa where no inventories are available (Longino et al. 2002; O'Hara 2005; Hortal et al. 2006).

Site similarity

Sites were classified using the CLUSTER routine in PRIMER Version 5 (Primer-E Ltd 2002). Cluster analysis was based on Bray-Curtis similarities of the pooled vegetation and pan trap data for each site which grouped sites according to similarity of their plant and anthophile assemblages respectively. From dendrograms produced by PRIMER, sites were classified according to subjective cut off values of 20% similarity for plants and 30% similarity for insects. Differences between these groupings were then tested using the analysis of similarity (ANOSIM, 1000 permutations) in PRIMER to confirm significance (Clarke & Warwick 2001).

Species turnover

The number of plant and anthophile species shared between all possible pairwise combinations of sites (120 pairs in total) was calculated using EstimateS (Colwell 2006). Additionally, for all 120 site pairs, the difference between the number of species observed at each site, and distance between sites (in kilometres) was calculated. To test for spatial relationships and species turnover, shared species and differences in species richness were plotted against distance for each site pair, using a simple linear regression in Statistica Version 8.0 (StatSoft Inc. 2007). Associations between site distance and number of shared species and site distance and species richness differences were also tested with Mantel tests (Sokal & Rohlf 1995), using the

PopTools (Hood 2008) plugin for Microsoft Excel. Associations were tested at a significance of $P = 0.05$ with 999 iterations run for each test (Legendre 2000).

Vegetation structure and composition

To compare the effects of vegetation structure and composition of the plant assemblage on flower visiting insect assemblages at each site a number of variables were compiled from the vegetation data (Table 3.1). Plant species composition at each site was summarised using detrended correspondence analysis (DCA) in CANOCO Version 4.53 (ter Braak & Šmilauer 2004) as the detrended segment lengths reported by CANOCO (maximum segment length >4) indicated that the data were unimodally distributed (Lepš & Šmilauer 2003). Scores from the first DCA axis, which accounted for 11.5% of total variation in the dataset were used as a measure of similarity between sites (Total inertia = 5.251, cumulative% variance described by 4 axes = 24.7).

Table 3.1 – Vegetations structure and composition variables calculated from 50 m line transect data for sixteen plots in the lowlands of the Cape Floristic Region.

Variable	Description
Plant cover	Total length (m) per transect covered by vegetation (excludes open ground, with litter, woody debris and sparse seedling cover).
Vegetation height	Mean height (cm) of vegetation per transect.
Flower cover	Total length (m) per transect covered by plants in flower at time of survey.
Open ground	Total length (m) per transect not covered by plant canopy (includes open ground with litter, woody debris and sparse seedling cover)
Plant composition	Index of similarity between all plots based on plant species composition using first axis scores from a detrended correspondence analysis
Plant richness	Estimated plant species richness per plot from Incidence Coverage Estimator, ICE (Chao et al. 2000)
Flower richness	Estimated species richness of flowering plants per plot from Incidence Coverage Estimator, ICE (Chao et al. 2000)
Annuals	Total length (m) per transect covered by annual species per plot. Plant species classified according to POSA (South African National Biodiversity Institute 2009)
Perennials	Total length (m) per transect covered by perennial species per plot. Species classified according to information in POSA.

The effects of vegetation structure and composition were tested in CANOCO using a canonical redundancy analysis (RDA) of anthophile assemblage data. Unlike the plant data, the segment lengths of an initial DCA indicated a linear distribution, more suited to an RDA (Lepš & Šmilauer 2003). The ordination was initially constrained by the nine vegetation variables in Table 3.1. Stepwise selection was used to select a subset of the four best fitting variables for the final model, based on partial Monte-Carlo

permutation tests to assess the usefulness of each potential variable (Lepš & Šmilauer 2003). Variance partitioning (Borcard et al. 1992) was used to calculate the relative contributions of the final four variables following procedures in CANOCO described by Lepš and Šmilauer (2003).

Results

Plant and flower visiting insect species richness

Observed and estimated plant species richness varied widely between plots, although there was no clear pattern of variation (Figure 3.1). The lowest observed plant species richness in a plot (18 spp.), was recorded at Elandsberg (EL2) and the highest (82 spp.) at Vergelegen Estate, in plot VG1 (Table 3.2a). Overall, mean number of observed species was 42 (± 1.03). Estimated species richness (ICE) ranged from 25 spp. (EL3) to 92 spp. (VG1), with a mean of 61 (± 1.16).

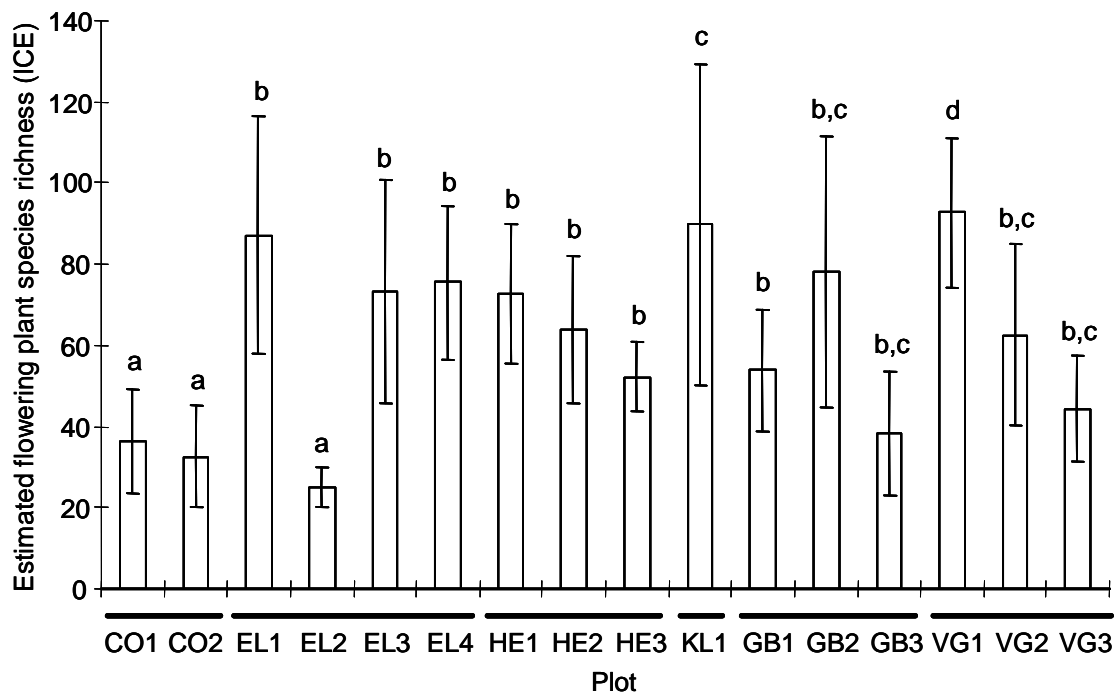


Figure 3.1 - Estimated (mean ICE \pm SD) flowering plant species richness in 16 plots in the lowlands of Cape Floristic Region. Solid bars above plot abbreviations denote grouping of plots by study site. Plots with the same letters are not significantly different (Z-test, $P > 0.05$).

There was similar variation in recorded and estimated species richness of flower visiting insects (Figure 3.2) ranging from a minimum of 31 observed species at Vergelegen Estate (VG1) and a maximum of 67 observed species at Helderberg Nature Reserve (HE2). A mean of $37 (\pm 0.18)$ species was observed across all sites. Estimated richness (ICE) was highest at Cordoba (CO1) with 71 species, and lowest at Veregelegen (VG1) at 36 species (Table 3.2b). Mean ICE across all plots was $50 (\pm 0.82)$.

Overall, anthophile species richness did not correspond well with plant species richness. Simple linear regressions revealed no significant relationships between estimated or observed insect species richness or abundance, and that of plant species at a site (for all regressions, $P > 0.05$).

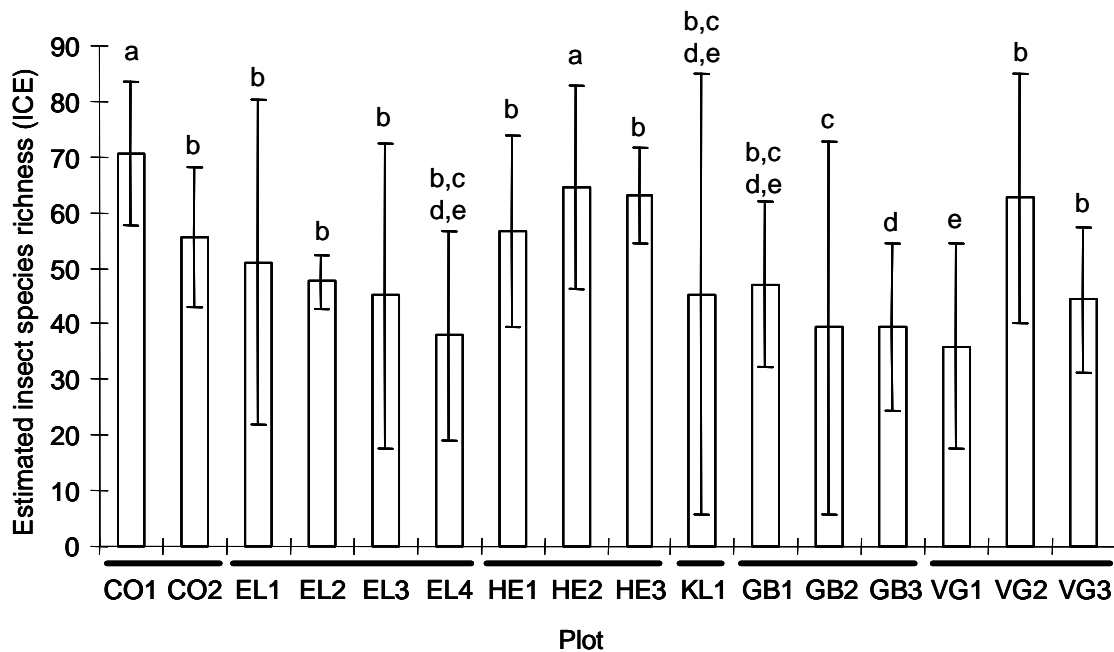


Figure 3.2 – Estimated (mean ICE \pm SD) species richness of flower visiting insects in 16 plots in the lowlands Cape Floristic Region. Solid bars above plot abbreviations denote grouping of plots by study site. Plots with the same letters are not significantly different (Z-test, $P > 0.05$).

Table 3.2 - Non-parametric species-richness estimates using four, abundance based species richness estimators for a) flowering plants and b) flower visiting insects from sixteen sites in the lowlands Cape Floristic Region.

a) Flowering plants						
	N [†]	Obs.	ICE (±S.D.)	Chao 2 (±S.D.)	Jack 1 (±S.D.)	Jack 2 (±S.D.)
CO1	3	29	36.31 (±12.94)	31.08 (±5.36)	30.38 (±4.04)	32.52 (±9.22)
CO2	3	28	32.53 (±12.52)	26.28 (±3.11)	28.19 (±3.92)	29.86 (±8.73)
EL1	3	70	87.15 (±29.23)	70.48 (±5.72)	74.88 (±8.77)	79.51 (±19.52)
EL2	3	24	25.11 (±4.87)	23.55 (±2.32)	24.65 (±2.34)	25.62 (±4.74)
EL3	3	62	73.19 (±27.31)	57.95 (±4.69)	62.92 (±9.96)	66.67 (±17.61)
EL4	3	69	75.53 (±18.98)	67.17 (±5.00)	70.7 (±9.07)	74.04 (±16.45)
GB1	3	51	72.69 (±17.28)	64.38 (±4.39)	68.8 (±7.75)	72.17 (±14.08)
GB2	3	62	63.82 (±18.37)	55.1 (±4.59)	58.25 (±7.60)	61.26 (±14.26)
GB3	3	33	52.18 (±8.64)	46.12 (±3.24)	50.18 (±6.10)	52.35 (±7.840)
HE1	3	67	89.67 (±39.63)	70.03 (±5.77)	74.44 (±10.23)	79.39 (±24.70)
HE2	3	57	53.9 (±14.85)	48.09 (±3.70)	51.01 (±6.21)	53.32 (±13.05)
HE3	3	48	78.05 (±33.52)	82.22 (±16.08)	64.37 (±10.87)	68.75 (±23.12)
KL1	3	74	38.3 (±15.17)	30.93 (±3.29)	33.33 (±4.98)	35.33 (±10.48)
VG1	3	82	92.64 (±18.56)	82.3 (±5.56)	87.08 (±10.18)	91.28 (±15.18)
VG2	3	67	62.63 (±22.37)	52.2 (±5.17)	54.45 (±6.46)	57.86 (±14.92)
VG3	3	66	44.34 (±13.03)	36.76 (±3.82)	39.41 (±5.68)	41.74 (±8.62)

b) Flower visiting insects						
	N [‡]	Obs.	ICE (±S.D.)	Chao 2 (±S.D.)	Jack 1 (±S.D.)	Jack 2 (±S.D.)
CO1	3	67	60.80 (±3.23)	62.07 (±3.68)	67.55 (±8.26)	70.47 (±13.97)
CO2	3	48	47.31 (±4.77)	47.49 (±4.46)	50.12 (±5.66)	53.08 (±13.16)
EL1	3	48	47.74 (±5.49)	47.24 (±4.51)	48.52 (±5.53)	50.92 (±10.60)
EL2	3	45	42.73 (±3.27)	44.32 (±4.05)	45.75 (±4.52)	47.84 (±9.53)
EL3	3	43	44.32 (±4.95)	41.5 (±2.97)	44.19 (±4.64)	45.89 (±8.22)
EL4	3	35	33.92 (±3.32)	33.1 (±2.69)	36.16 (±4.04)	37.82 (±6.75)
GB1	3	40	38.73 (±5.22)	38.48 (±4.52)	39.88 (±5.91)	42.47 (±13.34)
GB2	3	34	40.63 (±10.50)	37.43 (±7.20)	34.1 (±4.48)	36.25 (±10.08)
GB3	3	34	33.51 (±3.91)	33.04 (±3.40)	35.41 (±4.56)	37.41 (±9.47)
HE1	3	52	49.3 (±3.31)	51.64 (±4.54)	53.71 (±6.61)	56.04 (±12.16)
HE2	3	60	59.99 (±4.95)	58.39 (±3.81)	62.42 (±6.22)	65.14 (±12.38)
HE3	3	57	57.05 (±6.56)	56.06 (±5.84)	56.51 (±6.39)	59.82 (±15.71)
KL1	3	39	38.19 (±4.22)	37.87 (±3.58)	40.93 (±4.76)	43.29 (±9.75)
VG1	3	31	28.68 (±3.15)	34.48 (±7.11)	30.44 (±4.21)	32.18 (±11.29)
VG2	3	52	50.18 (±4.60)	52.2 (±5.17)	54.45 (±6.46)	57.86 (±14.92)
VG3	3	38	36.13 (±3.78)	36.76 (±3.82)	39.41 (±5.68)	41.74 (±8.62)

[†] Number of vegetation transects used to generate species richness estimates

[‡] Number of pan trap-arrays used to generate species richness estimates (Pooled data from 2005 pan trap survey)

Species assemblages

The sixteen plots separated according to their plant assemblages (Figure 3.3). At 20% similarity, four distinct groups could be discerned. Pair-wise comparisons showed that not all of these groups were significantly different, and the ANOSIM results suggested three groupings rather than four (Figure 3.3). Although groupings generally followed the spatial separation of the plots, with nearby plots from the same sites grouping together, there were exceptions, for example plot KL1 which grouped with sites from Elandsberg Nature Reserve, almost 70 km away, and plot EL2 which was quite distinct from all other plots (See Table A1.2, Appendix 1 for distances between plots).

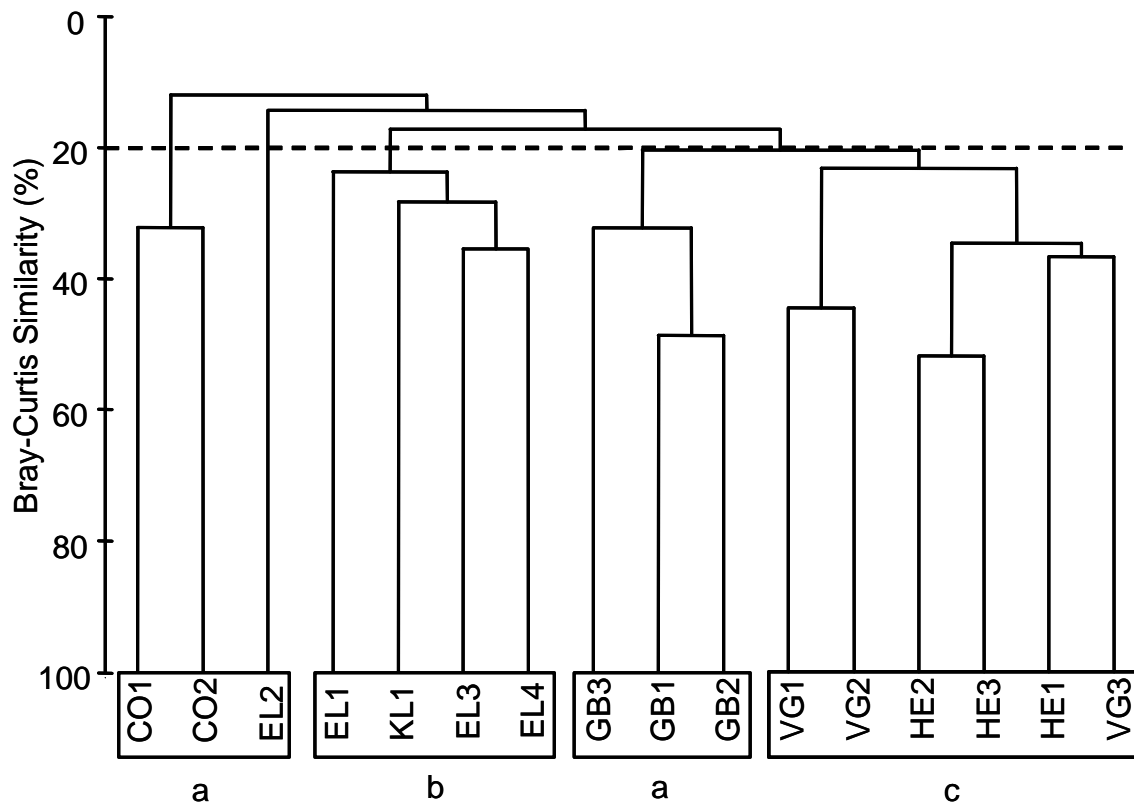


Figure 3.3 - Classification of sixteen sites in the lowlands of the Cape Floristic Region based on the similarity of flowering plant assemblages recorded from vegetation transects. Groups are divided at 20% similarity (indicated by dashed horizontal line). Groups sharing the same letter (a, b or c) below the diagram were not significantly different (ANOSIM, pairwise tests, $P > 0.05$).

There was a greater degree of similarity between anthophile assemblages at plots with the first major division occurring at about 25% similarity, but the grouping of plots was less spatially distinct with more intermingling of distant plots (Figure 3.4). Pair-wise comparisons found all groups to be significantly different (ANOSIM, Global R = 0.658, $P < 0.001$). Grouping plots by anthophile assemblages produced different associations than those based on plant assemblages in the same plots (cf. Figure 3.3).

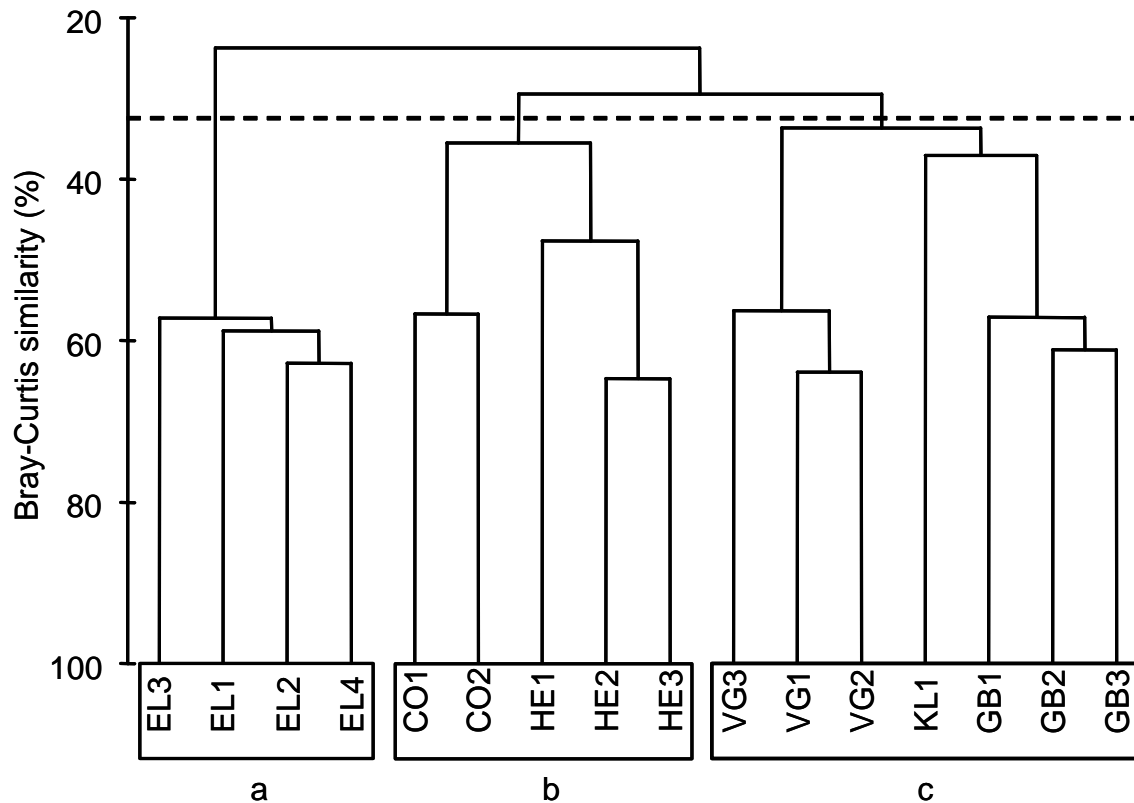


Figure 3.4 – Classification of sixteen sites in the lowlands of the Cape Floristic Region based on the similarity of flower-visiting insect assemblages recorded from coloured pan trap surveys. Groups are divided at approximately 30% similarity (indicated by dashed horizontal line). Letters below the diagram (a,b,c) indicate significantly different groups (ANOSIM, pairwise tests, $P < 0.05$).

Species turnover

The distance between sites significantly affected the number of shared species, differences in species richness and species assemblage (Bray-Curtis similarity), when tested using Mantel tests (Table 3.3).

Table 3.3 – Associations between the distance between plots, and differences in species richness and diversity of flowering plants and flower visiting insects observed in sixteen plots in the Cape Floristic Region.

	Mantel test statistic ¹	P-value ²
Shared plant species (%)	0.999	<0.01
Shared insect species (%)	0.999	<0.01
Plant species richness (change between sites)	0.662	0.03
Insect species richness (change between sites)	0.619	0.04
Plant assemblage similarity (Bray Curtis)	0.998	<0.01
Insect assemblage similarity (Bray Curtis)	0.998	<0.01

¹ Proportion of times coefficient of the original data is exceeded.

² 999 iterations, $\alpha = 0.05$.

Linear regressions of showed that for the entire set of 120 pairwise comparisons, number of species, and number of shared species decreased significantly for both plants ($R = -0.7991$, $P < 0.001$, Figure 3.5), and anthophiles ($R = -0.6008$, $P < 0.001$, Figure 3.6). Because the study sites were spatially grouped into three regions, pairwise comparisons separated out into three distinct distance classes, <10 km apart, 20-40 km apart and 60-80 km apart. Similar significant trends were evident within the different distance classes except for the 60-80 km group for plants and 20-40 km group for anthophiles which were not significant. Although Mantel tests indicated an association between the distance separating sites and differences in species richness, no significant relationships were found in linear regressions of differences in species richness vs. distance for plants or insects (all $P > 0.05$).

Within group regressions were significant only for the <10 km group for plants ($R = 0.4290$, $P = 0.0057$) and the 10-40 km group for insects ($R = 0.4958$, $P = 0.0039$), but the explanatory power of these trends was lower than those shown for all species.

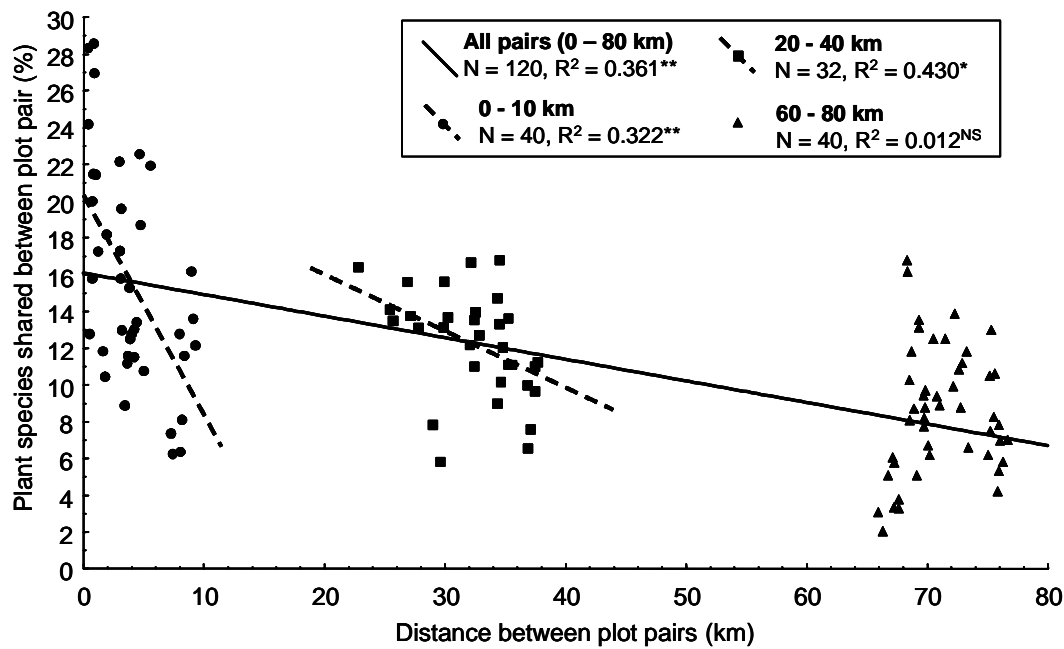


Figure 3.5 – Species turnover of plants, represented by the number of shared species between plot pairs at four spatial scales for sixteen plots in the lowlands of the Cape Floristic Region. Each point represents a pair of sites (120 possible combinations). Solid line indicates best fit of a simple linear regression for all points, while dashed lines are best fit for each subgroup of pairs in three distance classes. Only significant regressions are shown ($P < 0.05$).

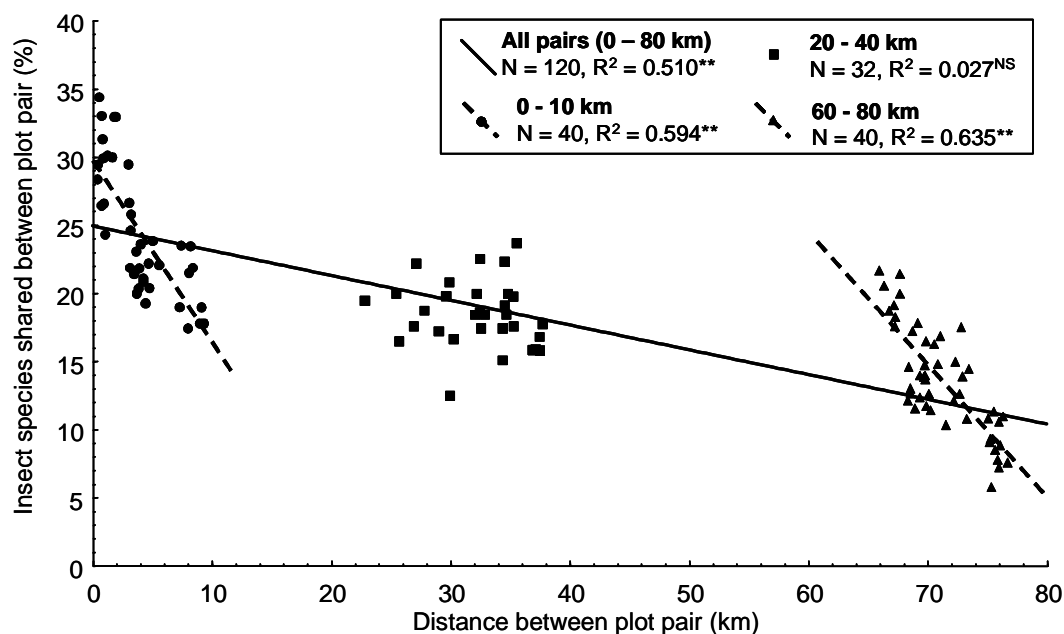


Figure 3.6 - Species turnover of flower visiting insects, represented by the number of shared species between plot pairs at four spatial scales for sixteen plots in the lowlands Cape Floristic Region. Each point represents a pair of sites (120 possible combinations). Solid line indicates best fit of a simple linear regression for all points, while dashed lines are best fit for each subgroup of pairs in three distance classes. Only significant regressions are shown ($P < 0.05$).

Effect of vegetation structure and community composition

Of the nine variables tested, stepwise selection showed that plant species composition, flower cover, plant species richness and average vegetation height were the four most influential variables, collectively explaining 51% of the total variation in the anthophile assemblage data (Figure 3.7). Variance partitioning suggested that flower cover was the most important variable, accounting for 22.1% of variation followed by plant composition (10%), mean vegetation height (6.9%) and plant species richness (3.4%). A further 8.7% of the variation could not be attributed to any particular one of these variables.

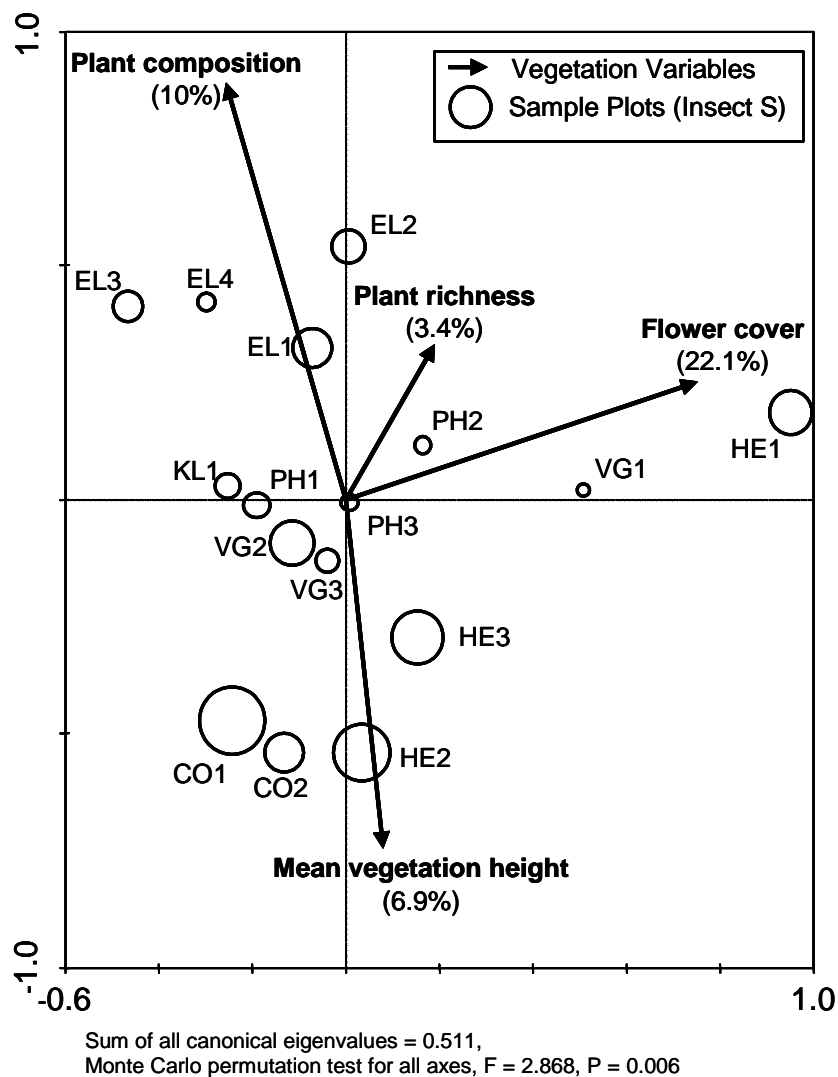


Figure 3.7 – Biplot from the RDA of anthophile assemblages at sixteen sites in the lowlands of the Cape Floristic Region. Sizes of the circles indicate relative species richness for each site. Arrows indicate the best subset of four vegetation structure variables chosen by forward selection during ordination. For each variable, the relative contribution to the total variation of 51.1% explained by the canonical axes is given in parentheses.

Discussion

Species richness and turnover

Species richness of anthophiles was similar to that of the flora for the region as a whole, as well as at individual sites. This is consistent with other findings emerging in the literature, as knowledge of arthropod diversity in the Cape Floristic Region improves (Wright & Samways 1998; Proches & Cowling 2006). The results here show a high turnover of insects across the landscape, highly similar to that the flora of the region. Even nearby sites showed a high degree of distinctness, with no site sharing more than 29% of plant species and 35% of anthophile species.

Species turnover is apparent at several spatial scales with distinct differences observable from the local (<10 km) to the regional (>60 km) scales. The high degree of species turnover, even at fine spatial scales made species richness an unstable measure, which may vary unpredictably across the landscape, unlike the number of shared species or degree of similarity between sites. Caterino (2007) found similar levels of spatial variability in a study of beetle fauna in the California Floristic Province, and it is likely that this may be characteristic of insect assemblages in mediterranean-type ecosystems. When comparing plant assemblages and their associated anthophile assemblages, both regions showed congruent patterns of similarity between sites, but incongruent patterns of diversity.

Congruence between plant and insect assemblages

Although similar patterns of species richness and turnover were observed for plants and anthophiles, the nature of the relationship between the two remains unclear. Procheş et al. (2009) found a consistently positive relationship between plant and insect diversity in the fynbos biome. In my study however, no consistent relationship was found between the two. Grouping based on assemblage data showed that areas with similar plant assemblages did not necessarily share similar insect assemblages. This decoupling between the two groups means that plant richness alone is not a wholly reliable surrogate for insect diversity, at least not at the scale examined here. Procheş et al. (2009) however, also note that plant-insect relationships are highly variable across biomes, scales and insect guilds, suggesting that in each case, different factors may drive insect diversity.

Factors affecting diversity of flower visiting insects

Flower visiting insects are highly mobile organisms that exhibit a wide range of specificity in terms of which plant species they visit. This is a well studied topic in pollination biology, with interactions between plants and

insects ranging along a continuum from highly specialised to extremely generalised interactions (Johnson & Steiner 2000). The needs of anthophiles are not only restricted to plants. They also include aspects not directly provided by plants, including resting, courtship and mating, oviposition or nesting, and avoiding death (Kevan & Baker 1983; Buchmann & Nabhan 1996; Kearns et al. 1998; Kevan & Baker 1999). This means that anthophiles are sensitive to a range of factors that may not affect plants. Mobility also means that they are able to respond to changes in the environment much faster than plants, introducing a temporal component of variation that could not be accounted for in this study.

Given the diverse range of taxa encompassed by an entire assemblage of anthophiles, it is difficult to generalise about which factors are most important. The four most influential variables here are likely to represent some of the resource needs of this assemblage, but do not account for all of the observed variation. The fact that flower cover (a measure of the relative abundance of resources for anthophiles) was far more important than plant richness and diversity suggests that resource availability is an important determinant of flower-visitor diversity and abundance, particularly at the local scale (Hegland & Boeke 2006). The species rich, temperate flora of southern Africa has a remarkable prevalence of highly specialised pollination systems (Johnson & Steiner 2003), so it may seem strange that plant diversity is not a reliable estimator of anthophile diversity. However, functional relationships between plants and anthophiles and plant are characterised by a high degree of asymmetry (Jordano 1987). Anthophiles visiting a specialised plant can be taxonomically diverse, although even specialised pollinators may visit a range of non-specialised plants. The degree of ecological specialisation observed at any one time can be affected by various spatial and temporal factors (Ollerton 1996; Petanidou & Potts 2006), meaning that plant and pollinator diversity may not be as tightly coupled as would be expected. Although resources for anthophiles are affected by the richness and diversity of the local flora, the abundance and quality of suitable resources is not necessarily directly related to plant species richness alone.

Conclusions

In the absence of complete knowledge of biodiversity, surrogacy remains a vital tool for conservation planning (Rodrigues & Brooks 2007). However, in a recent meta-analysis of correlations between species richness of different taxa, Wolters et al. (2006) found no single taxon to be a universal, or even good predictor of the richness of other taxa. Diversity indicators should be used cautiously, in conjunction with other approaches, until we have a

better understanding of the mechanisms that drive species richness correlations.

The discordance between these results and those of other studies such as Procheş et al. (2009), as well as the inconsistencies noted by those authors, indicate that the factors affecting distributions differ between various taxonomic groups and can confound attempts to draw general conclusions about the relationships between plant and insect species-richness.

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The landscape mosaic. The lowlands around Helderberg mountain consist of a complex patchwork of suburban development, vineyards, orchards, a golf course and exotic tree plantations. Embedded within this anthropogenically altered matrix are scattered remnants of natural vegetation providing small islands of habitat for endemic plants and invertebrates.

4

Farmland biodiversity complements nature reserves for plants and their flower visiting insects

SUMMARY

An increasing challenge is to integrate conservation and agricultural production to create multiuse, ecoagricultural landscapes. Although protected areas form the core of biodiversity conservation worldwide, the value of farmland biodiversity cannot be overlooked, if we are to meet the conservation goals set through systematic conservation planning. Here, in the Cape Floristic Region, a biodiversity hotspot, I compare the diversity of plants and their flower visiting insects among sites within reserves and those representing transformed, remnant and semi-natural landscape components. Species richness of sites outside reserves was found to be similar to those within reserves for flower visiting insects. Species richness was more variable for plants, although sites outside reserves often retained a high diversity of flowering plants. Comparisons of assemblages among sites found that sites shared 20-38% of their insect species and 12-28% of plants species, although each category of sites (transformed, heavily disturbed, natural remnants and reserves) retained species that were not found elsewhere in the landscape. This means that habitats outside reserves make a major contribution to the overall biodiversity of the region. Successful biodiversity conservation in the Cape Floristic Region should consider the entire landscape as a heterogeneous, ecoagricultural system that integrates natural and agricultural components.

Introduction

Agricultural intensification and expansion in the latter half of the 20th century have been major drivers of loss of biodiversity at local, regional and global scales through the continuing degradation of natural and semi-natural habitats (Norris 2008). In the face of widespread land transformation there is a growing need for agroecosystems to play a major role in biodiversity conservation (Perrings et al. 2006; Fischer et al. 2006). This is particularly pertinent for biodiversity hotspots, which as defined by Myers et al. (2000), have already lost at least 70% of their natural habitat.

In general, the global coverage of protected areas is far from complete (Brooks et al. 2004; Rodrigues et al. 2004), especially in areas with high levels of endemism (Rodrigues & Gaston 2001). Although protected areas are central to effective conservation strategies (Margules & Pressey 2000), much remaining natural habitat exists outside formally protected areas, with most species now living in human-managed ecosystems (Pimentel et al. 1992). Consequently, the need for conservation outside protected areas has become widely recognised (Norris 2008). This has led to the challenge of conserving biodiversity in the context of so called 'ecoagriculture', the creation of integrated conservation-agriculture landscapes (Scherr & McNeely 2008), based upon the integration of ecological principles into the design and management of multiuse landscapes for agricultural production and biodiversity conservation (Fischer et al. 2006; Samways 2007).

Biodiversity of an agroecosystem is maintained at different levels within each of the different landscape components (Figure 4.1). The entire landscape may be home to certain generalists and opportunists, while specific components of the landscape, especially the transformed ones, only host certain species which have adaptations to survive transformation and its ongoing dynamics. These, speculatively, will only be a subset of those occurring in neighbouring, large untransformed patches such as nature reserves, which will support a more diverse range of species, including species eliminated from the transformed landscape components. The variation in species from one patch to another will be determined by a range of anthropogenic and natural factors, with organisms responding differently to transformation, as they disappear, appear or are replaced along gradients of agricultural intensification (Burel et al. 2004).

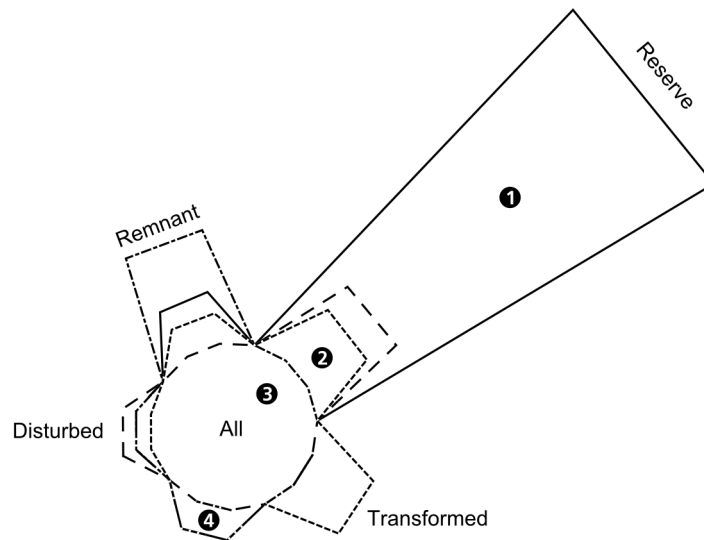


Figure 4.1 – Conceptual diagram of how biodiversity might be apportioned within a transformed agricultural landscape. The area of each region represents the number of species occurring within a particular landscape component. For example, region 1 represents species found only in reserves, region 2 represents species occurring in reserves, remnant and disturbed habitats, region 3 represents species that occur within all four landscape components and region 4 represents species occurring in reserves and transformed habitats. Reserves are expected to hold the greatest number of species, many of which would not occur elsewhere. Heavily disturbed, remnant and transformed habitats hold proportionally fewer species. A number of species would be shared across all habitat types, while others would only be shared between some habitat types. (Based upon an area proportional Euler diagram (Chow 2007).)

In the Cape Floristic Region (CFR), a global biodiversity hotspot (Cowling et al. 2003; Mittermeier et al. 2004), most of the remaining lowland vegetation exists as scattered remnants on privately owned land (Kemper et al. 2000). The fragmented nature of natural habitat means that effective biodiversity conservation, by default, has to be implemented in an ecoagricultural context. High levels of endemism and species turnover, and the high conservation value and degree of irreplaceability of most habitat types in the CFR mean that even small remnants are likely to be valuable in terms of achieving the goals of conservation planning (Rouget et al. 2003a; Rouget et al. 2003b).

Towards this end, there have been various schemes such as CapeNature's Stewardship Programme (Winter 2004a) and the Biodiversity and Wine Initiative (Winter 2004b) instituted to encourage farmers and landowners to actively undertake conservation action on their lands. Although such schemes are based upon sound principles, little quantifiable data has been presented as to the levels of biodiversity that might be maintained within natural and semi-natural habitat remnants making it

difficult to determine their true conservation value. This is especially true for lesser known groups such as insects, where we have little information about diversity and distributions in natural, let alone transformed, areas. Here, I assess the diversity of flowering plants and their associated flower visiting insects (anthophiles) in sites representing a range of transformed and semi-natural landscape components to compare the complementary biodiversity value of farmland habitats with those in protected natural areas. I address two key questions: 1) How many plant and anthophile species are retained in these remnant and marginal agricultural habitats, outside protected areas? 2) How well do these species complement those that occur in existing protected areas?

Methods

Study sites

The study area was the lowlands of the CFR, the most highly transformed and threatened part of the region (Rouget et al. 2003a). Sites were situated in three localities, where a reference site was selected within a reserve area. At each locality several sites were selected within adjacent or nearby remnants of natural and semi-natural vegetation embedded within agricultural land. All sites were below 400 m.a.s.l. and were selected to represent the botanical heterogeneity in the region.

Remnant sites were all within vicinity of protected areas, situated on farms where the owners/managers have shown an interest in conservation either by joining conservancies, or have incorporated some form of conservation measures into management of their land.

The three localities formed a triangle with the Elandskloofberge (ELKB) in the north. The reserve site was situated in the Elandsberg Nature Reserve (33.27° S, 19.03° E). The reserve, proclaimed in 1973 covers 4000 ha. It protects the largest remaining contiguous area of West Coast Renosterveld and some bordered by abandoned farmland (Ashwell et al. 2006). The surrounding farmland includes wheat fields and sheep and cattle pasture. Outside the reserve three sites were selected, one in an old field on the boundary of the reserve, and a further two sites in fragments of natural vegetation surrounded by wheat fields. Vegetation in the two fragments was in a near natural state with minimal artificial disturbance although one site was disturbed by feral pigs.

In the south-west, sites lay around Helderberg Mountain (HEBR) (34.06° S, 18.87° E). The Helderberg Nature Reserve (HE) was chosen as a reserve site. Declared in 1964 on former farmland and encompassing areas of natural vegetation, recovering vegetation and an alien tree plantation (mainly

Pinus pinea) the reserve is surrounded by urban residential use, a golf course and wine estates. Two remnant sites were situated on the nearby Cordoba Estate (CO). One site was an old vineyard, where natural vegetation had been replanted, and another in a small fragment of moderately degraded natural vegetation adjacent to vineyards. A further three sites were situated on Vergelegen Estate (VG) a champion of the Biodiversity and Wine Initiative (BWI) (Winter 2004b). The estate has embarked upon extensive invasive alien plant (IAP) eradication programme to remove IAPs such as black wattle (*Acacia mearnsii*), pine (*Pinus pinea*) and eucalyptus (*Eucalyptus* spp.) and restore up to 300 ha of natural vegetation on the estate. One site was situated in a 60 ha block of relatively undisturbed natural vegetation, a second on recently cleared land with some remaining aliens, and a third in a 40 m wide firebreak, with grass and natural vegetation between dense stands of *P. pinea* and *A. mearnsii*. Because of the number of sites outside the reserve at this locality, a second reference site was selected within the Helderberg nature reserve to ensure equal sampling effort across the different site categories at this locality.

In the south-east, the reserve site was situated at Klipfontein (KL), part of the 42 000 ha Hottentots Holland Nature Reserve (33.98° S, 19.13° E). Remnant sites were in the Diepkloof Private Nature Reserve (GB) in the Bot River valley about 10 km from the Klipfontein reserve site. Diepkloof is part of the Groenlandberg Conservancy (GLBC) of 34 000 ha (IUCN 2009). One site was situated in natural, but moribund vegetation dominated by renosterbos (*Elytropappus rhinocerotis*) and another in a recently mowed firebreak in similar vegetation. The third site was in a remnant patch of more slightly disturbed vegetation adjacent to a fallow wheat field.

Anthophile sampling

Insects were sampled using coloured pan traps. Anthophiles in the Western Cape (Picker & Midgley 1996) and elsewhere (Leong & Thorp 1999; Campbell & Hanula 2007) have differential colour preferences to pan traps, so a range of colours were used, namely red, orange, yellow, blue, violet, and white. Pans were 115 mm diameter by 50 mm deep and were painted with gloss enamel paint. The plastic pans were 115 mm diameter by 50 mm deep and were painted with gloss enamel paint. For each site, three arrays of six coloured pan traps were used, arranged in a — | — configuration of three 50 m lines in each site, with the six colours arranged randomly at 10 m intervals on each line.

Pans were elevated and set at the level of flowers in the surrounding vegetation and half filled with water, with a little detergent added to reduce surface tension. Elevating pantraps to the level of the canopy where insects

are actively foraging has been shown to significantly increase catches (Tuell & Isaacs 2009). Trapping took place only on sunny days, from 08h00 until 17h00. At the end of each day trapped insects were removed from the water and preserved in 80% ethanol for later identification. Whenever possible, trapping was done on two consecutive days per site, although as the weather at this time of year is highly variable often the next suitable day was used. Anthophiles were sampled in the spring (August-December), in 2004 and 2005, to coincide with times of peak flowering at each site.

Upon completion of sampling, anthophiles were identified and counted under a Leica Microsystems Ltd. (Heerbrugg, Switzerland) M-Series stereo-microscope. Initial identifications were as morphospecies, with later refinement by comparison to specimens held in the entomology collection at the Iziko South African Museum in Cape Town and consultation with experts on certain groups. Morphospecies have been used as surrogates for species and can provide satisfactory estimates of formal species (Oliver & Beattie 1996) All insects were identified to at least family level or to lower taxonomic levels in most cases. A voucher collection is housed in the museum at the Department of Conservation Ecology and Entomology, Stellenbosch University.

Vegetation transects

Vegetation at each site was sampled during the 2005 season, the day before the first day of pan-trapping at each site. Vegetation composition, height and cover were measured over three, 20 m transects per site. The transects overlaid the three pan-trap lines used per site. All plants that touched the transect line were measured (height, length of transect covered), identified and their flowering status noted (not flowering, flowering, in bud, in seed).

Site Classification

Sites in each of the three localities were divided into four categories depending upon their habitat, condition and situation in the landscape (Table 4.1). At Elandskloofberge, there was no frequently disturbed site, but two remnant sites were considered separately. The Helderberg Region had more sites than the other two localities, with two sites in each category, compared to the single sites per category at Elandskloofberge and Groenlandberg Conservancy. Because comparisons were made between sites within rather than across localities, this did not affect the analyses.

Table 4.1 – Description of site categories used to classify anthophile and vegetation sampling sites from three localities in the lowlands of the Cape Floristic Region.

Habitat category		Description	Sites
Heavily disturbed	(D)	Frequently disturbed areas, marginal areas such as firebreaks that are regularly mowed	GB2 HE1 VG3
Remnant	(F)	Patches of natural vegetation that are relatively undisturbed, but surrounded by transformed land.	GB1 EL1 EL4 VG1 CO1
Protected	(R)	Sites within formally protected areas such as national or private nature reserves.	EL3 HE2 HE3 KL1
Transformed	(T)	Semi-natural habitat that, was either transformed in the past and is now fallow, or has undergone some restoration.	CO2 EL2 GB3 VG2

*See Appendix 1 for further site descriptions. Elandskloofberge sites are prefixed 'EL'; Groenlandberg Conservancy sites are prefixed 'KL' or 'GB'; and Helderberg Region sites are prefixed 'CO', 'HE' or 'VG'.

Data analyses

Data were analysed separately within each sampling locality. Insect data for each category were pooled for each array and year (2004 and 2005), yielding six samples per site. Vegetation was sampled only once, so pooled data for the three transects per site were used. Estimated species richness was calculated for each locality, using EstimateS Version 8.0 software package (Colwell 2006). To assess sampling adequacy, species accumulation curves were constructed for each locality and each category per locality by plotting Sobs (Mao Tau) against cumulative numbers of individuals trapped for insects and cumulative coverage measured along vegetation transects for plants (Gotelli & Colwell 2001). There are a wide range of species-richness measures available, all of which vary in accuracy (a combination of each measure's precision and bias). Here, non-parametric estimators of species richness were used, following the recommendations of Hortal et al. (2006). The four measures used were the Incidence-based Coverage Estimator (ICE), Chao 2, and Jackknife 1 & 2, all of which Hortal et al. (2006) recommend as robust diversity estimates for abundance data at collected at small grain size (the spatial scale at which data are collected).

The apportioning of plants and anthophile species-diversity across the landscape was visualised using Euler diagrams. An Euler diagram is a collection of simple closed curves depicting connected subsets each enclosed by a unique combination of curves and are used to visualise the distribution of discrete entities across a sample population (Chow 2007). First, the number of species was counted within each habitat category, and possible combinations of categories (four categories creating a total of 15 possible

subsets). These figures were then used to draw proportional Euler diagrams (the area of each subset being proportional to the number of species it includes) for each locality, using the web based application DrawEuler (Chow 2006).

Further comparison of habitat categories were made using EstimateS to calculate the total numbers of shared species and Jaccard's index of similarity for all pairwise comparisons of categories at each locality. An Analysis of Similarity (ANOSIM) in PRIMER Version 5.0 (Primer-E Ltd 2002) was undertaken to test the significance of differences in the species assemblages between categories at each locality.

The anthophile assemblage structure of habitat categories at each locality were compared by using relative abundance (total number of individuals captured), family-richness (total number of families recorded) and species-richness (total number of species recorded), broken down by insect order. A similar analysis was performed for plants, but the vegetation data were categorised into plant growth form, as defined for each species in the Plants of Southern Africa (POSA) online checklist (South African National Biodiversity Institute 2007), as life-form has been found to be a useful classification for characterising the effects of disturbance on plant communities (McIntyre et al. 1995; Lavorel et al. 1997).

Results

Species richness

Species accumulation curves showed that sampling was adequate, although not complete as curves for plants and anthophiles, although not completely asymptotic, leveled-off for most of the sites sampled (Figure 4.2). Anthophile species-richness estimates per habitat category ranged from 65 to 75 at Elandskloofberge, 56 to 85 in the Groenlandberg Conservancy, and 81 to 113 in the Helderberg region (Table 4.2a). Estimated plant species-richness for the same localities ranged from 24 to 85, 37 to 99, and 78 to 131 respectively (Table 4.2). Within each locality, ICE varied more between sites for plants than for insects (Figure 4.3). Plant ICE was markedly lower in the transformed sites at Elandskloofberge and Groenlandberg conservancy, whereas the estimated diversity of anthophiles was similar across all categories.

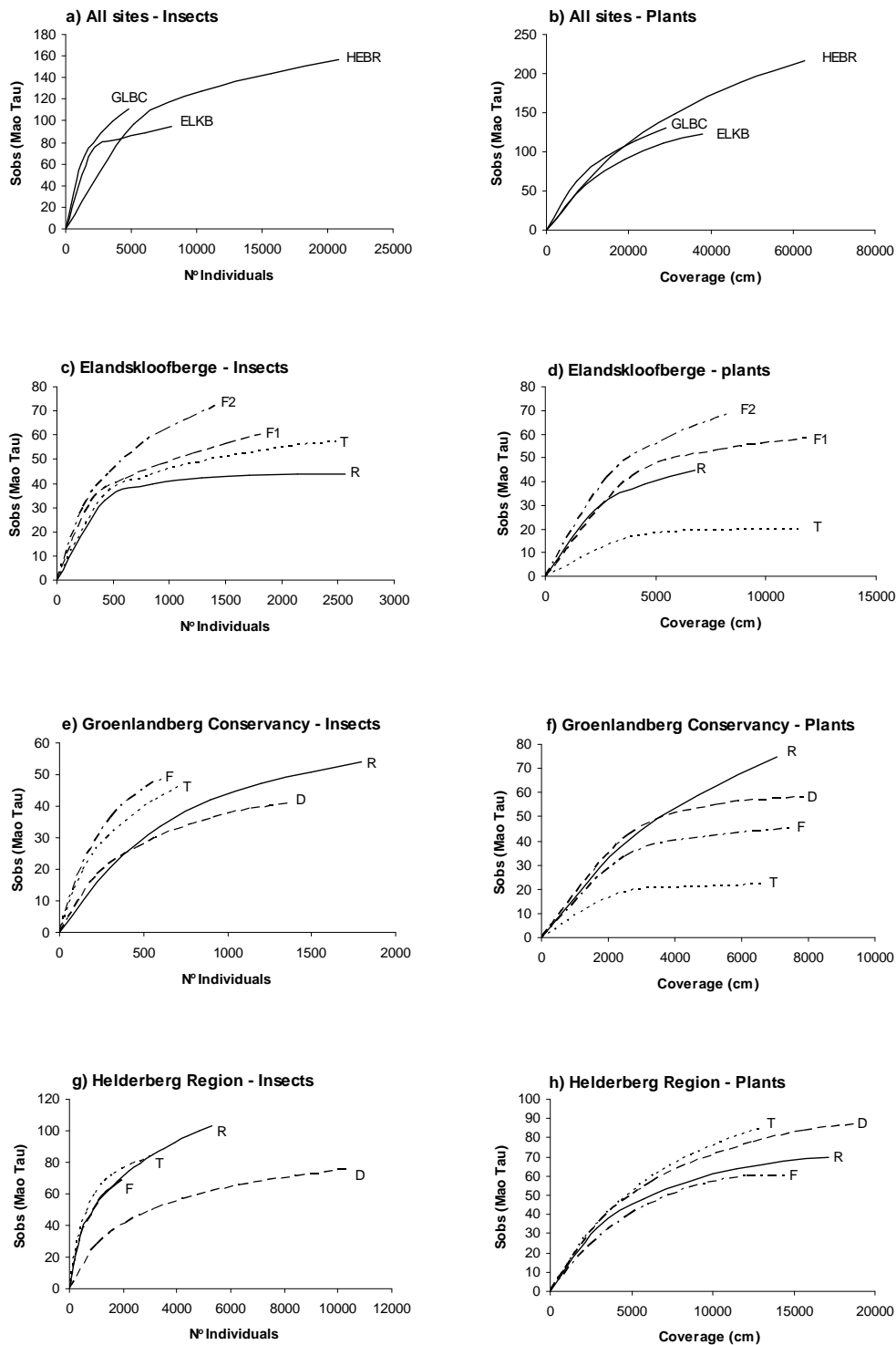


Figure 4.2 – Sample based rarefaction curves for flowering plants and flower visiting insects sampled in disturbed (D), remnant (F), protected (R) and disturbed habitats in three localities in the Cape Floristic Region. The cumulative number of species observed (Sobs, Mao Tau) was plotted against the cumulative number of individuals caught for insects and the total cumulative coverage measured along vegetation transects for plants. For the Elandskloofberge Region two remnant sites were used (F1 and F2).

Table 4.2 - Non-parametric species-richness estimates for a) flower visiting insect and b) flowering plants in disturbed (D), remnant (F) protected (R) and transformed (T) habitats from three localities - Elandskloofberge (ELKB), Groenlandberg Conservancy (GLBC) and the Helderberg Region (HEBR) in the Cape Floristic Region. For the Elandskloofberge Region two remnant sites were used (F1 and F2). See text for further explanation of estimators used.

a) Flower visiting insects							
		N [†]	Obs.	ICE (±S.D.)	Chao 2 (±S.D.)	Jack 1 (±S.D.)	Jack 2 (±S.D.)
ELKB	F1	1	72	72.52 (±9.01)	70.24 (±4.95)	74.35 (±6.82)	74.35 (±12.62)
	F2	1	72	74.68 (±14.6)	73.73 (±7.96)	74.40 (±7.92)	74.40 (±17.80)
	R	1	67	71.52 (±11.5)	72.35 (±6.98)	72.91 (±7.29)	72.91 (±16.52)
	T	1	72	64.84 (±9.43)	65.00 (±5.56)	66.52 (±5.28)	66.52 (±14.01)
GLBC	D	1	54	59.29 (±13.67)	64.48 (±15.51)	56.43 (±6.65)	56.43 (±14.64)
	F	1	58	63.07 (±16.69)	59.88 (±8.64)	59.6 (±7.90)	59.60 (±16.20)
	R	1	63	68.08 (±13.43)	67.49 (±9.08)	66.95 (±8.09)	61.39 (±18.33)
	T	1	60	66.21 (±20.12)	85.39 (±17.90)	61.39 (±9.07)	66.95 (±16.88)
HEBR	D	2	89	93.35 (±15.49)	89.80 (±8.42)	93.02 (±9.23)	93.02 (±19.23)
	F	2	77	83.35 (±14.98)	82.67 (±12.08)	80.58 (±8.53)	80.58 (±16.37)
	R	2	108	113.21 (±18.46)	112.40 (±11.99)	110.80 (±8.76)	110.80 (±22.01)
	T	2	101	101.34 (±14.26)	99.06 (±7.71)	103.58 (±8.66)	103.58 (±19.53)
b) Flowering plants							
		N [†]	Obs.	ICE (±S.D.)	Chao 2 (±S.D.)	Jack 1 (±S.D.)	Jack 2 (±S.D.)
ELKB	F1	1	71	82.61 (±30.74)	68.17 (±5.42)	71.96 (±7.96)	76.31 (±22.14)
	F2	1	69	79.01 (±19.39)	69.19 (±5.45)	73 (±9.45)	76.96 (±16.40)
	R	1	62	75.72 (±29.04)	59.10 (±5.16)	63.69 (±9.84)	67.86 (±18.31)
	T	1	25	26.14 (±5.05)	24.39 (±2.31)	25.68 (±2.44)	26.69 (±5.05)
GLBC	D	1	62	74.4 (±31.51)	66.62 (±7.76)	63.48 (±9.74)	66.74 (±21.39)
	F	1	51	54.93 (±15.56)	48.72 (±3.77)	51.66 (±5.99)	54.07 (±13.45)
	R	1	75	98.55 (±42.98)	75.23 (±6.60)	79.19 (±10.07)	84.91 (±25.03)
	T	1	33	39.97 (±15.11)	31.93 (±3.52)	34.44 (±5.32)	36.62 (±10.32)
HEBR	D	2	104	108.52 (±20.06)	108.06 (±10.46)	108.25 (±11.67)	114.46 (±24.75)
	F	2	104	111.64 (±37.56)	131.24 (±20.32)	106.26 (±14.43)	109.78 (±33.27)
	R	2	75	78.18 (±14.45)	78.72 (±8.58)	78.56 (±8.50)	82.48 (±18.34)
	T	2	90	102.8 (±32.02)	102.31 (±14.39)	94.95 (±15.20)	103.62 (±28.81)

[†]Number of sites sampled per habitat category

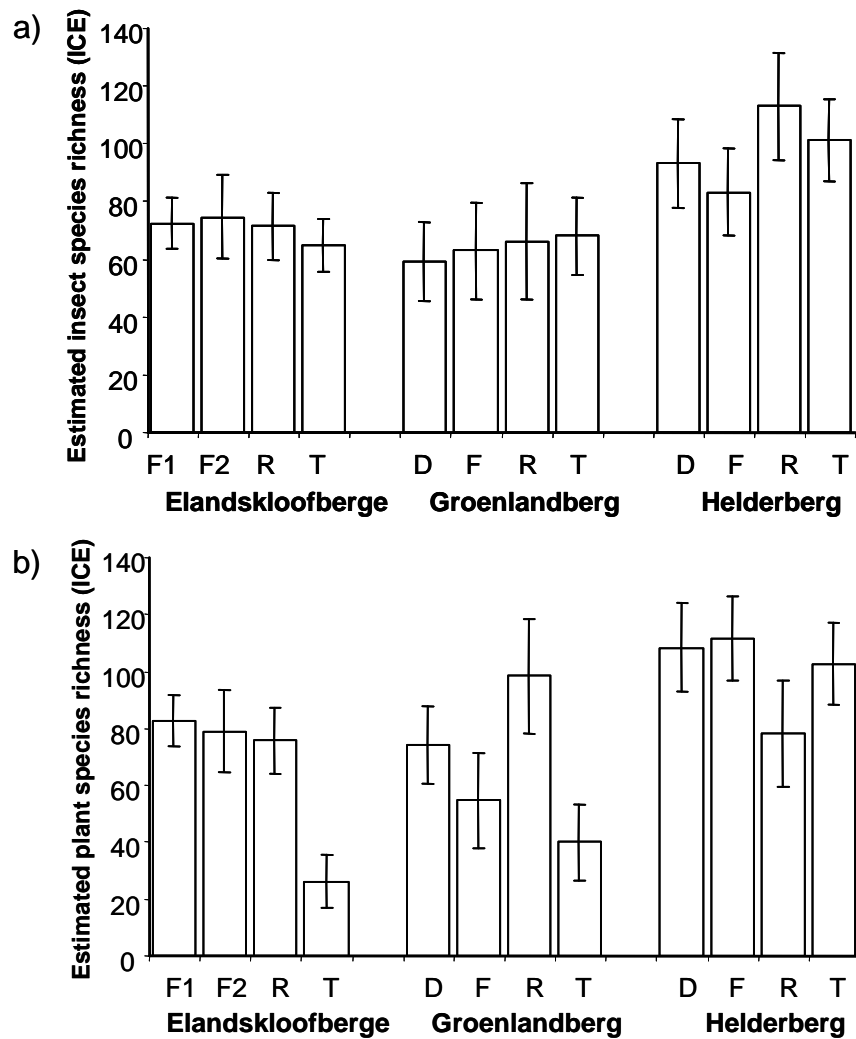


Figure 4.3 – Estimated species-richness of a) flower visiting insects) and b) plants in frequently disturbed (D), remnant (F), protected (R) and transformed (T) habitats in three localities in the Cape Floristic Region (ELKB=Elands Kloofberge, GLBC=Groenlandberg Conservancy, and HEBR=Helderberg). Bars represent estimated richness using the Incidence-based Coverage Estimator (ICE ± 1 SD). Note that for Elands Kloofberge, no disturbed site was sampled, but an additional remnant site was included.

Shared species

Across all localities, site categories shared 20-38% of their insect species and 12-28% of plants species. The increased proportions of shared insects compared to plants were reflected by Jaccard's index for each pair-wise comparison, which tended to be higher (indicating greater similarity) for insects than plants (Table 4.3). Across all three localities species composition for plants and anthophiles were significantly different. Only two comparisons were non-significant (Table 4.3).

Table 4.3 – Comparisons of plants and flower visiting insect assemblages in frequently disturbed (D), remnant (F), protected (R) and transformed (T) habitats in three localities in the Cape Floristic Region. Figures represent the total percentage of species shared between each category, Jaccard's index of similarity based on species occurrences in each category and R values for a pairwise Analysis of Similarity (ANOSIM) of presence-absence data for each category. Significance for ANOSIM are indicated as ***P <0.01; **P<0.05; *P<0.1; nsNot significant.

Pair-wise comparisons of species assemblages												
		% shared species			Similarity (Jaccard)			ANOSIM				
		F1	T	R	F1	T	R	F1	T	R		
Elandskloofberge	Insects	T	38.13			0.616			1.00*			
		R	35.42	33.81		0.548	0.511		1.00*	1.00*		
		F ₂	34.03	35.25	35.42	0.516	0.544	0.548	0.963*	1.00*	0.963*	
	Plants	T	12.77			0.146			0.796**			
		R	18.18	10.47		0.222	0.117		1.00**	0.889**		
		F ₂	17.27	11.83	22.14	0.209	0.134	0.284	0.963**	0.759**	0.963**	
	Groenlandberg	Insects	F	33.04			0.493			0.593*		
			R	20.51	20.66		0.258	0.260		0.926*	0.963*	
			T	30.70	27.97	20.33	0.443	0.388	0.255	1.00*	1.00*	1.00*
Plants		F	28.32			0.395			0.111 ^{ns}			
		R	16.06	13.49		0.191	0.156		0.981**	0.889**		
		T	20.00	21.43	12.04	0.250	0.273	0.137	0.810**	0.654**	1.00**	
Helderberg		Insects	F	25.90			0.350			0.411***		
			R	30.96	25.95		0.449	0.350		0.252**	0.681***	
			T	31.41	35.20	30.95	0.458	0.543	0.448	0.319***	0.203*	0.627***
	Plants	F	20.87			0.264			0.356***			
		R	25.28	16.29		0.338	0.195		0.726***	0.430***		
		T	18.13	24.35	14.55	0.222	0.322	0.17	0.334**	0.036 ^{ns}	0.400**	

The distribution of species among the four categories varied from locality to locality, but some common patterns were evident. Most species at all three localities occurred in more than one habitat category. Anthophiles tended to have a large pool of species that occurred across all sites (Figure 4.4), while for plants (Figure 4.5), there was greater partitioning and relatively few species occurred in all four categories. Even with a high proportion of shared species, all categories retained a portion of species not found elsewhere. The proportions of species in habitat categories other than protected areas was variable, but sites in all categories contained many species that were not found in formally protected areas.

In all categories, sites held a sizable proportion of the entire pool of species recorded for each locality. For anthophiles the mean percentage of species held per category (including species occurring in multiple categories) was 54.3 (± 2.4), reflecting the fairly uniform distribution of species across all sites (Figure 4.4).

For plants, each category contained, on average 44.8% (± 4.1) of the total number of recorded species (including species occurring in multiple categories). The transformed site at Elandskloofberge held few plant species (17.5%), while in the Groenlandberg Conservancy the reserve site held a very high 53.7% of all plants recorded for that locality (Figure 4.5).

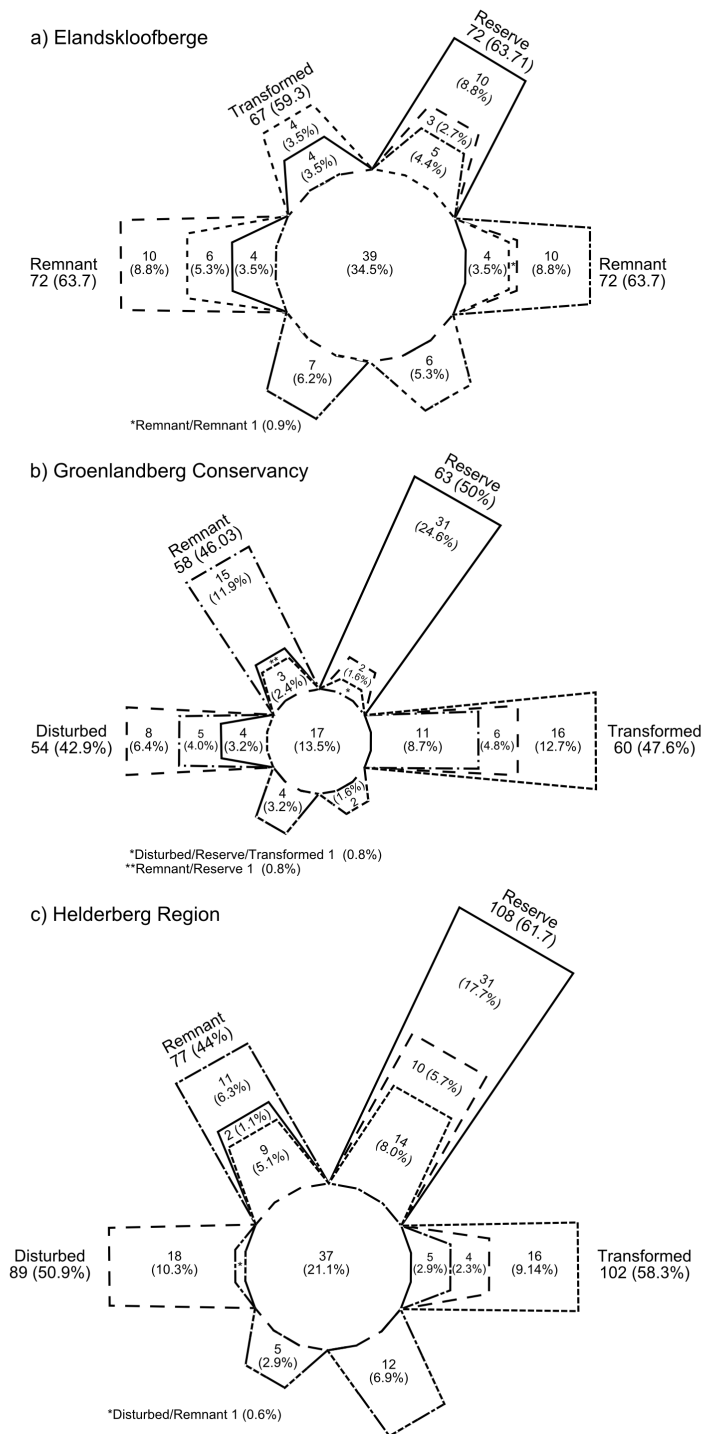


Figure 4.4 – Area proportional Euler diagrams showing the partitioning of anthophile species richness between disturbed, remnant, reserve and transformed sites in each of three localities in the Cape Floristic Region. At Elands Kloofberge, no disturbed site was sampled, but an additional remnant site was included. The area of each region represents the number of species occurring within that category. Different line styles denote categories to differentiate regions of overlap (Disturbed - long dashes; Remnant - dots and dashes; Reserve - solid; Transformed - short dashes).

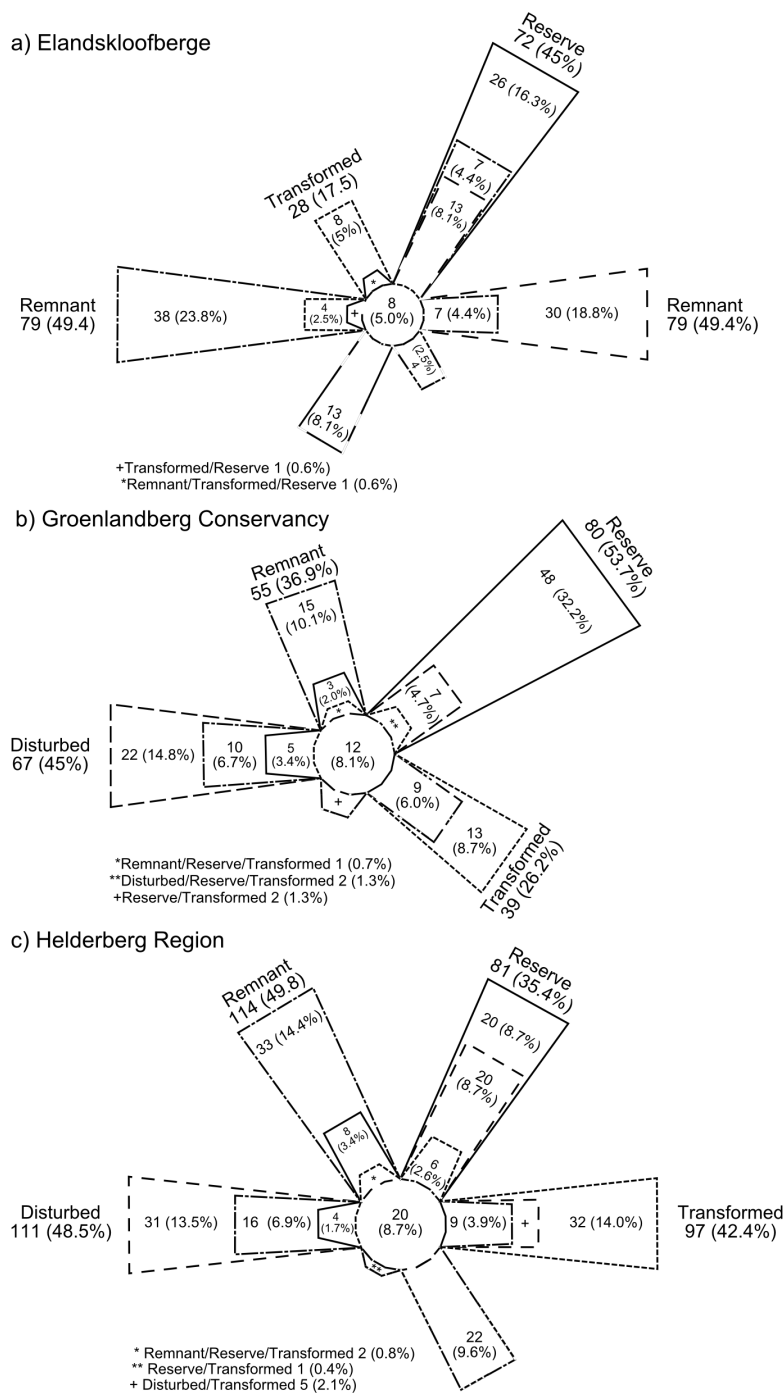


Figure 4.5 - Euler diagrams showing the partitioning of flowering plant species richness between sites disturbed, remnant, reserve and transformed habitats in each of three localities in the Cape Floristic Region. At Elands-kloofberge, no disturbed site was sampled, but an additional remnant site was included. The area of each region represents the number of species occurring within that category. Different line styles denote categories to differentiate regions of overlap (Disturbed - long dashes; Remnant - dots and dashes; Reserve - solid; Transformed - short dashes).

Assemblage structure

Numerically, pan trap catches were dominated by the Coleoptera, mostly monkey-beetles (Scarabaeidae: Ruteliinae). An exception were the reserve sites in the Helderberg Region, where far more Diptera, mostly Bibionidae, were caught. Abundance was particularly high for the disturbed category at this locality Helderberg region. This super-abundance was due to very high catches of Coleoptera, again mainly monkey-beetles, at these sites. Patterns of family and species richness remained consistent across site categories and localities, with trap catches dominated by Coleoptera, Hymenoptera and Diptera (Figure 4.6).

Plant assemblages and vegetation structure at each site (reflected by the proportional abundance of different growth forms) were varied, changing between the different site categories and localities. This makes it difficult to define any clear patterns, although plant assemblages tended to be dominated by shrubs, herbs graminoids and geophytes, in varying proportions. Likewise, family and species richness was mostly included within these four growth forms, but graminoids were less important (Figure 4.7).

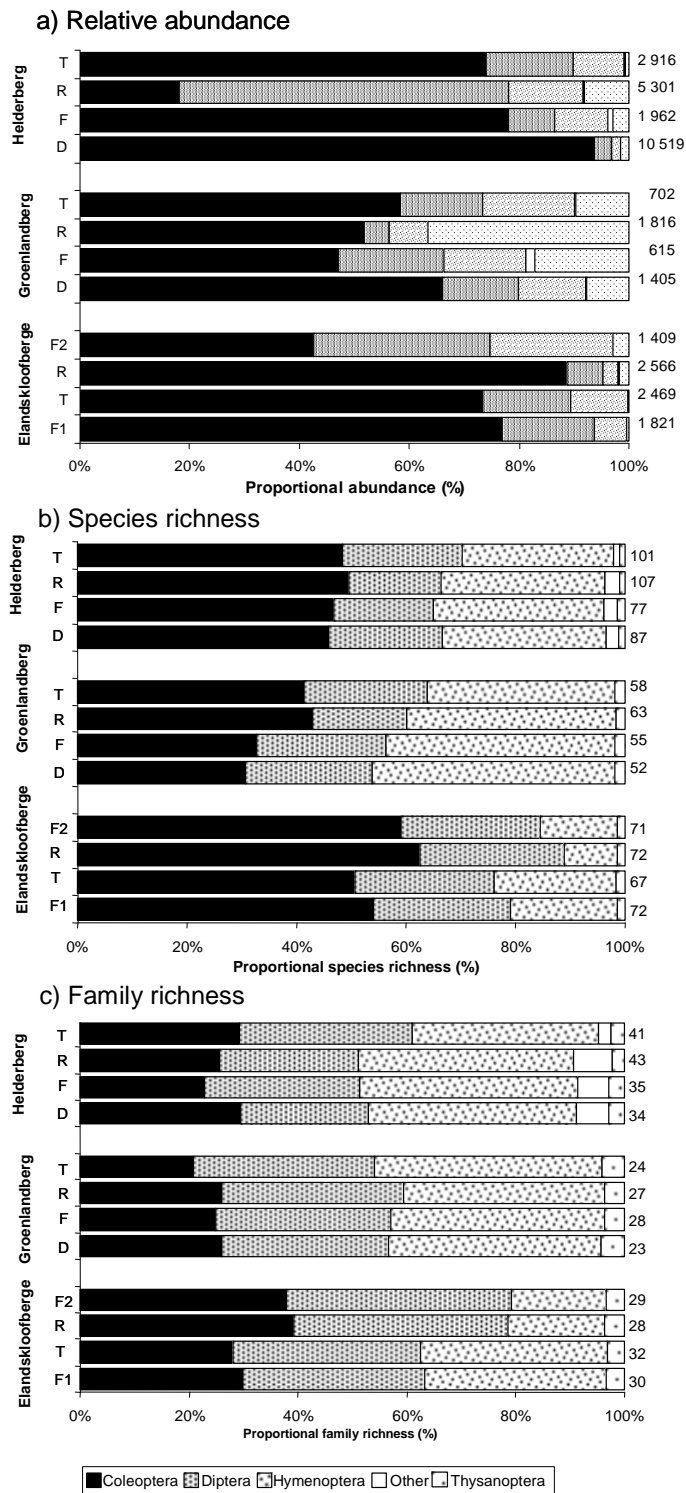
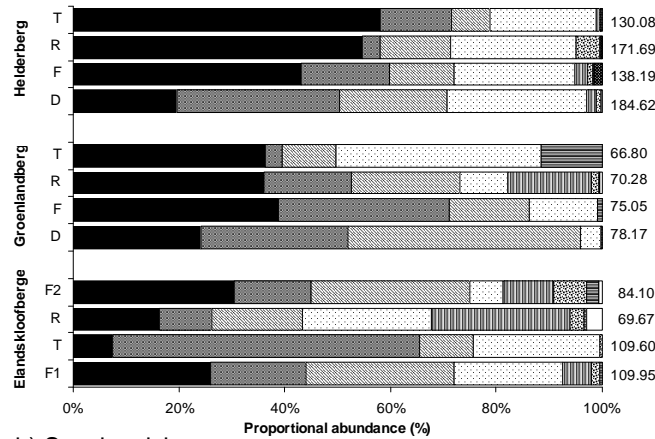
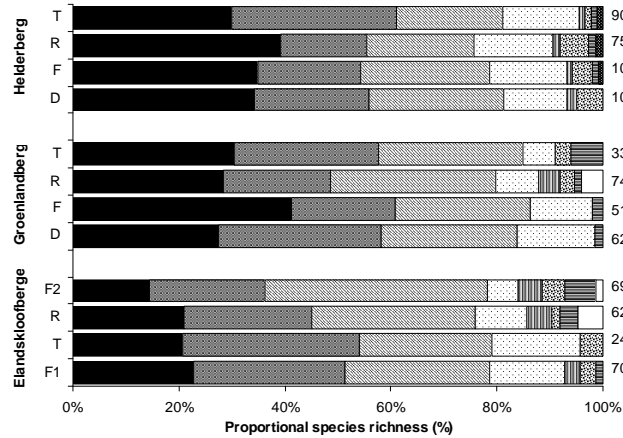


Figure 4.6 – Categorisation by taxonomic order of pan-trap catches from sites in highly disturbed (D), remnant (F), protected (R) and transformed (T) habitats in three localities in the Cape Floristic Region. Numbers at the ends of the bars on each graph represent a) total abundance (individuals trapped), b) species richness, and c) family richness per site. ‘Other’ includes Hemiptera, Lepidoptera and Dermaptera which were caught infrequently.

a) Relative abundance



b) Species richness



c) Family richness

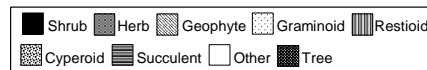
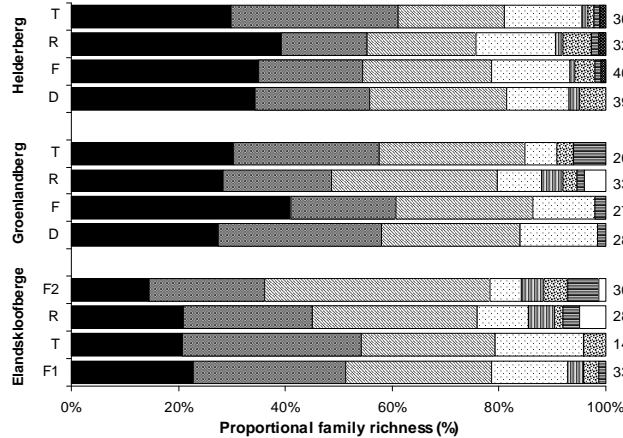


Figure 4.7 - Categorisation by growth-form of vegetation transect data from sites in highly disturbed (D), remnant (F), protected (R) and transformed (T) habitats in three localities in the Cape Floristic Region. Numbers at the ends of the bars on each graph represent a) total abundance (total coverage in meters along all transects), b) species richness, and c) family richness per site. 'Shrub' includes shrubs, dwarf shrubs and suffrutexes. 'Other' includes carnivorous plants and climbers.

Discussion

Systematic conservation planning is built around the paradigm of protected areas and setting aside sufficient land to preserve remaining biodiversity and the natural processes that sustain it (Margules & Pressey 2000). This approach views reserves as islands within an inhospitable matrix of transformed land. Agriculture is a major driver of biodiversity loss, and, although many agricultural landscapes do justify this stark outlook, there is also growing recognition that much biodiversity can be retained within agricultural landscapes (Perrings et al. 2006; Fischer et al. 2006). Managed (agricultural) land and natural/semi-natural habitats cannot be viewed in isolation but should rather be considered as part of a functional ecosystem comprising managed and natural components (Norris 2008). The paradigm shift towards ecoagriculture (Scherr & McNeely 2008) is evident in the number of agri-environmental schemes that have been implemented, particularly in Europe (Kleijn & Sutherland 2003) to encourage farming practices that enhance the retention of biodiversity in agricultural lands. The success of agri-environmental schemes has been difficult to quantify so far, with much discordance in the assessment of their efficacy (Tscharntke et al. 2005; Kleijn et al. 2006). However, the degree to which biodiversity is retained within the components of agricultural landscapes is important to understand and manage effectively if agriculture is to make a meaningful contribution to biodiversity conservation (Scholes & Biggs 2005).

Apportioning of species

My results show, at least at a local scale, that sites outside protected areas can retain similar levels of biodiversity to those within reserves. Species richness of plants and anthophiles within all three localities tested was similar regardless of their context (within reserves or transformed land), although less consistently so for plants. Even where there was variation in the species richness of each category of site, it was not always consistent, and reserve sites did not always hold a greater number of species than those outside reserves.

The conservation value of the sites outside reserves is evident in two ways. Firstly, they retained a considerable proportion of the total diversity recorded at each site (40-60% of anthophiles and 18-50% of plants). Secondly, at all three localities, partitioning of species between the different site categories, meant that a substantial portion of the total diversity occurred only in sites outside protected areas. This is particularly important in areas such as the CFR where reserves are generally small, and there is a high species turnover over various spatial scales (see Chapter 3, this dissertation).

In such landscapes, remnants can complement reserves by retaining species that may not occur within protected areas.

Although the conservation value of the remaining natural habitat in the CFR is generally acknowledged, surprisingly few studies have attempted to quantify biodiversity in remnants of natural, semi-natural and transformed habitat in the region. In a neighbouring biome, xeric succulent thicket, Fabricius et al. (2003) found that a diverse landuse mosaic helped promote the gamma diversity, of arthropods and reptiles, although the authors emphasised the importance of reserve areas rather than the contribution of agricultural land. In the CFR, Witt & Samways (2004) emphasised the importance of habitat remnants for maintaining diversity between highly-transformed, species-poor fruit orchards. Boonzaaier (2006) also recognised the value of remnant habitats for the conservation of ants in human influenced, lowland areas. Pryke & Samways (2009) found, in an urban context, that a botanical garden of indigenous plants had major conservation value as a refugium for invertebrates.

Implications for conservation and other considerations

The high heterogeneity of plants and anthophiles indicated that remnants of natural and semi-natural habitat can make a meaningful contribution to biodiversity conservation in the CFR. This is not to downplay the central role that reserves play, but rather to recognise the complementary value that habitat remnants and transformed areas have in addition to reserves.

There are, however, a number of questions that remain to be answered before ascribing a true conservation value to these remnants. The deleterious effect of land transformation on biodiversity is not always immediately apparent, as ecological relaxation and extinction debt (Tilman et al. 1994) may still result in future species loss in remnant and transformed habitats. Another important consideration is the dispersal abilities of species through the landscape. Transformed land may be permeable to some species, but can act as a barrier or a filter to others (Wood & Samways 1991), limiting the movement of individuals and genes between populations resulting in their gradual decline (Noss & Csuti 1997). For anthophiles, which are highly mobile, remnants may act as stepping stones, facilitating movement through the landscape (which may account for the greater number of shared insects between categories than plants). For plants, on the other hand, remnants may provide habitat for certain narrow-range endemics that would otherwise be excluded by the spatial configuration of protected areas. But these benefits cannot persist in the long term if the surrounding matrix isolates remnant habitats.

Finally, species richness, although providing a useful currency for comparisons between areas, does not necessarily convey complete information about ecological function which may be more affected by functional substitution than by species loss per se (Loreau et al. 2001). It would be useful to explore functional considerations such as the relative proportions of functional groups, or specialist vs. generalist species retained within various landscape components. For finer scale conservation planning, further consideration of particular species is also necessary. Species richness does not necessarily capture information on, say, rare endemics which might require more focused, species specific conservation efforts.

Conclusions

The plant and anthophile diversity of the CFR comprises species that occur within the various landscape components that make up the landscape mosaic of transformed and natural/semi-natural habitat. Some remnant and transformed habitats can support representative numbers of species and include species that may not be found elsewhere. Therefore, habitats outside reserve areas do make a meaningful contribution to the conservation of these groups in a global biodiversity hotspot, and should be managed accordingly. Successful biodiversity conservation in the CFR should not take a binary approach, where protected areas are considered separately to production areas but should rather view, and manage the entire landscape as a heterogenous ecoagricultural ecosystem

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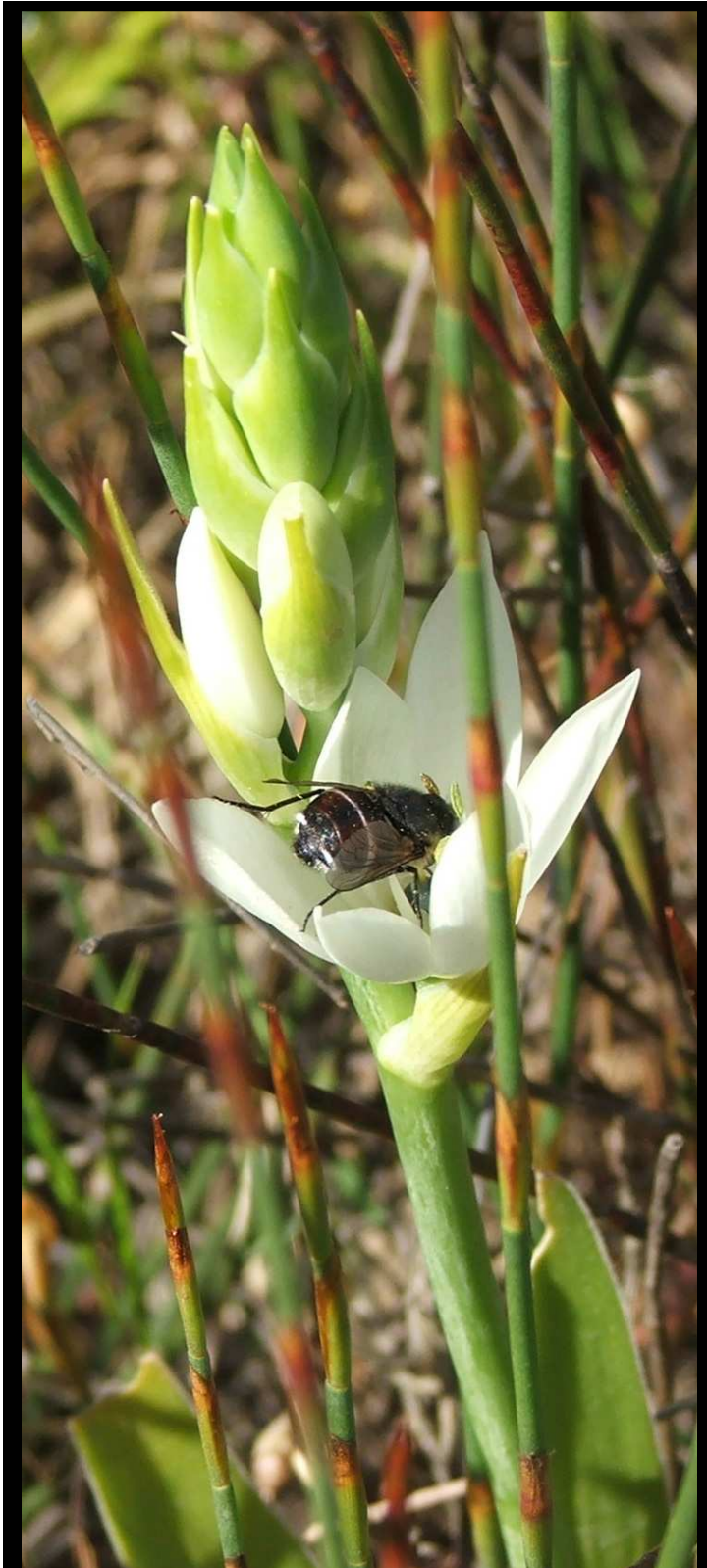
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Anthophilous tabanid fly of the genus *Philoliche* visiting chinkerinchee (*Ornithogalum thyrsoides*) at Elandsberg Private Nature Reserve

Sven Vrdoljak, 2007

5

Importance of floral traits and visual display area on insect visitation rates in mixed stands of flowers

SUMMARY

Pollination services have vital roles in terrestrial ecosystems, with an indirect, yet significant effect on structuring plant communities. Addressing worldwide pollinator declines requires ecological data on plant-pollinator interaction for integrated landscape management. Floral advertisement plays an important role in determining the behaviour of foraging anthophiles, which will be affected by both the density and type of flowers on display. I investigated the importance of visual floral traits for attracting visitation by insects to plants in mixed species patches in a lowland plant community in the Cape Floristic Region, which is rich in narrow range endemics. There was a strong positive relationship between visitation frequency and total number and area of visual displays. Categorical floral traits (e.g. colour and floral form) affected visitation less consistently than continuous traits (e.g. visual display area). There was a positive relationship between visitation frequency and measures of floral similarity for all traits combined, and for continuous traits alone, but not for categorical traits alone. At the community level, visitation frequency was influenced more consistently by floral density than by traits specific to individual flowers, making continuous floral traits more reliable predictors of visitation frequency. Interactions in this highly endemic, southern hemisphere community mirrored those in a northern temperate grassland community, although composition of the visitor pool differed markedly.

Introduction

Insect pollinators play an essential role in ecosystem processes, contributing towards both diversity and function. The importance of pollinators and their apparent worldwide decline (Buchmann & Nabhan 1996) has led to concern that we may be facing a “pollination crisis” (Allen-Wardell et al. 1998; Kearns et al. 1998; Kevan 1999). The International Pollinator Initiative (São Paulo Declaration on Pollinators 1999) points out that we need more sound ecological data on plant-pollinator interactions to develop strategies for integrated landscape management.

The CFR of South Africa is a global hotspot of plant diversity (Goldblatt & Manning 2002) where a number of specialised pollination systems have been described (Johnson & Steiner 2000). The study of pollination biology is well established in South Africa (see Johnson 2004 for an extensive list of pollination studies in South Africa). However, a recent review of African pollination studies (Rodger et al. 2004) highlighted studies at the community level and those relevant to pollinator conservation as two apparent gaps in the pollination literature for the region. Some recent studies of relevance to pollinator conservation in the Cape flora have addressed issues such as the effects of habitat fragmentation (Donaldson et al. 2002; Pauw 2007) disturbance (Colville et al. 2002) and land-use (Gess & Gess 1993; Mayer 2004; Mayer et al. 2006) on plant and pollinator communities. While these studies link differences in pollinator communities to various anthropogenic disturbances, they do not consider the role of pollinator attraction in determining the activity and abundance of flower visitors in these areas. In Chapter 3 of this dissertation, relative floral abundance was an important variable affecting the richness and diversity of anthophiles among sites surveyed in natural remnants across the CFR lowlands. Anthropogenic changes to the landscape affect anthophile populations through the destruction of resources such as food, nesting or oviposition sites, and resting or mating sites (Kevan 2001). Flowers provide a number of these resources and are a key component in determining the suitability of habitat for anthophiles (Committee on the Status of Pollinators in North America 2007) and the loss of floral hosts through anthropogenic disturbance has been linked to pollinator declines (Rasmont et al. 2005). In this chapter and the next, I examine the relationship between anthophile activity (represented here by visitation frequency), and visual traits and floral abundance in a community of plants in the lowlands of the CFR.

The diversity of floral colours, forms, odours and nectar producing have evolved as a means of attracting potential pollinators. In this context, flowers can be considered as ‘attraction units’, which attract pollinators from

different distances depending upon the visual acuity of the foraging anthophile and whether single flowers (or part thereof) or aggregations of flowers (an inflorescence, an entire plant or patches of plants) are operating as the attraction unit (Dafni et al. 1997). From an anthophile perspective, the role of these attraction units provide more than just advertisement of rewards, because combination of various visual cues also allow anthophiles to discriminate between flowers. The ability to distinguish different flowers from each other enables 'floral fidelity' or 'floral constancy' (these terms are reviewed in Slaa & Biesmeijer 2005) so anthophiles can recognise and memorise rewarding species and optimise foraging efficiency by foraging mainly on these species. Anthophile activity at a variety of spatial scales will be affected by both the abundance of flowers as well as their various floral traits. If anthophiles choose between among floral patches in the landscape they may select species with higher a higher density of floral displays (Steffan-Dewenter et al. 2001; Westphal et al. 2003). The size and density of floral patches within the landscape can be expected to influence the number of anthophiles within a patch, as well as their behaviour (Kunin 1997), which may in turn affect the efficiency of pollinators, through density dependence effects and intraspecific competition for pollination. The higher density of certain plant species, may also increase the constancy of flower visitors, increasing the quality of pollinator visits (Kunin 1993).

While visitation and even an anthophile's ability to carry pollen does not imply pollination *per se* (Kevan & Baker 1983; Kevan 1999), there is a link between visitation rate and pollination service (Vazquez et al. 2005). Information at the community level is essential for the construction of plant-pollinator interaction webs (Memmott 1999), drawing general conclusions about pollination interactions (Memmott 1999; Johnson & Steiner 2000) and understanding the broader implications of these interactions for pollinator conservation.

I address a number of questions. 1) What is the relationship between the density of visual displays and visitation rates of flower visiting insects in a mixed community of flowers? 2) Can a set of categorical visual traits explain why groups of flower loving insects tend towards preferring some plant species, or, do continuous traits such as visual density and flower size have a greater effect on visitation rates? 3) Do plant species with similar visual traits have similar attractiveness to anthophiles, and can this information be useful in predicting interactions between species at the community level? I address these questions by examining the relationship between visitation frequency to a number of plant species within this community and a subset of visual traits (flower colour, flower shape, flower symmetry, abundance of species within

the community, the size and number of visual displays, and the visual display area) during a period of high anthophile activity.

Methods

Study site

I worked in the Elandsberg Private Nature Reserve (33.27° S, 19.03° E) and on the surrounding Bartholomeus Klip farm, near Hermon, Western Cape Province, South Africa. Situated in the lowlands (below 300 m asl) at the foot of the Elandskoof Mountain Range, the reserve covers approximately 4000 ha encompassing the largest remaining contiguous patch of West Coast Renosterveld, and some marginal abandoned farmland (Ashwell et al. 2006). Renosterveld is an evergreen, fire prone, shrubland, dominated by the cupressoid leaved Asteraceae, in particular renosterbos (*Elytropappus rhinocerotis*), with an understory of grasses (Poaceae) and a rich diversity of spring flowering geophytic plants (Mucina & Rutherford 2006). Renosterveld has been highly transformed. Less than 10% of the original Renosterveld remains (Rebelo 1992), existing mainly as scattered fragments in agricultural land (Kemper et al. 1999) The two main vegetation types in the Elandsberg Reserve are Swartland Alluvium Fynbos and Swartland Shale Renosterveld, both critically endangered (Mucina & Rutherford 2006). The surrounding farmland includes wheat fields and areas under grazing by sheep and cattle. The area receives a mean annual rainfall of about 500 mm. During this study, 32 plant species were observed to be flowering, of which 25 were recorded frequently enough to be used in subsequent analyses (Table 5.1).

Table 5.1 - Basic characteristics and mean visitation frequency per observation period by all insects and selected insect visitor group (Table 5.2) for plant species in a lowland Renosterveld community. Blank spaces indicate that the plant was not visited by that group.

Flower	Code	Display ¹	Shape ²	Symmetry ³	I° Visitor	Colour ⁴	Abundance ⁵	All	BUP	SCA	OTH	MUS	TAB	SYR	HYM
<i>Albica flaccida</i>	Albfla	S	T	Z	Beetles	Y	R	0.180		0.091	0.091				
<i>Aspalathus</i> sp.	Aspsp1	G	O	Z	Syrphids	Y	R	0.467		0.033				0.200	0.2
<i>Aspalathus</i> sp2	Aspsp2	G	O	Z	Scarabs	W	R	0.130		0.692	0.385	0.154			0.385
<i>Aster</i> sp.	Astsp	S	O	A	Buprestids	Y	R	3.600	1.200	0.800	0.400			0.067	0.267
<i>Aster</i> sp2	Astsp2	S	O	A	Bees	Y	R	0.056							0.056
<i>Babiana angustifolia</i>	Babang	I	T	Z	Scarabs	BV	Ab	0.522	0.008	0.159	0.076	0.015	0.129	0.076	0.008
<i>Berkheya armata</i>	Berarm	S	O	A	Scarabs	O	In	0.700	0.050	0.450	0.050				0.050
<i>Cotula turbinata</i>	Cottur	S	O	A	Beetles	Y	In	0.296	0.037	0.019	0.130			0.111	
<i>Cyanella lyacinthoides</i>	Cyahya	S	O	Z	Muscoids	BV	In	0.507		0.053	0.213	0.027	0.147	0.04	
<i>Dimorphotheca pluvalis</i>	Dimplu	S	O	A	Ants	W	R	0.038							
<i>Dorotheanthus bellidiformis</i>	Dorbel	S	O	A	Buprestids	PR	R	0.009	0.056						
<i>Felicia</i> sp.	Felsp1	S	O	A	Muscoids	W	Ab	0.174			0.018	0.092	0.037	0.018	0.009
<i>Heliophila</i> sp.	Helsp.	S	O	A	Beetles	W	In	0.060	0.020	0.040					
<i>Hermannia scabra</i>	Hersca	S	T	Z	Scarabs	Y	R	0.692		0.308	0.154	0.077			
<i>Lachenalia</i> sp.	Lacsp.	I	T	Z	Tabanids	W	In	1.453		0.021	0.063	0.842	0.305	0.032	
<i>Lapeirousia corymbosa</i>	Lapcor	I	O	Z	Scarabs	BV	R	1.000	0.067	0.600	0.067	0.200		0.067	
<i>Moraea lewisiae</i>	Morlew	S	O	A	Beetles	Y	In	0.378	0.027	0.054	0.081	0.027	0.027	0.108	
<i>Muraltia heisteria</i>	Murhei	G	O	Z	Scarabs	BV	In	0.661		0.464	0.018	0.054	0.018	0.054	
<i>Ornithogalum thyrsoides</i>	Ornthy	I	O	A	Bees	W	In	0.346		0.019	0.019	0.019	0.019	0.135	
<i>Osteospermum tomentosum</i>	Osttom	S	O	A	Buprestids	Y	In	0.583	0.271	0.063	0.208			0.021	
<i>Pelargonium myrrhifolium</i>	Pelmyr	G	T	Z	Bees	PR	R	0.267						0.267	
<i>Relbunium fruticosum</i>	Relfru	S	O	A	Muscoids	Y	Ab	4.871	0.264	0.143	1.807	1.943	0.150	0.279	0.121
<i>Salvia chamaeleagnae</i>	Salcha	G	T	Z	Scarabs	BV	R	15.833	0.067	12.867	0.467	0.433	0.467	2.040	
<i>Senecio elegans</i>	Senele	S	O	A	Buprestids	BV	In	1.756	0.689	0.111	0.267	0.156	0.044	0.022	0.444
<i>Senecio</i> sp.	Sensp.	S	O	A	Tabanids	Y	In	0.015			0.015				
All flowers					Scarabs			1.326	0.09	0.40	0.26	0.26	0.11	0.08	1.96

Codes refer to visitor groups defined in Table 5.2.
 BUP = buprestid beetles; SCA = scarabaeid beetles; OTH = other flower visiting beetles
 MUS = muscoid (Calyptrata) flies; TAB = tabanid flies; SYR = syrphid flies
 HYM = Hymenoptera (bees and wasps)

¹G – Group; I – Inflorescence; S – Single.
²O – Open; T – Tubular
³Z – Zygomorphic and A – Actinomorphic
⁴Colours as perceived by the human eye. W – white; Y – yellow; BV – blue-violet; PR – pink-red.
⁵Ab – Abundant (occurring in 7-10 plots); In – Intermediate (occurring in 4-6 plots); R – Rare (occurring in 1-3 plots)

Data collection

The methodology was based on that of Hegland and Totland (2005) who conducted a similar study in a northern temperate grassland community. The study was short, but highly intensive, involving a team of four coordinated observers, who conducted visitation surveys in 20, marked, 2 x 2 m plots. Over four days (9-12 October 2007) we collected over 46 hours of simultaneous observation in four sets of observation plots. The brief duration of data collection ensured comparison between the sample plots without the confounding effects of variable weather or phenological changes in floral abundance and composition. The sampling time fell within the spring flowering period in the area, which is associated with high floral abundance and pollinator activity. All days were sunny, with temperatures ranging from 15 to 31 °C at the nearest weather station, Diemerskraal (33.35° S, 18.55° E) between 09h00 and 17h00 over the four days. Weather data were provided by the AgroMet-ISCW Agricultural Research Council. Five plots, each at least 10 m apart were located randomly in four sites chosen to represent the reserve area and its surrounding remnants of natural vegetation. Two sites fell within the main reserve area, and two outside the reserve, in patches surrounded by wheat fields.

Before starting the observations, flowering plants in the plots were identified and counted, and the number of visual displays per plant species in the entire plot, was recorded. Depending on the plant species, a visual display could be a single flower, an inflorescence, or a group of flowers that formed a recognisable visual unit (Table 5.1). Mean visual display area was determined per plant species by measuring 10-20 randomly selected plants per species and calculating the inflorescence size (as an area) according to the shape of the flowers. Visual displays with a circular outline were calculated using the formula: πr^2 . For other flat visual displays the formula: length×width was used. When visual displays also had a depth dimension the formula: $2\pi r^2 + \pi r^2$ was used. The daily visual display counts per plot and mean visual display areas per species were used to calculate total visual display areas per plot as a measure of visual density.

Visitations were surveyed within the plots by counting visits by identified insect visitor groups (Table 5.2) to visual displays of insect-pollinated plant species during 10 min observation periods. Visits were only recorded when the visitor landed on, or made contact with, the visual display for more than 1 s. Plots were observed four times daily in two morning (09h00-10h30; 11h00-12h30) and two afternoon (13h30-14h30; 15h00-16h30) sessions, run concurrently in each of the four sites. In total, 1771 visits were recorded in 280 observation periods (2800 min).

Table 5.2 - Flower visiting insects recorded during 280 observation periods in a lowland Renosterveld community.

	Visitor Group	Description
Coleoptera	Scarabs	Monkey beetles (Scarabaeidae: Hopliini) including the genera <i>Dichelus</i> , <i>Heterochelus</i> , <i>Lepithrix</i> and <i>Peritrichia</i> .
	Buprestids	Buprestidae, mainly the genus <i>Acmaeodera</i> and others.
	Other beetles	Smaller, flower visiting beetles including Chrysomelidae (<i>Pagurodactylus</i> spp., <i>Dasytes</i> spp.), Meloidae (<i>Ceroctis</i> spp.), Byrrhidae, Dermestidae
Hymenoptera	Xylocopids	Carpenter bees, <i>Xylocopa</i> spp.
	Small Bees	Small bees and wasps. Including Halictidae, Sphecidae, Redivividae
	Large bees	Larger bees including Apidae (<i>Apis mellifera</i>) Anthophoridae.
Diptera	Tabanids	Flower visiting Tabanidae mainly <i>Philoliche</i> spp.
	Bombyliids	Bombyliidae
	Syrphids	Syrphidae, mainly the genera <i>Allograpta</i> spp. and <i>Eristalis</i> spp.
	Muscoids	Calyptrate flies. Mainly Calliphoridae (<i>Chrysoma</i> spp.) and including Muscidae (<i>Musca</i> spp.), Scathophagidae (<i>Scathophaga</i> spp.) and Tachinidae.
Other Taxa	Butterflies	Butterflies and day flying moths including <i>Vanessa cardui</i> and <i>Melampias huebneri</i>
	Thrips	Thysonaptera including Thripidae and Phlaeothripidae
	Ants	Formicidae

Data analyses

I examined the relationship between single visual traits and the visitation frequencies of species using simple linear regressions for continuous variables and generalised linear models (GLM), in this case a Poisson loglinear model, suited to the type of count data generated from the visitation surveys (Agresti 2007). To determine the relative importance of combined visual traits (categorical and continuous) in explaining variation in visitation rates at the community level I used analysis of co-variance (ANCOVA) using a loglinear Poisson model, corrected for overdispersion. Floral advertisements, or 'anthia' (Faegri & van der Pijl 1979) operate as an entire unit, with their attractiveness to potential pollinators depending on the corporate identity of the advertisement as a whole rather individual traits that operate independently (Leppik 1953). For the purposes of measurement and comparison it is necessary to break this identity down into individual traits. Here, I focus on visual traits, even though other traits such as odour are also important. However, given that analysing floral odour in the field is

technically quite complicated and would require manipulating flowers in some manner (Dobson et al. 2005), it has not been examined in the present study.

The visitation frequency of each species was defined as the mean number of visits per observation period. This provides a measure of that species' attractiveness to potential pollinators. Predictors included the categorical variables: (1) flower shape (open or tubular flowers), (2) flower symmetry (actinomorphic or zygomorphic flowers), (3) flower colour (white, yellow, blue-violet, pink-red flowers; as perceived by human eyes), (4) community abundance (rare: occurring in 1-3 plots ; intermediate: occurring in 4-7 plots ; and abundant: occurring in 8-10 plots), and the continuous variables: (5) number of visual displays (mean per species calculated from mean per plot), (6) visual display area (mean per species calculated from mean per plot) and (7) inflorescence size (mean per species calculated from 20 inflorescences on each plant measured). These are referred to hereafter as visual traits. Plants included in the final analyses were restricted to those recorded in more than 10 observation periods. This yielded a sample size of 29 plant species of which 25 received at least one visit during the study.

To ordinate the plant species according to their visual similarity I used principal component analysis (PCA) (Jongman et al. 1995). Structure of the visual trait dataset was analysed first using detrended correspondence analysis (DCA), detrended by segments, to determine linearity of the dataset. Gradient lengths for all axes were less than 1 SD suggesting very little unimodality in the dataset (ter Braak & Šmilauer 2002) that would make PCA unsuitable for this analysis. First axis PCA scores were used to measure the degree of visual similarity between species. Species with similar visual traits will occur closer together on this axis than dissimilar species that will occur further apart. PCAs were run for all visual traits combined, and categorical and continuous traits separately. To determine the relationship between visual similarity and visitation frequency I used a simple linear regression between the first axis scores and visitation frequency for all insects. Multivariate analyses (DCA and PCA) were performed using CANOCO version 4.53 (ter Braak & Šmilauer 2004). All other analyses were performed using Statistica version 8.0 (StatSoft Inc. 2007).

Results

Of the 1771 recorded visits, the visitor pool was dominated by Coleoptera and Diptera, which accounted for 46% and 36% respectively of all visits (Figure 5.1). The top three visitor groups were scarabs (29%), calyptrate flies (19%) and other flower visiting beetles (19%). All other groups accounted for no more than 10% each of the total visitations.

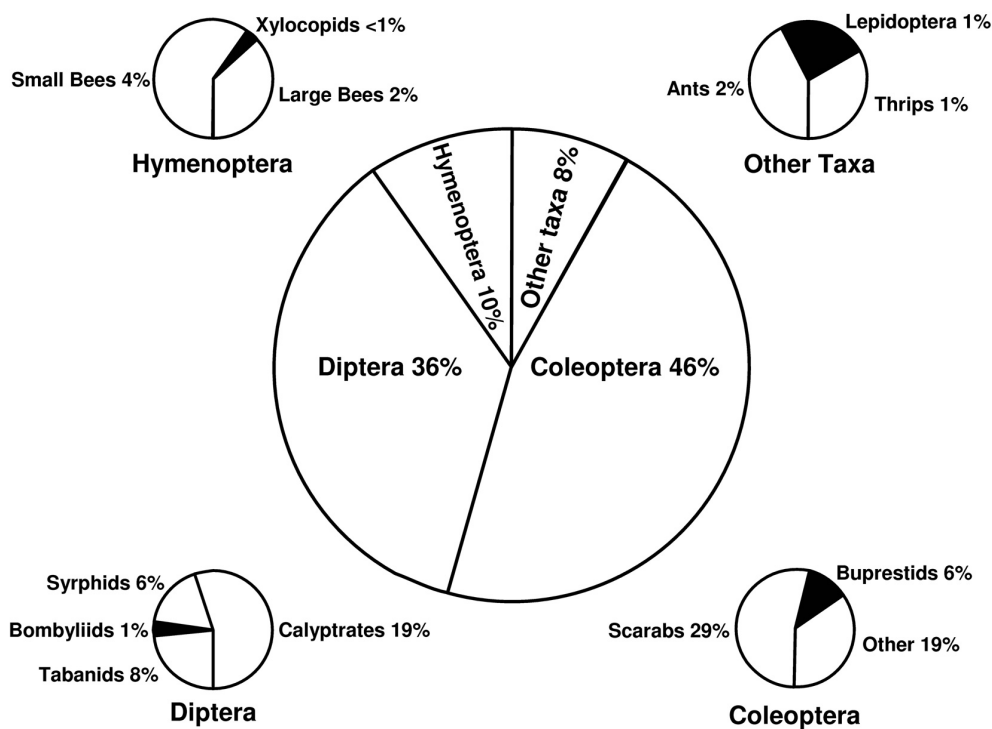


Figure 5.1 - Breakdown of visitation to plants by all insects observed in 20 observation plots in a Renosterveld community. In total 1771 visits were recorded during 280 ten minute observation periods (2800 mins).

For most visitor groups at least 30 % of all their recorded visits were made to a single plant species (Figure 5.2). For most visitor groups, three to five plant species accounted for 90% of recorded visits. This was one-third of the plant species visited by buprestid beetles, other beetles and calyptrate flies (Figure 5.2 b,d,g), and half of the plants visited by scarabid beetles, tabanid flies and syrphid flies (Figure 5.2 c,e,f).

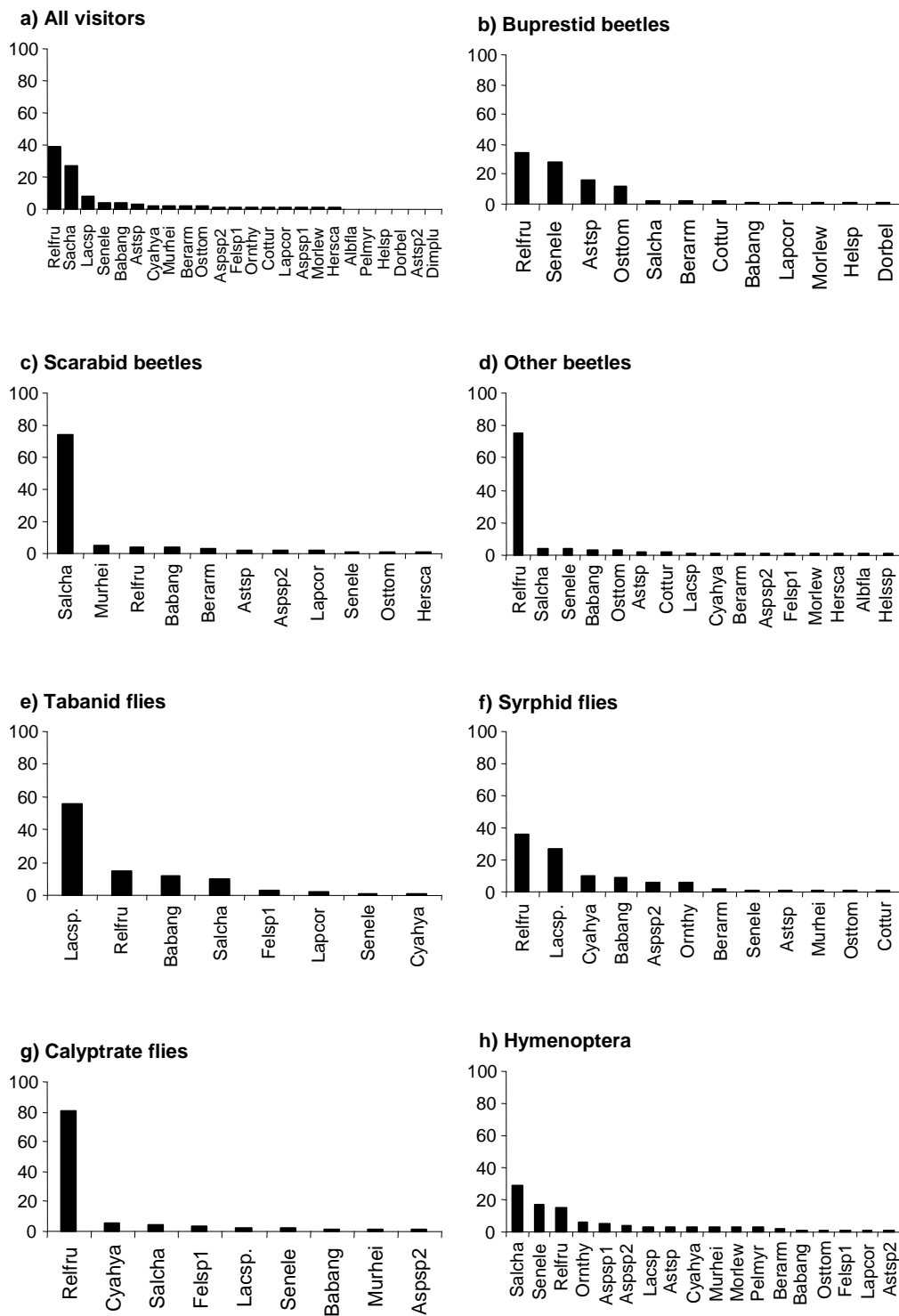


Figure 5.2 – Relative visitation frequency for different plant species by selected groups of anthophiles in a lowland Renosterveld community. Columns represent the percentage of total visits recorded for that anthophile to each plant species on the category axis. Species codes follow those used in Table 5.1.

Single predictor models

Visitation frequency for all insect visitors combined, increased with the number (N=29, P=0.006) and area (N=29, P=0.001) of visual displays per plant and per plot, but was not significantly affected by inflorescence size. Visual display area positively affected visitation frequency of all Coleoptera (N=21, P=0.021), and Diptera (N=17, P=0.001) (Figure 5.3).

Plots with more visual displays, received more visits from all insects combined (N=29, P=0.006), Coleoptera (N=21, P=0.024), and Diptera, (N=17, P=0.001,) (Figure 5.4).

Within Coleoptera, the visitation frequency, of scarabid beetles (N=15, P=0.015) increased with increasing visual display area (Figure 5.5a), while within the Diptera visitation rate of tabanid flies (N=9, P=0.022) was positively affected by visual display area (Figure 5.5b) and flower size per species (N=9, P<0.001). Calyptrate flies (N=12, P=0.003) were most strongly influenced by the number of visual displays per plot (Figure 5.5c). However, the increased visitation frequency to plants with a high number or area of visual displays did not result in a higher number of visits per flower (Figure 5.6). Plants with more flowers (numerically) tended to receive fewer visits per flower (Figure 5.6a) although this trend was only weakly significant (N=29, P=0.048). There was also a trend towards species with larger individual flowers receiving more visits per flower (Figure 5.6c) although this too was non-significant (N=29, P=0.117).

Categorical traits had significant effects on visitation frequencies for all insects combined (Figure 5.7a), as well as for Coleoptera and Diptera (Figure 5.7b; d) but not Hymenoptera (Figure 5.7c). Within these orders, scarabid and buprestid beetles (Figure 5.8a; b) showed significant responses to categorical variables, as did tabanid and calyptrate flies (Figure 5.8c; d). Overall, flower colour and symmetry as well as the relative abundance of flower species were the most influential variables affecting insect visitation rates in this community.

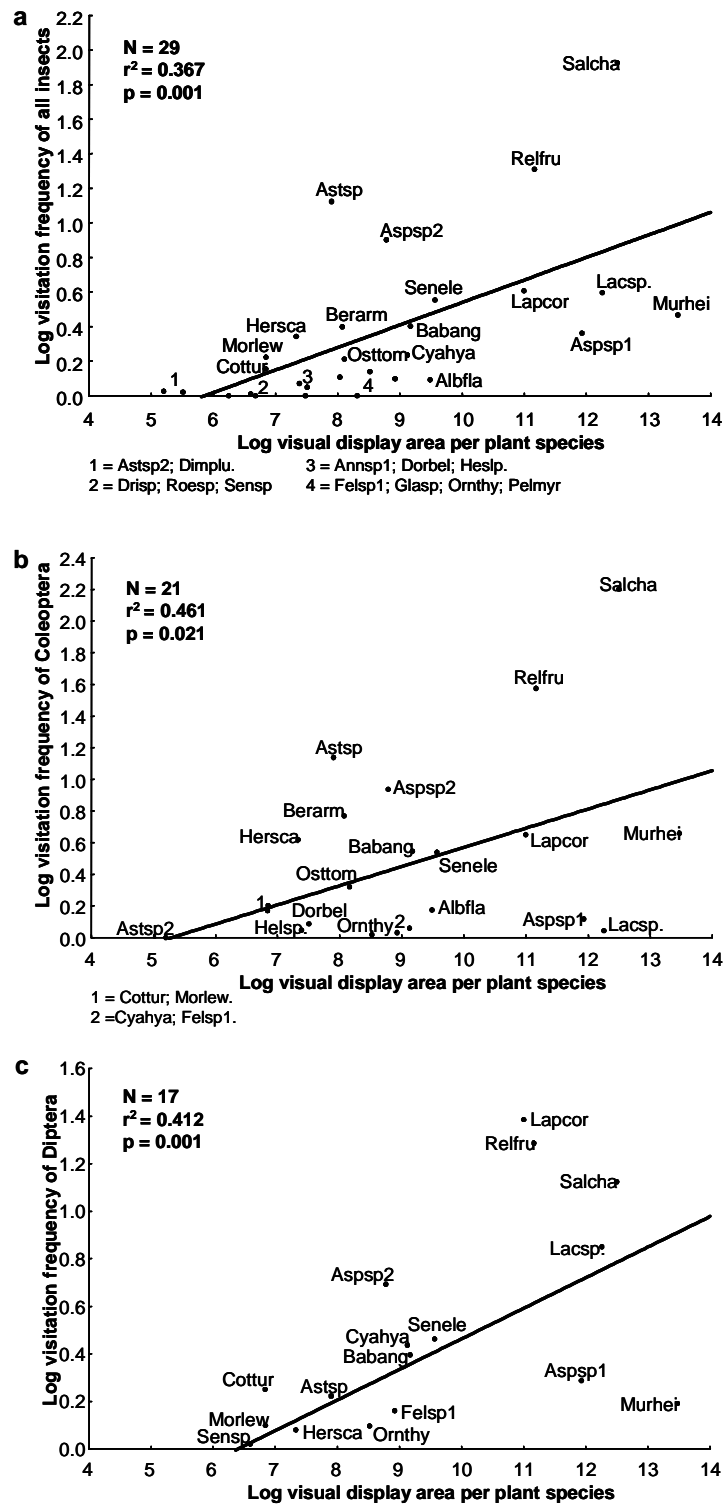


Figure 5.3 - Visitation frequency plotted against visual display area per plot for selected orders of insect visitors to flowering plants in a lowland Renosterveld community. A – All insects; B – Coleoptera; C – Diptera. Plant codes follow those used in Table 5.1. For clarity, some clusters of plant species are numbered and listed below the graph.

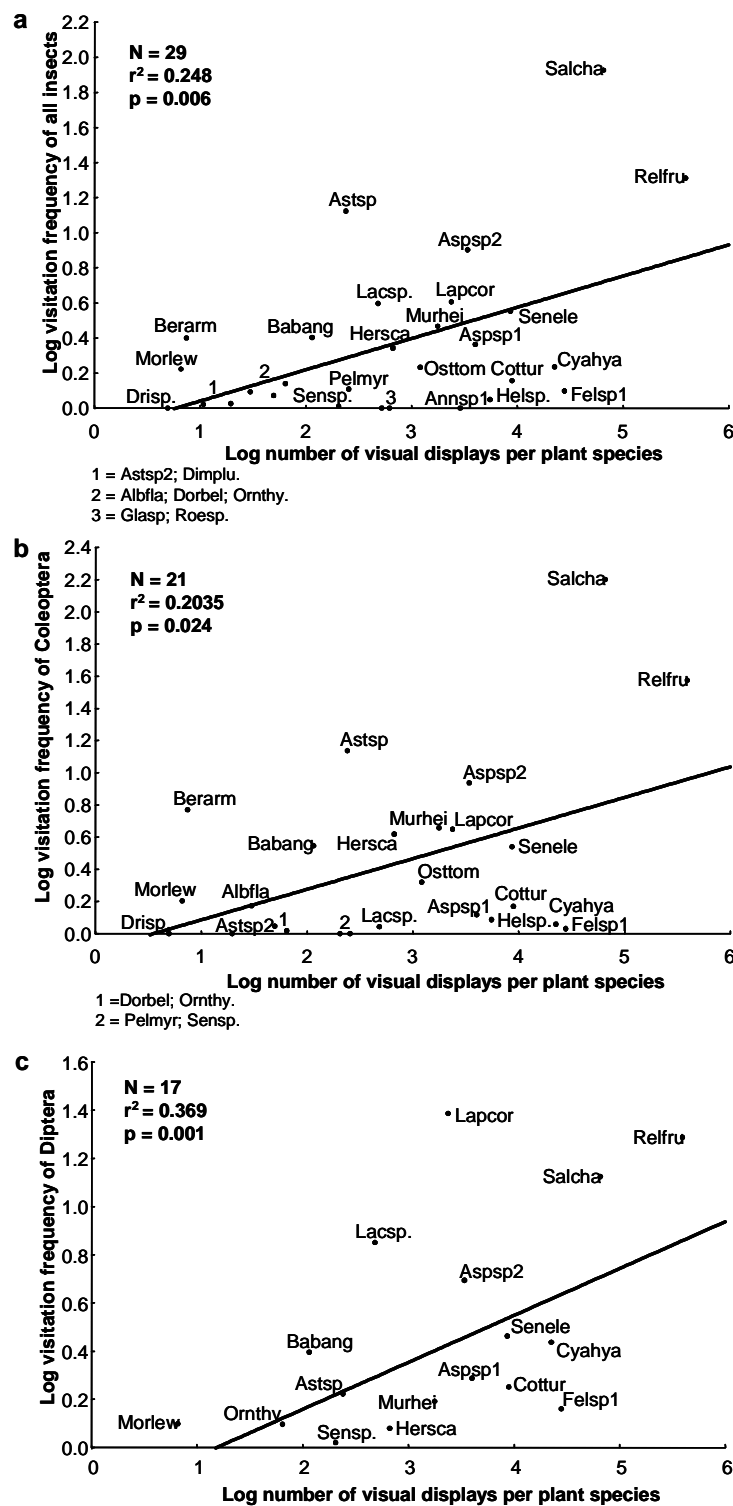


Figure 5.4 - Visitation frequency plotted against number of visual displays per plot for selected orders of insect visitors to flowering plants in a lowland Renosterveld community. A – All insects; B – Coleoptera; C – Diptera. Plant codes follow those used in Table 5.1. For clarity, some clusters of plant species are numbered and listed below the graph.

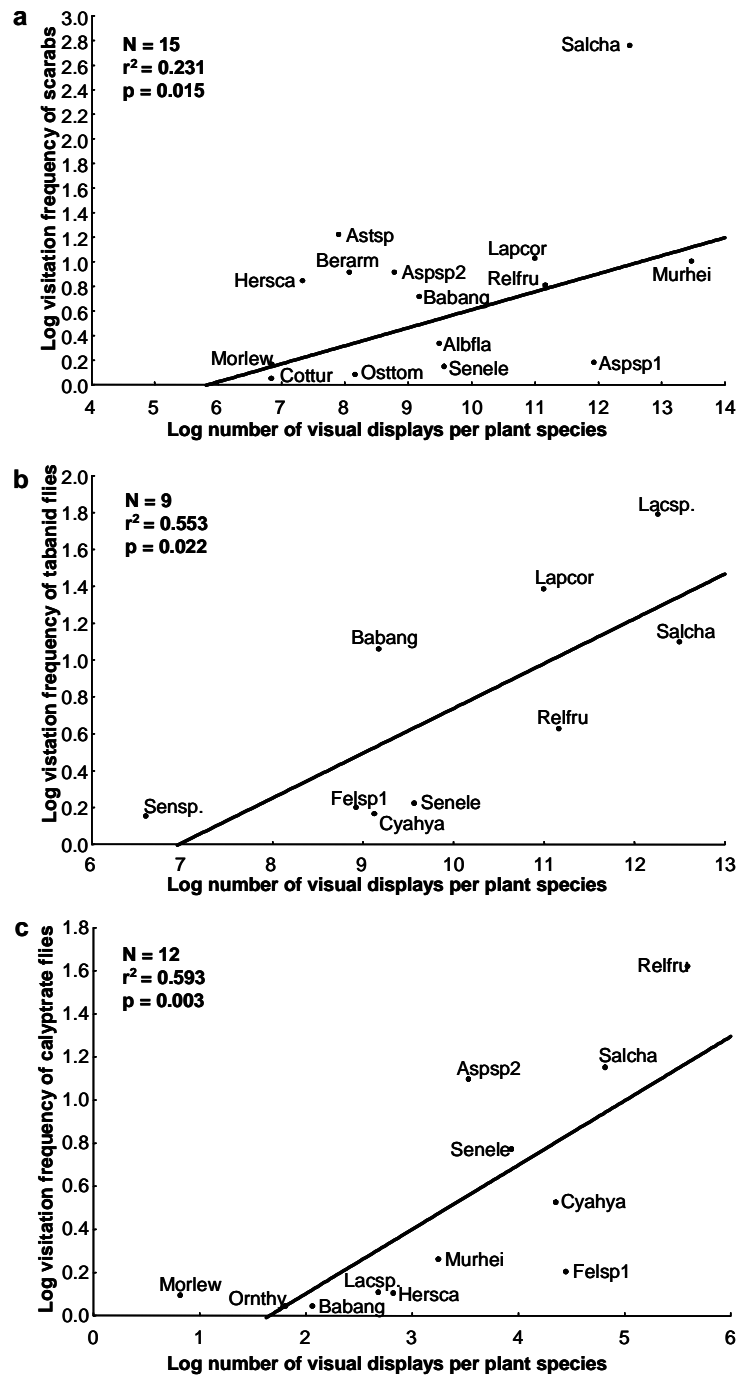


Figure 5.5 - Visitation frequency plotted against number of visual displays per plot for selected groups of insect visitors to flowering plants in a lowland Renosterveld community. A – scarabid beetles; B – tabanid flies; C – calyptrate flies. Plant codes follow those used in Table 5.1.

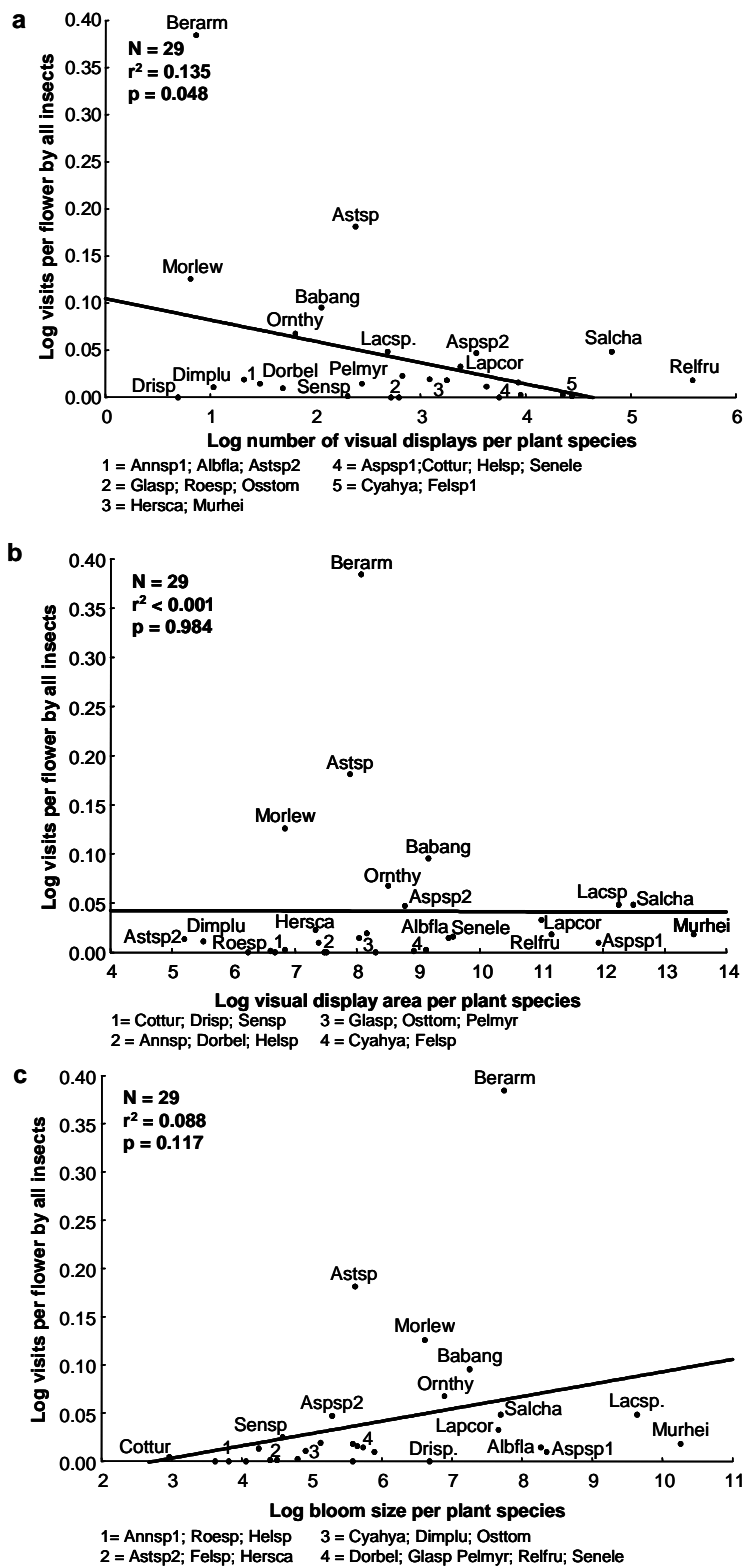


Figure 5.6 – Visits per flower by all insect visitors plotted against a - number of visual displays per plot , b - total area of visual display per species and c – average bloom size for flowering plants in a lowland Renosterveld community. Plant codes follow those used in Table 5.1.

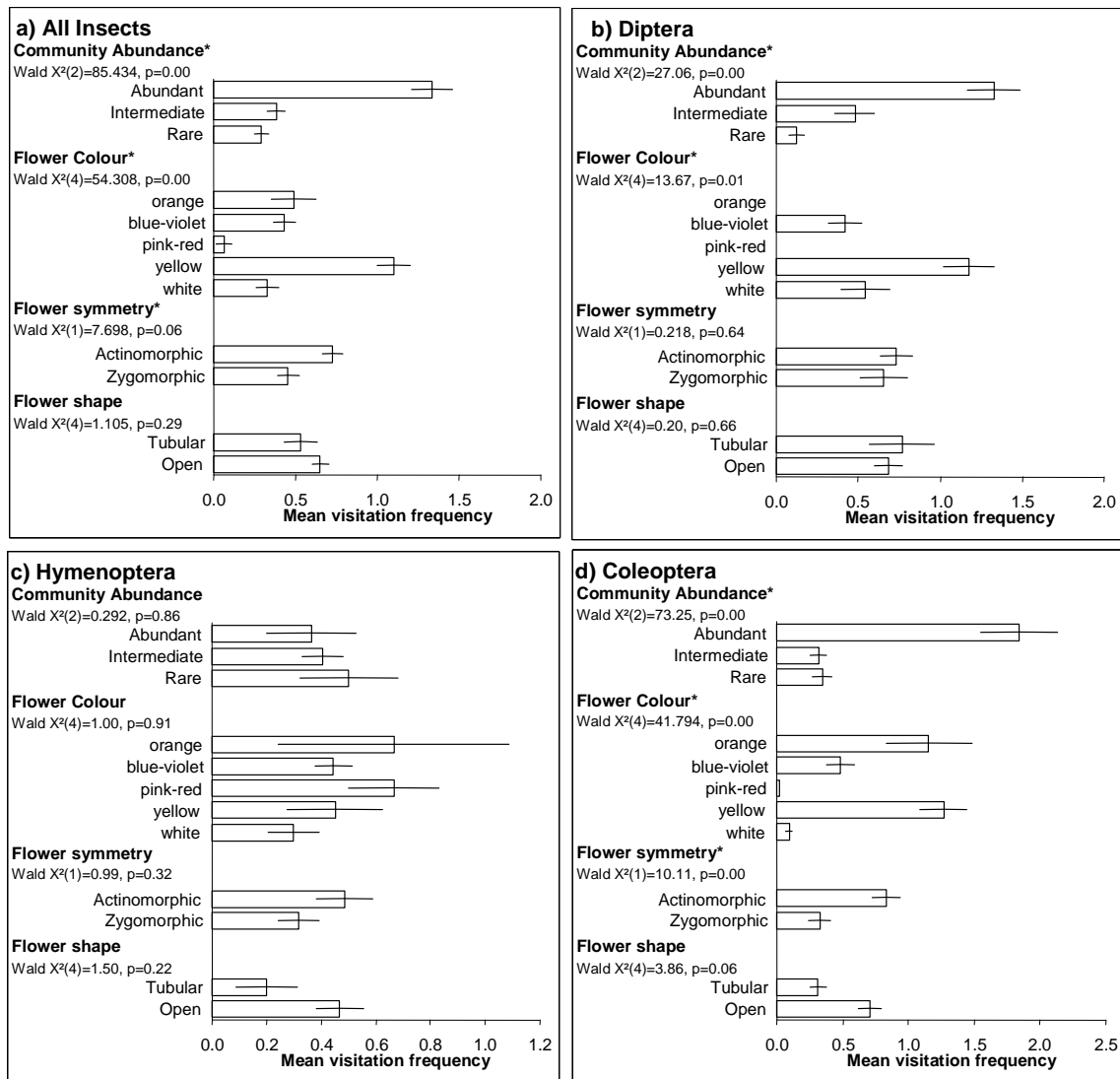


Figure 5.7 - Mean visitation frequency/observation period (± 1 SE) of all anthophiles (a) and selected insect orders (b – Diptera; c – Hymenoptera; d – Coleoptera) to flowers grouped by five categorical variables (community abundance, flower colour, flower symmetry and flower shape) in a lowland Renosterveld community. Variables marked with an asterisk(*) showed significant differences between classes within that category (GLM ANOVA, $P < 0.05$).

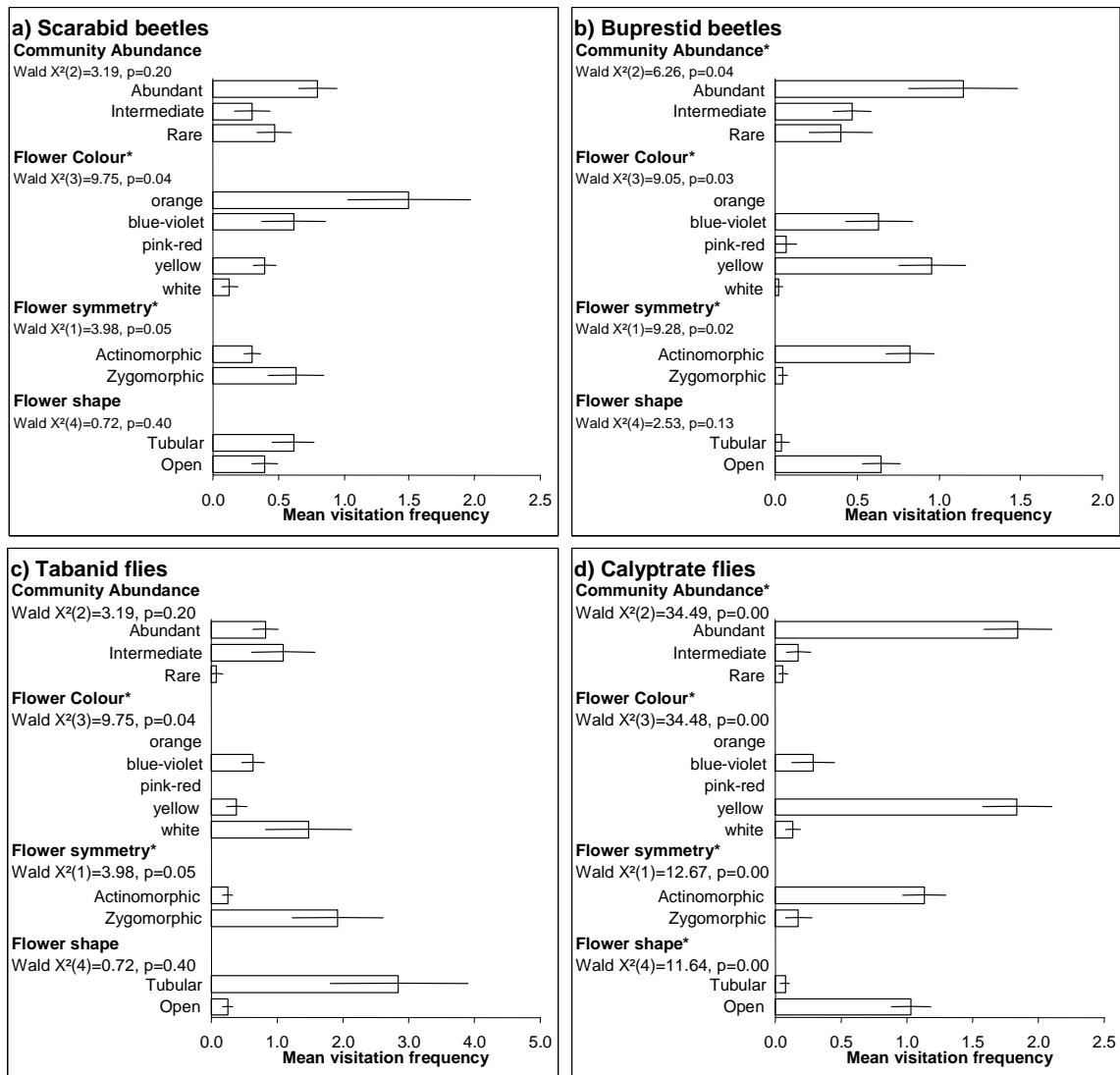


Figure 5.8 - Mean visitation frequency/observation period (± 1 SE) of selected anthophile groups (a - scarabid beetles, b – buprestid beetles, c – tabanid flies and d – calyptrate flies) to flowers grouped by five categorical variables (community abundance, flower colour, flower symmetry and flower shape) in a lowland Renosterveld community. Variables marked with an asterisk(*) showed significant differences between classes within that category (GLM ANOVA, $P < 0.05$).

Multiple predictor models

The ANCOVA models presented very similar results to the single predictor models, with continuous variables affecting visitation frequency across the range of taxa observed and categorical traits also showing significant effects for most groups (Table 5.3). For all insects combined, all continuous variables tested (number, total area and size of visual display per species) had a significant effect on visitation (all $P < 0.01$). Of the categorical variables measured, flower colour, shape and community abundance affected visitation frequency ($P < 0.01$). At order level, there was some variation in which variables had a significant effect, and this brought about some discrepancies with single predictor models, but the overall pattern here is that both continuous and categorical variables affect visitation frequency across the range of anthophiles groups observed.

The first axis of the PCA of combined visual traits explained 64.8% of total variation in visual traits between species. First axis PCA scores for combined visual traits showed a significant relationship with visitation frequency ($N=29$, $P < 0.001$) indicating that plant species with similar combinations of visual traits had more similar visitation frequencies than those with dissimilar visual trait combinations (Figure 5.9a). Similarly, the first axis of the PCA of only continuous visual traits explained 71.9% of the total variation in these traits between species and scores showed a significant relationship with visitation frequency ($N=29$, $P < 0.001$, Figure 5.9b). On the other hand, although the first axis of a PCA of only categorical visual traits explained 36.3% of total variation between plant species, these scores showed no significant relationship with visitation frequency ($N=25$ $P=0.364$, Figure 5.9c).

Table 5.3 - Analysis of covariance for the relationship between visual traits (predictor variables) and visitation frequency (response variable) for insect pollinated plant species from a lowland Renosterveld community. Numbers of plant species visited by each of the visitor groups and in each visual trait category per group (*N*) are in parentheses. Only significant models for each group are listed ($P < 0.05$) but all visual traits were included in analyses.

Visitor Group	Predictor Variable	DF	Log-likelihood	X ²	P
All Insects (25)	Intercept	1	-1800.63		
	Number of visual displays per plot	1	-1728.58	144.09	<0.001
	Inflorescence size	1	-1725.16	6.85	0.008
	Visual display area per plot	1	-1720.28	9.77	0.001
	Symmetry	1	-1711.82	14.21	<0.001
	Colour	4	-1685.63	52.38	<0.001
	Abundance	2	-1657.44	56.37	<0.001
	Shape* Colour	3	-1618.55	77.79	<0.001
	Symmetry*Colour	2	-1606.75	23.60	<0.001
Hymenoptera (17)	Colour*Abundance	3	-1588.73	35.72	<0.001
	Intercept	1	-137.68		
	Shape*Colour	2	-128.14	9.47	0.008
	Symmetry*Colour	2	-119.53	17.20	<0.001
Coleoptera (21)	Colour*Abundance	1	-111.54	15.99	<0.001
	Intercept	1	-812.47		
Diptera (19)	Number of visual displays per plot	1	-778.43	68.08	<0.001
	Visual display area per plot	1	-765.67	25.49	<0.001
	Symmetry	1	-757.89	15.56	<0.001
	Colour	4	-723.19	69.40	<0.001
	Abundance	2	-678.94	88.50	<0.001
	Symmetry*Colour	2	-664.51	25.62	<0.001
	Colour*Abundance	1	-658.24	12.28	<0.001
	Intercept	1	-836.25		
Scarabs (15)	Number of visual displays per plot	1	-792.60	87.30	<0.001
	Inflorescence size	1	-785.96	13.27	<0.001
	Colour	3	-766.70	25.19	<0.001
	Abundance	2	-745.22	42.96	<0.001
	Shape*Colour	3	-721.84	46.74	<0.001
	Intercept	1	-193.21		
Calyptrate Flies (12)	Inflorescence size	1	-186.06	13.73	<0.001
	Visual display area per plot	1	-176.54	19.04	<0.001
	Shape	1	-173.23	6.62	0.010
	Colour	4	-157.23	31.88	<0.001
	Abundance	2	-147.62	19.23	<0.001
	Symmetry*Colour	1	-141.01	13.11	<0.001
	Symmetry*Abundance	1	-138.67	4.69	0.030
	Intercept	1	-504.46		
Tabanids (9)	Number of visual displays per plot	1	-422.74	163.43	<0.001
	Inflorescence size	1	-419.75	5.99	0.014
	Colour	3	-392.61	39.49	<0.001
	Abundance	2	-363.93	57.35	<0.001
	Symmetry*Colour	3	-352.17	23.52	<0.001
	Shape*Abundance	1	-346.64	11.068	<0.001
	Intercept	1	-254.50		
Tabanids (9)	Inflorescence size	1	-220.61	67.78	<0.001
	Visual display area per plot	1	-216.24	8.75	0.003
	Shape	1	-187.03	58.42	<0.001
	Colour	3	-181.76	10.03	0.018
	Abundance	2	-178.23	7.06	0.029
	Shape*Colour	2	-170.92	14.63	<0.001
	Intercept	1	-170.92		

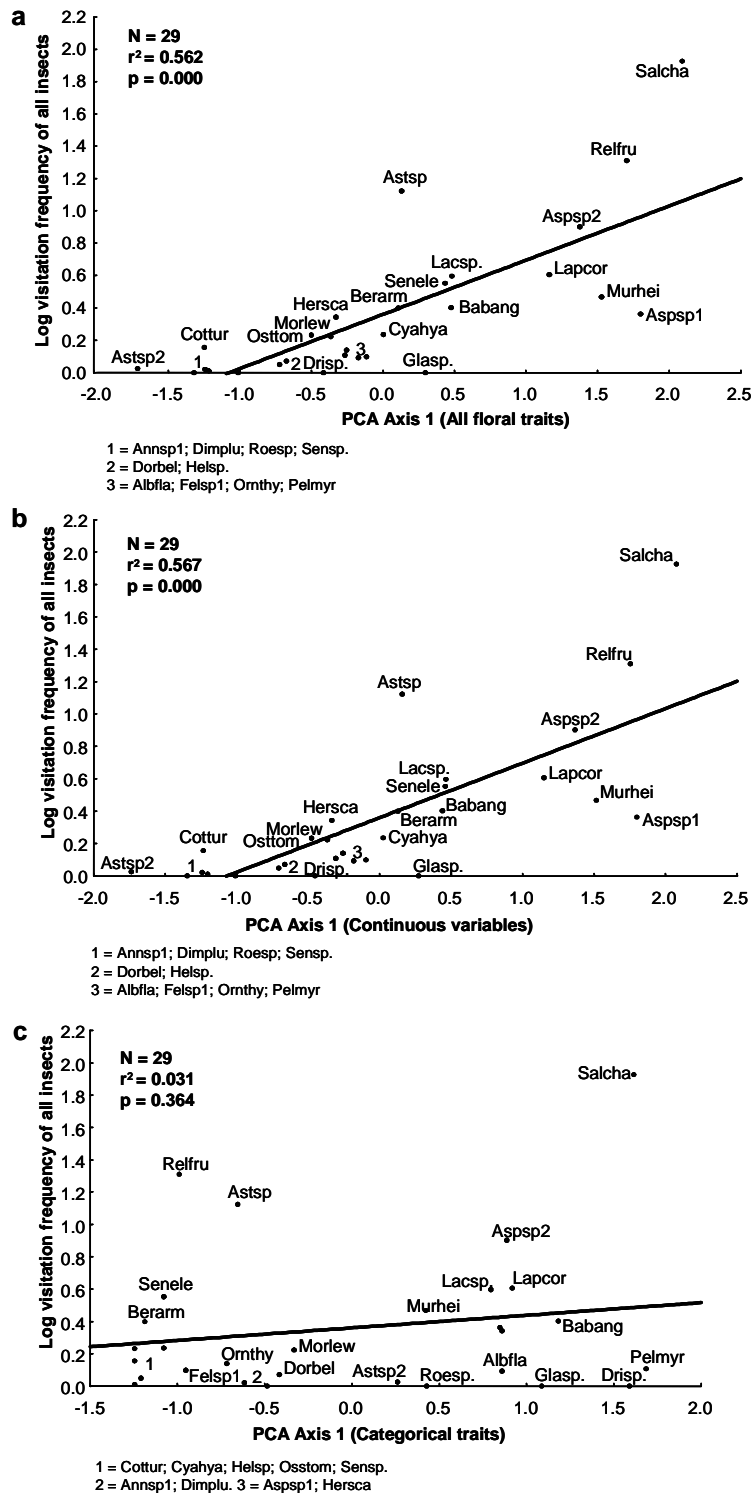


Figure 5.9 - Mean visitation per species for insect pollinated plants in a lowland Renosterveld community by all insects plotted against the first PCA axis for: a - all floral traits combined; b - continuous floral traits; c - categorical floral traits. For clarity, some clusters of plant species are numbered and listed below the graph.

Discussion

Patterns of visitation: northern and southern hemisphere comparisons

Hegland and Totland (2005) examined the relative importance of species' visual traits for the attraction of potential pollinators at the interspecific level. My study makes a direct comparison to theirs and is the first, to my knowledge, in a threatened community of lowland vegetation in the CFR. Although Hegland and Totland's (2005) study community was in a northern hemisphere temperate grassland, similar patterns emerge from the community studied here in southern hemisphere, species-rich, lowland fynbos vegetation. In both cases, visual display area is a particularly important factor in determining a species' ability to attract potential pollinators. However, both studies show that it is difficult to uncouple visual display area and visual density (i.e. total number of visual displays) in patches, as there was a strong significant correlation between number of visual displays and total area per plot, and many species with a large area of visual display, for example *Relhania fruticosa* (Asteraceae) and *Salvia chamaeleagnea* (Gerinaceae), in a plot will have a similarly high visual density.

Attractiveness of areas with great area or density of visual displays to pollinators may be a function of anthophiles optimising their foraging to minimise costs of searching for rewards, 'choosing' to visit areas with high floral density (Hegland & Boeke 2006). Similar patterns have been found in intraspecific studies where individual plants with many flowers or those occurring in dense conspecific patches tend to have higher visitation frequency (Goulson et al. 1998; Totland & Matthews 1998; Pickering 2001), although this relationship may be variable (Grindeland et al. 2005), suggesting that other factors may also play a role in determining the attractiveness of patches of flowers to anthophiles.

One major difference between my study community in the CFR and the temperate grassland community of Hegland and Totland (2005) is the composition of anthophile groups that dominate the pool of potential pollinators. Where the grassland community visitor pool was dominated by bumblebees and flies, the visitor pool in here was composed largely of beetles (mostly hopliine monkey beetles) and flies (mostly calyptrate flies) which was manifested by roughly equal proportions of the total visits. This is not surprising given that both monkey beetles (Goldblatt et al. 1998; Steiner 1998; Mayer et al. 2006) and flies (Goldblatt & Manning 2000) are known to be important pollinators of the Cape flora. Importantly, although there are broad similarities between the processes observed in both communities, the groups of taxa involved are very different. In a comparison across three different plant communities, McCall and Primack (1992) also found that although

certain visual traits and environmental variables may consistently influence visitation frequency, these relationships are non-specific and vary between communities. When comparing interactions between these communities, the functional relationships remain similar, even though they differ taxonomically.

Importance of floral traits for predicting visitation frequency

In the lowland Renosterveld community studied here, anthophile visitation rates were affected by a combination of traits intrinsic to visual displays themselves (the colour, shape and form of flowers) as well as density and abundance (measured here as the area and number of visual displays). This is consistent with the well established concept of floral syndromes (Faegri & van der Pijl 1979) where combinations of floral traits have co-evolved according to certain pollinators' sensory and learning capacities, dietary needs, mobility and ability to handle different types of flowers (Kevan & Baker 1983; 1999). Pollinators are unlikely to base their foraging choices on a single visual trait. Rather, they will distinguish co-flowering species from each other on several visual traits (Dafni et al. 1997; Gegear & Lavery 2001). The correlation between visitation frequency and similarity between the combined visual traits of plant species showed that species with similar combinations of visual traits were similarly attractive to anthophiles. However, this correlation seemed to be driven largely by pollinator response to continuous variables such as the number and area of visual displays. The floral traits examined can be broadly divided into two groups – traits that affected visitation consistently across the entire anthophile community, and traits where the effects observed varied among the defined groups of anthophiles. This is indicated by the highly significant relationship between visitation frequency and the first axis scores of the PCA of continuous visual traits, whereas the relationship between visitation frequency and categorical visual traits was non-significant, although a trend was still evident. So, while quantitative traits such as floral abundance may be a good indicator of overall anthophile activity in a floral patch, qualitative traits that impart a particular identity to flowers of a particular plant species will be more important in determining the different responses of different groups of flower visitors. Different floral forms (the combination of traits that characterise a particular flower) can be assigned to particular groups of visitors (Faegri & van der Pijl 1979; Rebelo & Jarman 1987; Dafni 1994; and various studies summarised in Dafni et al. 1997). However, flowers of most plant species are visited by more than one type of pollinator, so this should not be considered a unilateral relationship (Dafni et al. 1997). In my study, visitation was not distributed

evenly among plant species. Most anthophile groups made the bulk of their visits to only a few of available the plant species (Figure 5.2) . This suggests some degree of constancy towards particular flowers, although overall, the plant species receiving most visits were the more abundant species in the community (e.g. *R. fruticosa*, *S. chamaeleagnea* and *Lachenalia* sp.) indicating that this may be more of a labile preference (Waser 1986) to more abundant species. Nonetheless, the most favoured species differed among anthophiles and did not always correspond to the most abundant plant species, indicating preference for different species, if not floral constancy *per se*.

The flexibility of foraging anthophiles in terms of their constancy to particular floral forms (Waser et al. 1996; Waser & Price 1998) in response to changes in abundance (Fontaine et al. 2008) or species composition (Petanidou et al. 2008) of floral resources, combined with the complexity of plant-anthophile interaction webs (Memmott 1999) makes generalisation about the effect of particular traits on floral visitation at the community level difficult. Additionally, datasets that cover a number of different species or groups of organisms often have the problem of random variation or 'noise' that may obscure the effects under study. In my study, there was no single categorical trait or even set of categorical traits consistently explained visitation frequency, but rather a number of alternative combinations could be invoked depending upon the visitor group being examined. Continuous traits on the other hand, produced a much more predictable response that was consistent across most anthophile groups.

Anthophiles may use continuous visual traits such as visual display area and density to gauge abundance of resources in an area. For certain species it has been found that larger flowers or plants with a greater area of visual display hold more nectar (Frankie et al. 1983; Herrera 1985; Dafni 1991; Duffield et al. 1993; Inoue et al. 1995; Gomez et al. 2008) and it is possible traits such as petal size may be used by anthophiles as cues to nectar production (Ashman & Stanton 1991). If anthophiles are using these traits as a cue for resource abundance across a range of plant species in the community, the importance of traits such as the area and density of flowers could be explained by anthophiles, particularly generalist species, acting as predicted by optimal foraging theory (MacArthur & Pianka 1966; Emlen 1966). This would maximise rewards by utilising more abundant plants, or patches of plants with more abundant flowers and hence a larger area of visual display. Flower visitors will be attracted to patches with high floral abundance, and this is an important variable to consider when examining the effects of landscape change on anthophile communities.

While anthophiles benefit from foraging in potentially resource rich floral patches, this higher visitation frequency will not necessarily translate

into higher pollination rates in these patches. Not all anthophiles are pollinators. Flower visitation, and even the ability to carry pollen do not qualify an anthophile as a pollinator (Kevan & Baker 1983; 1999). Those that do transfer pollen will vary in their effectiveness (Primack & Silander 1975; Schemske & Horvitz 1984). Visitation does not necessarily result in successful pollination and seed set, which may be affected by other factors besides visitation rates (Price et al. 2005). Although it is recognised that there is a link between visitation rates and pollination service (Vazquez et al. 2005), visitation alone is a rather crude measure given the variation in pollinator effectiveness (Price et al. 2005). Additionally, higher visitation frequency in high density patches of floral patches does not imply that individual flowers will be visited more often. Although numerous studies have shown that visitation frequency is higher in larger plants or patches of flowers (Beattie 1976; Schmitt 1983; Geber 1985; Andersson 1988; Schmid-Hempel & Speiser 1988; Klinkhamer et al. 1989; Klinkhamer & De Jong 1990; Robertson & Macnair 1995; Goulson et al. 1998; Grindeland et al. 2005), it has also been found that a smaller proportion of available flowers receive visits in large floral displays (Schmitt 1983; Geber 1985; Andersson 1988; Schmid-Hempel & Speiser 1988; Klinkhamer & De Jong 1990; Robertson & Macnair 1995; Goulson et al. 1998; Goulson 2000). Visitation rate will likely increase as floral resources in a patch until anthophiles reach a saturation of floral resources (Rathcke 1983), after which competition between individual plants causes visitation rates to decrease (Goulson et al. 1998), as was the case here where although visitation increased with the floral area per plot, yet visitation per flower declined (Figure 5.6a). Alternatively, anthophiles may visit fewer flowers in large patches, as it is easier in small patches to avoid flower depleted by previous visits (Goulson 2000).

The results of the short term study presented in this chapter show that the floral abundance and density (which can be considered to approximate floral resources) at the scale of individual plant species within patches of flowers is an important factor in determining the activity and abundance of pollinators. A recent study by Dauber et al. (2010) using a much larger pan-European dataset similarly found that density of floral resources influenced both visitation and seed set at the patch scale. These interactions are reflected at a larger scale within the lowlands of CFR, as the results of landscape level surveys reported in Chapter 3 of this dissertation, found that floral abundance influenced the diversity and abundance of anthophiles among different areas. Fine scale effects are particularly relevant when considering pollinator conservation in the CFR lowlands, given the highly fragmented nature of much of the remaining habitat.

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A buprestid beetle visits the abundant aster *Relhania fruticosa* in a remnant patch of natural vegetation adjacent to Elandsberg Private Nature Reserve

Sven Vrdoljak, 2007

6

Pollinator conservation at the local scale: the role of density, diversity and community structure in attracting flower visiting insects to mixed floral stands.

SUMMARY

Insect pollinators play a keystone role in terrestrial ecosystems. The closely linked nature and evidence of parallel declines in plant and pollinator communities emphasizes that the understanding plant-pollinator interactions at the community level is highly relevant for biodiversity conservation. Here I examine relationships between plants and flower-visiting insects (anthophiles) at the scale of local floral patches. I conducted a visitation survey during the spring flowering season, a peak time for pollinator activity in a highly threatened lowland Renosterveld community in the Western Cape. I tested floral density, diversity and composition as predictors of anthophile visitation rates in observation plots in multispecies stands of flowers. anthophile visitation was positively affected by density and diversity of flowers in plots, but was also influenced by floral community structure. Responses to these variables also differed between the various anthophile groups observed. The results show that anthophile activity is affected by very localised, small-scale factors, which should be included in landscape level plans for pollinator conservation.

Introduction

Insect pollinators play a keystone role in most terrestrial ecosystems. Decline in pollinator populations has serious consequences for the long-term sustainability of natural and managed ecosystems (Rathcke & Jules 1993; Buchmann & Nabhan 1996; Allen-Wardell et al. 1998; Kearns et al. 1998; Kevan 1999; Biesmeijer et al. 2006). At the same time habitat loss and fragmentation decreases the local abundance and diversity of plants (Bascompte & Rodriguez 2001; Lienert 2004). The nature of plant-pollinator interactions means that a decline in one group of these mutualistic partners can lead to parallel declines in the other (Aizen & Feinsinger 1994; Steffan-Dewenter & Tschardt 1999; Steffan-Dewenter et al. 2001; Donaldson et al. 2002; Biesmeijer et al. 2006; Taki et al. 2007; Pauw 2007), leading to the possibility of cascading community-level decline and extinctions (Chapin et al. 1997). Consequently, an understanding of the interactions between plants and pollinators is highly relevant for biodiversity conservation, particularly when considering the value of remnant habitats for biodiversity conservation in the long term.

Foraging anthophiles respond to a number of different cues, such as floral odours, colours and other parameters that allow them to discriminate among flowers in their foraging area (Dafni et al. 1997). The ability to learn and memorise the scent and appearance of rewarding flowers allows anthophiles to optimise efficiency by foraging mainly on this species until it is no longer rewarding (Grant 1950; Waser 1986; Goulson & Cory 1993). Plant-pollinator interaction webs in ecosystems will contain a mix of specialised and generalised interactions (Kevan & Baker 1983; 1999), although most seem to be more dominated by generalised interactions (Procter 1978; Herrera 1988; Waser et al. 1996; Johnson & Steiner 2000). Abundance of floral resources is likely to be an important determinant of activity patterns, particularly when pollinators behave as predicted by optimal foraging theory (MacArthur & Pianka 1966; Emlen 1966). Large floral displays may act as long distance cues for anthophiles (Waser 1983; Dafni et al. 1997) affecting foraging behaviour in a number of ways. The size and density of floral patches will be expected to affect both the number of anthophiles attracted to a patch, and the way in which they forage in that patch (Kunin 1997). Plants with larger floral displays may improve foraging efficiency, making them more attractive to foraging anthophiles (Goulson 2000). If anthophiles choose among available floral patches they may select those with a higher density of flowers (Steffan-Dewenter et al. 2001; Westphal et al. 2003). High floral density of particular species may also increase the effective constancy of anthophiles, increasing the number of visits to those species (Kunin 1993).

Plant species with large floral displays may also affect visitation to their neighbours. Although co-flowering plants can be thought of as competing for pollinators (Kevan & Baker 1999), it is also possible that they facilitate visitation and pollination to neighbours (Waser & Real 1979; Brown & Kodric-Brown 1979; Rathcke 1983; Callaway 1995). Indeed, visitation to single plant species are affected by the surrounding community (Johnson et al. 2003 and references therein) and the quality and quantity of pollination services may be improved by proximity to floral resources or through facilitation by 'magnet species' (Lavery 1992). The downside of these interactions is increased competition for pollination services in large patches of flowers (Rathcke 1983). However, some studies have shown that common plant species do have the also likely to affect the attractiveness of a patch to anthophiles, positively affecting both richness and abundance of insect visitors (Hegland & Boeke 2006; Ebeling et al. 2008). This is thought to occur through increased resource provision (nectar and pollen availability) over time and space, and specific preferences of different pollinators for certain plant species (Linsley 1958; Steffan-Dewenter & Tschardt 2001; Potts et al. 2003; Hegland & Totland 2005; Fontaine et al. 2006; Holzschuh et al. 2007; Kwaiser & Hendrix 2008). As well as species richness, the community structure of floral patches also needs to be considered, but also (i.e. which species occur there and in what proportions). Understanding these interactions at the patch scale can have important implications for conservation planning, especially in a region such as the Cape Floristic Region (CFR), where lowland habitats exist only as small scattered fragments, embedded within a transformed matrix (Kemper et al. 1999).

Here I examine whether relationships between plants and anthophiles observed at the landscape level persist at the local patch scale. I address the following questions: 1) Is there a positive relationship between anthophile activity and floral density and diversity in mixed floral patches? 2) Is there a positive relationship between anthophile diversity and floral density and diversity? 3) How does the composition of mixed floral patches affect anthophile activity? 4) Do abundant, mass-flowering species affect anthophile visitation to nearby plant species?

To answer these questions I conducted visitation surveys in a highly threatened lowland Renosterveld community in the CFR during the spring flowering season, a peak time for pollinator activity. More specifically, the study tested how well anthophile presence and activity were predicted by floral diversity, floral density and floral composition in observation plots, and how the effects of these predictors differed between different anthophile groups.

Methods

Study area

The study area was in the Elandsberg Private Nature Reserve (33.27° S, 19.03° E) and on the surrounding Bartholomeus Klip farm, near Hermon, Western Cape Province, South Africa. Situated in the lowlands (below 300 m 4000 ha, the reserve encompasses the largest remaining contiguous patch of West Coast Renosterveld, and some marginal abandoned farmland (Ashwell et al. 2006). Renosterveld is an evergreen, fire prone, shrubland, dominated by the cupressoid leaved Asteraceae, in particular renosterbos (*Elytropappus rhinocerotis*), with an understory of grasses (Poaceae) and a rich diversity of spring flowering geophytic plants (Mucina & Rutherford 2006). Renosterveld has been highly transformed. Less than 10% of the original Renosterveld remains (Rebello 1992), existing mainly as scattered fragments in agricultural land (Kemper et al. 1999). The two main vegetation types in the Elandsberg Reserve are Swartland alluvium fynbos and Swartland shale Renosterveld, both critically endangered (Mucina & Rutherford 2006). The surrounding farmland includes wheat fields and areas under grazing by livestock. The area receives a mean annual rainfall of about 500 mm. During this study, 32 species plant species were observed to be flowering, of which, 25 were recorded frequently enough to be used in subsequent analyses (see Chapter 5 for more information on the occurrence of and visitation to these plant species).

Data collection

I conducted a visitation survey within 20 plots in the Elandsberg reserve and surrounding area. Although brief, the study was highly intensive, involving a team of four co-ordinated observers, who conducted visitation surveys in marked, 2 x 2 m plots. Over four days (9-12 October 2007) more than 46 hours of simultaneous observation data were collected from four sets of observation plots. The brief, but intensive, data collection ensured comparison between the sample plots without confounding effects of variable weather or phenological changes in floral abundance and composition. The sampling time fell within the spring flowering period in the area, which is associated with high floral abundance and pollinator activity. All days were sunny, with temperatures ranging from 15 to 31°C at the nearest weather station, Diemerskraal (33.35°S, 18.55°E) between 09h00 and 17h00 over the four days. Weather data were provided by the AgroMet-ISCW, Agricultural Research Council. Five plots, each at least 10 m apart, were located randomly in four sites chosen to represent the reserve area and its surrounding remnants of natural vegetation. Two sites fell within the main reserve area,

and two outside the reserve, in patches of natural vegetation surrounded by wheat fields.

Visitations were surveyed within the plots by counting visits by insects to visual displays of insect-pollinated plant species during 10 min observation periods. Visits were only recorded when the visitor landed on, or made contact with, the visual display for more than one sec. Plots were observed four times daily, twice in the morning (09h00-10h30; 11h00-12h30) and twice in the afternoon (13h30-14h30; 15h00-16h30), run concurrently in each of the four sites. In total, 1771 visits were recorded in 280 observation periods (2800 min). The visitor pool was dominated by Coleoptera and Diptera, which accounted for 46% and 36% respectively of all visits. The top three visitor groups were scarabs (29%), calyptrate flies (19%) and other flower-visiting beetles (19%). All other groups accounted for no more than 10% each of the total visitations.

Before starting the observations, the flowering plants in the plots were identified and counted, and the number of visual displays per plant species in the entire plot, was recorded. Depending on the plant species, a visual display could be a single flower, an inflorescence, or a group of flowers that formed a recognisable visual unit. Counts were repeated each day, and this information was used to calculate the floral density and diversity of plots (see *Variable calculations* for more details).

Variable calculations

To investigate absolute and relative importance of floral density, diversity and composition to anthophile activity, standardised variables were calculated. The number of flowers per plot could not be used, as such a measure is dependent upon flower size, as well as what the observer defines as a single floral unit, both of which differ between species. To obtain a standardised measure of floral density I instead calculated the total area of floral display in each plot.

Mean floral area was determined per plant species by measuring 10-20 randomly selected plants per species, and calculating the inflorescence size (as an area) according to the shape of the flowers. Visual displays with a circular outline were calculated using the formula: πr^2 . For other flat visual displays the formula: length \times width was used. When visual displays also had a depth dimension the formula: $2\pi r^2 + \pi r^2$ was used. The daily floral counts per plot and mean floral areas per species were used to calculate total floral areas per plot as a measure of total floral density as different visitor groups may respond differently to such flowers (see Table 5.1, Chapter 5 for classification of plant species). Separate variables were calculated for tubular and open flowers, called 'tubular floral density' and 'open floral density' respectively.

For diversity variables, the species richness of insect pollinated plants in bloom in each plot, called 'total floral diversity', was used, as well as separate variables for plants with tubular (tubular floral diversity) and open flowers (open floral diversity). To obtain a measure of the floral composition of each plot I used a Detrended Correspondence Analysis (DCA) (Jongman et al. 1995) of the floral area per plant species in each plot. First axis DCA scores were used to measure the compositional similarity between plots (called here 'floral composition'). Plots with similar plant community structure will occur closer together on this axis than dissimilar species that will occur farther apart. Multivariate analyses were performed using CANOCO 4.53 (ter Braak & Šmilauer 2004).

Two locally abundant plant species, *Relhania fruticosa* and *Salvia chamaeleagnea*, which had high floral density and high visitation frequency in plots in which they occurred, were chosen as 'mass-flowering' (MF) plant species. Samples were coded as '+MF' or '-MF' depending on the presence or absence of MF species and for each sample, the area and number of visits were calculated separately for non-MF and MF plants. Fifteen plant species occurred in both +MF and -MF plots. These species were used to test the effect of the potential magnet species on neighbouring plants. To account for the effect of floral display area on visitation, a Visitation Index (VI) was calculated for each species. For a species in a particular sample $VI = \text{number of visits} / \text{floral area}$ to give the visits/cm²/10 min observation period.

Data analyses

To gain statistical power, anthophile groups that were observed in less than 30 observation periods were excluded from the analyses. This left scarab beetles, other beetles, calyptrate flies, tabanid flies, and syrphid flies for inclusion in the analyses. To check for spatial autocorrelation, a matrix of distance between plots and matrices of differences (Bray-Curtis) between plots for the measured variables were constructed. The associations between plot distance and variable difference for all variables was tested with a Mantel test (Sokal & Rohlf 1995) using the PopTools add-in for Microsoft Excel (Hood 2008). No significant associations were found for any of the variables tested (all $r < 0.14$, $P > 0.06$), showing that the study design successfully minimised the probability of spatial autocorrelation.

Stepwise multiple regressions were applied to account for inter-correlation among predictor variables. To investigate the effects of floral density, diversity and composition on the probability of presence in the community of anthophiles, I used a stepwise logistic regression with backward selection ($P < 0.05$ to enter and $P > 0.1$ to remove) was used. For this analysis, all visitation data were transformed into a binomial dataset of

visitation. Models with a final P-value greater than 0.05 were rejected. Simple linear regression was used to investigate relationships between floral variables and the number of anthophile groups visiting the plots. To examine the relationship of anthophile activity (number of visits to each plot) to floral density, diversity and composition, linear multiple regression, of log transformed visitation counts from all periods where anthophile groups entered the plots was used. Variables were selected using backward selection. ($P < 0.05$ to enter and $P > 0.1$ to remove). Models with a final P value > 0.05 were rejected.

Multivariate analysis was used to test the effect of floral composition on anthophile visitation to plots. A Canonical Correspondence Analysis (CCA) was performed on a matrix of visits to each plot by anthophile groups. A matrix of floral areas by plant species in each plot was used to constrain the ordination. The CCA was performed in CANOCO 4.53 (ter Braak & Šmilauer 2004).

To test the potential magnet effects of MF species, I compared total VI per plot and VI per each of the fifteen co-occurring plant species as well as total visits, area and area of non-MF species per plot using non-parametric Mann-Whitney U tests, as sample sizes, and sample variance of +MF versus -MF plots were not equal for most species. All statistical analyses were performed using Statistica 8 (StatSoft Inc. 2007).

Results

Presence of different flower visitor groups

Significant stepwise multiple binary logistic regressions were found for all anthophile groups (Table 6.1). Overall, floral composition was a better predictor of visitor presence in plots than floral density or diversity, affecting all groups except for the other beetles and tabanids. All groups were significantly affected in some way by at least one of the density or diversity variables measured. Of the variables that could be modelled, probability of anthophile presence increased with total floral density per plot (Figure 6.1a). Total floral diversity within plots had a similar positive effect on buprestid presence (Figure 6.1b), yet the probability of scarabs entering plots decreased in higher diversity plots (Figure 6.1c). Tabanid presence was more likely in plots with higher floral density (Figure 6.1d), while the probability of syrphid presence increased with both total (Figure 6.1e) and open (Figure 6.1f) floral diversity.

Table 6.1 - Relationships between flower visiting insect presence in plots and floral density, diversity and composition variables in a lowland Renosterveld community, analysed by stepwise logistic regression.

Visitor Group	Predictor Variable	DF	Log-likelihood	Chi ²
All Insects	Intercept	1	-187.800	
	Floral composition	1	-147.839	5.753*
	Total floral density	1	-145.959	3.759*
	Floral density (open)	1	-143.276	5.366*
Coleoptera	Intercept	1	-187.800	
	Floral diversity (open)	1	-177.931	17.631**
	Floral composition	1	-169.441	16.981**
	Floral density (open)	1	-164.149	9.710**
Diptera	Intercept	1	-183.535	
	Total floral diversity	1	-171.040	24.990**
	Floral diversity (open)	1	-168.055	5.96885*
	Floral composition	1	-165.007	6.09604*
	Total floral density	1	-160.252	9.510**
	Floral density (open)	1	-150.372	19.760**
Buprestids	Intercept	1	-115.323	
	Floral diversity (open)	1	-109.847	10.572**
	Floral composition	1	-99.064	21.566**
	Floral density (open)	1	-94.220	9.470**
Calyptrate flies	Intercept	1	-157.195	
	Total floral diversity	1	-140.929	32.531**
	Floral diversity (open)	1	-133.657	14.544**
	Total floral density	1	-129.780	5.497*
Other Beetles	Intercept	1	-163.893	
	Floral density (open)	1	-157.276	5.698*
Scarabs	Intercept	1	-163.893	
	Total floral diversity	1	-159.975	7.836**
	Floral diversity (open)	1	-157.309	5.330*
	Floral composition	1	-136.091	42.436**
Syrphids	Intercept	1	-92.3127	
	Total floral diversity	1	-90.0212	4.583*
	Floral diversity (open)	1	-87.1852	5.672*
	Floral composition	1	-84.3680	5.634*
Tabanids	Intercept	1	-102.481	
	Total floral density	1	-99.563	4.511*
	Floral density (open)	1	-93.201	12.723**

Backward stepwise selection procedures, α 0.05 to enter and 0.10 to remove, were applied for multiple models. Only significant relationships are shown and indicated by * $P < 0.05$ and ** $P < 0.01$ (See materials and methods for explanation of variables). Model fit was assessed using the Goodness-of-fit *Chi*-square, test where significant values indicate that the estimated models is a significantly better fit than the null model.

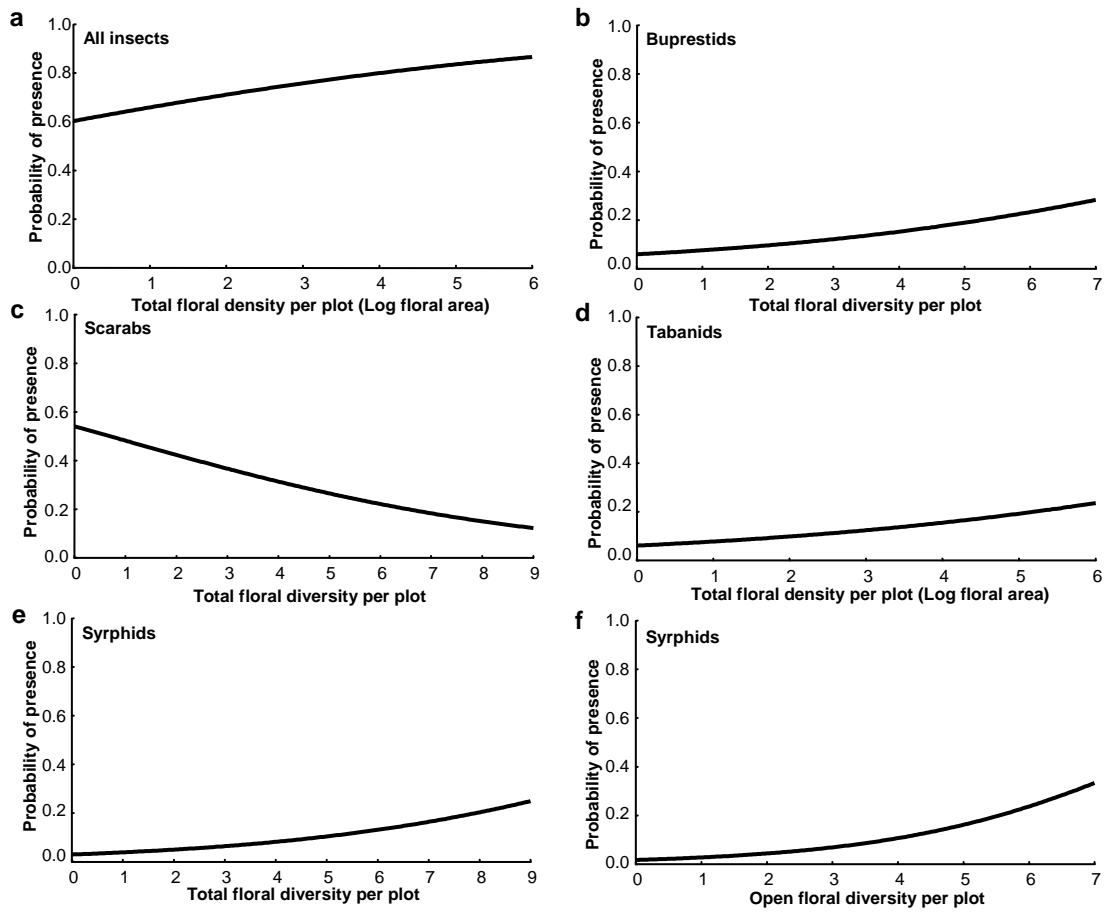


Figure 6.1 - Probability of presence of flower visiting insects in plots in relationship to floral diversity and density in a lowland Renosterveld community. Only significant variables from multiple stepwise regression in Table 6.1 (that were also significant in the simple regressions in this figure) are shown.

Activity of different visitor groups

Visitation rates of all anthophile groups were affected by either density, diversity and composition of flowers in the plots (Table 6.2). The importance of these effects varied between different groups. The simple linear regressions were only significant for the pooled set of all insect visitors (Figure 6.2a) and for scarabaeid beetles (Figure 6.2b). Visitation for both of these groups increased with floral density. However the scarabaeid beetles also showed a negative relationship with total and open floral diversity (Figure 6.2c,d).

Table 6.2 - Relationships between flower visiting insect activity (no. visits/10 min observation period) and floral density, diversity and composition in a lowland Renosterveld community, analysed by stepwise linear regression.

Visitor group		DF	R ²	Predictor variable	β
All Insects	Regression:	2	0.109**	Total floral density	0.182
	Residual:	277		Floral composition	-0.246
All Coleoptera	Regression:	1	0.256**	Floral composition	-0.506
	Residual:	278			
All Diptera	Regression:	2	0.163**	Total floral density	0.314
	Residual:	277		Floral composition	0.312
All Hymenoptera	Regression:	3	0.044**	Floral composition	-0.176
	Residual:	276			
Buprestids	Regression:	3	0.124**	Floral diversity (open)	0.219
	Residual:	276		Total floral density	-0.141
				Floral composition	-0.337
Calyptrate flies	Regression:	4	0.186**	Floral diversity (tubular)	0.682
	Residual:	275		Total floral density	0.179
Scarabs	Regression:	4	0.463**	Floral diversity (open)	-0.396
	Residual:	275		Floral diversity (tubular)	0.144
				Floral composition	-0.679
Syrphids	Regression:	4	0.053**	Floral diversity (open)	0.185
	Residual:	275		Floral diversity (tubular)	-0.607
				Floral composition	0.157
Tabanids	Regression:	4	0.034*	Floral diversity (tubular)	-0.494
	Residual:	275		Total floral density	0.164

Backward stepwise selection procedures, α 0.05 to enter and 0.10 to remove, were applied for multiple models. Only significant relationships are shown and indicated by * $P < 0.05$ and ** $P < 0.01$ (See materials and methods for explanation of variables). The explanatory values of the models are indicated by standardised regression coefficients (β) for variables and the multiple coefficient of determination R^2 for whole models.

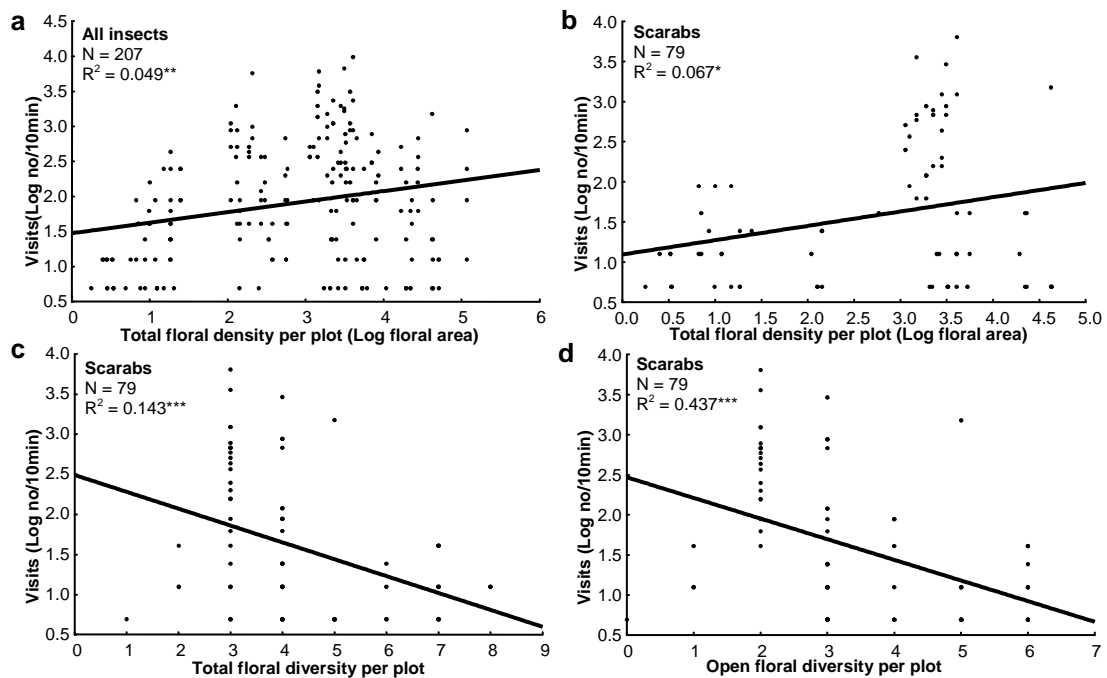


Figure 6.2 - Flower visiting insect activity (log no. visits/10 min) in plots in relationship to floral density (A – All insects; B – scarabaeid beetles); total floral diversity (C – scarabaeid beetles) and open floral diversity (D – scarabaeid beetles) in a lowland Renosterveld community. Only significant variables from the multiple stepwise regression in Table 6.2 that were also significant in simple regressions are shown.

Visitor diversity

Simple linear regressions showed that anthophile diversity was weakly, but positively, significantly correlated to both floral density ($n = 280$, $R^2 = 0.0475$; $P = 0.0002$, (Figure 6.3a), and floral diversity ($n = 280$, $R^2 = 0.0127$; $P = 0.0284$, Figure 6.3b).

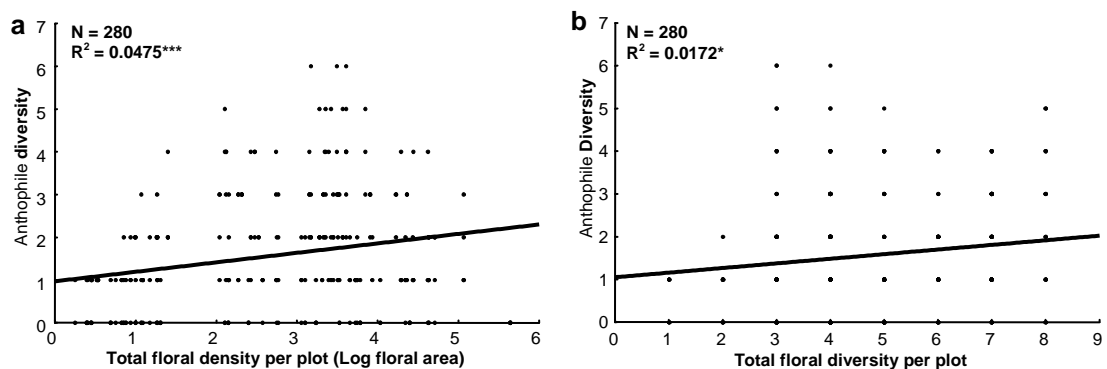


Figure 6.3 - Simple linear regressions of the relationship between flower visiting insect diversity and A – floral density and B – floral diversity in a lowland Renosterveld community.

Effects of floral composition

Floral composition of the plots was a consistently significant variable in multiple regressions for both presence (stepwise logistic regressions, Table 6.1) and activity (stepwise linear regressions, Table 6.2) for all anthophile groups, except calyprate and tabanid flies. The DCA showed that plots within the same sites tended to be more similar in terms of their floral composition and plots grouped by site, with only a small degree of overlap (Figure 6.4, sum of all eigenvalues = 5.914; cumulative percentage variance of first four axes = 30.5). In terms of both anthophile presence (sum of all canonical eigenvalues = 0.873; cumulative percentage variance of first four axes = 34.4) and visitation rates (sum of all eigenvalues = 1.177; cumulative percentage variance of first four axes = 41.1), a similar separation of the sites can be seen in the CCA biplots of visitation data (Figure 6.5), constrained by the floral composition of the plots.

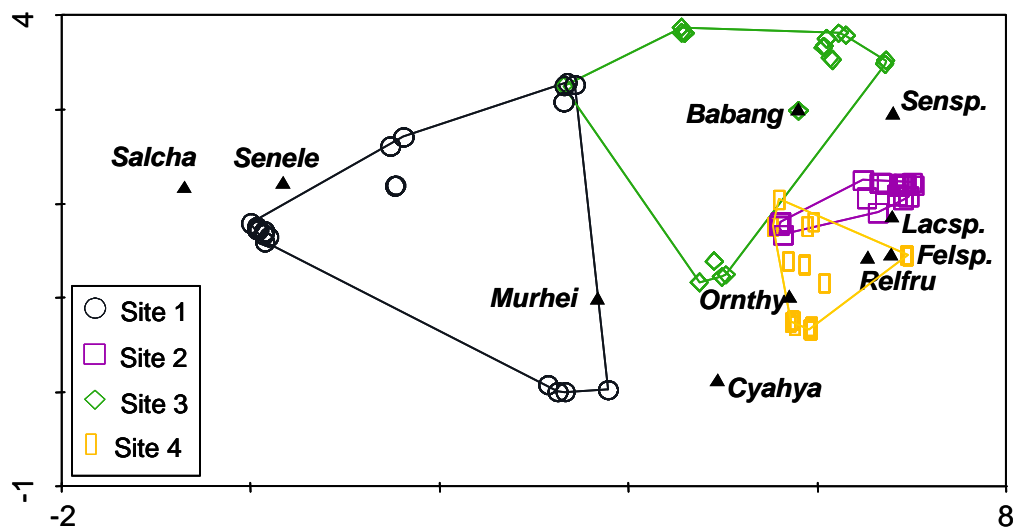


Figure 6.4 - DCA biplot of floral composition of 2x2 m plots used in visitation surveys in a lowland Renosterveld community (Eigenvalues: Axis 1 = 0.908; Axis 2 = 0.437. Sum of all eigenvalues = 5.915). The top 10 out of 36 plant species in terms of weight in the DCA model are indicated by solid triangles (Babang = *Babiana angustifolia*; Cyahya = *Cyanella hyacinthoides*; Felsp = *Felicia* sp.; Lacsp = *Lachenalia* sp.; Murhei = *Murhertia heisteria*; Ornthy = *Ornithogalum thyrsoides*; Salcha = *Salvia chamaeleagna*; Senele = *Senecio elegans*; Sensp = *Senecio* sp.).

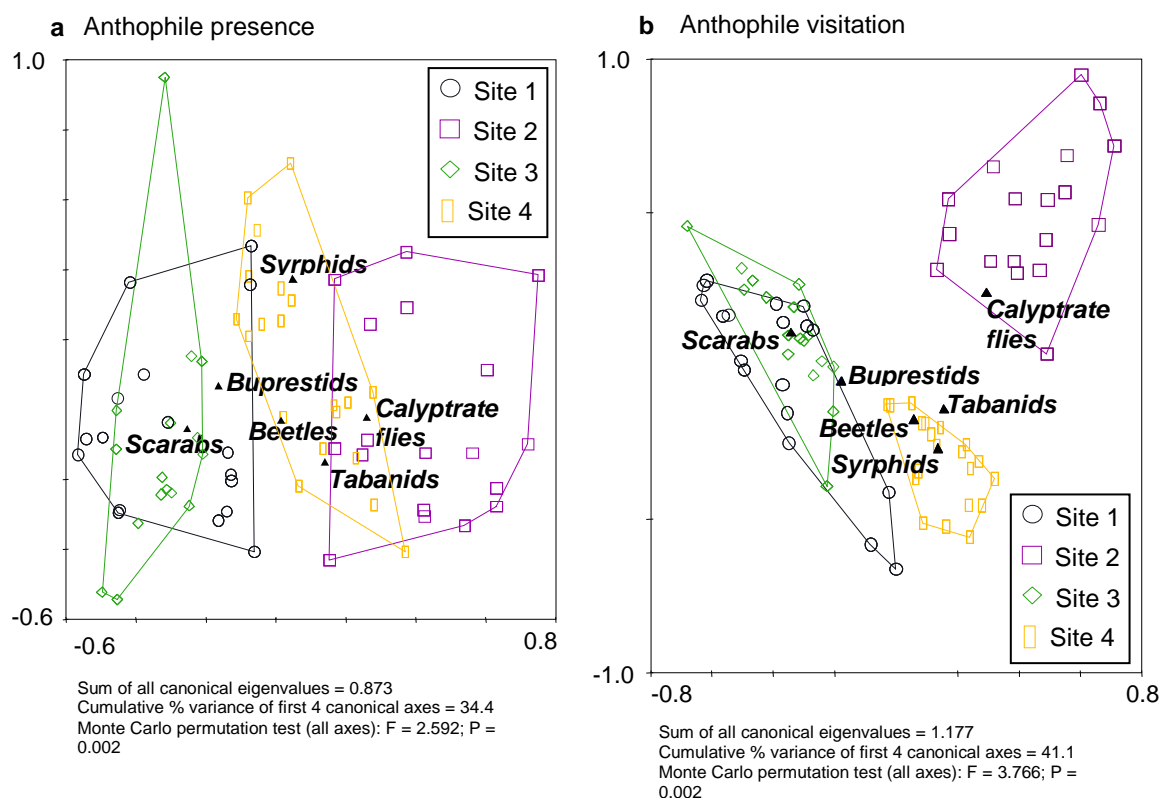


Figure 6.5 - CCA biplots of flower visiting insect presence (a) and visitation (b) in plots in four sites in a lowland Renosterveld community. Anthophile groups are indicated by solid triangles. Sites 2 and 3 are situated within the Elandsberg Nature Reserve. Sites 1 and 4 are remnants of natural vegetation in agricultural land outside the reserve.

Effects of mass-flowering plant species

Plots containing *S. chamaeleagnea* or *R. fruticosa* (+MF plots) had a lower floral display area than -MF plots where these species were absent (Figure 6.6a, Mann-Whitney $U = 6716$; $P < 0.001$). Floral diversity was also lower in plots with *S. chamaeleagnea* and *R. fruticosa*, but not significantly so. Overall, plots with high floral diversity also tended to have high floral density (Figure 6.7). Despite the lower floral density, total visitation per plot was significantly higher in +MF plots (Mann-Whitney $U = 4675$; $P < 0.001$) compared to -MF plots (Figure 6.8a). However, most of visits in +MF plots were made to whichever of these two mass-flowering, magnet species were present, with far fewer made to -MF plants (Figure 6.8b). The area of other -MF species in the plots ($U = 8629$; $P = 0.276$) was not significantly different between plots that contained MF plants and those that did not.

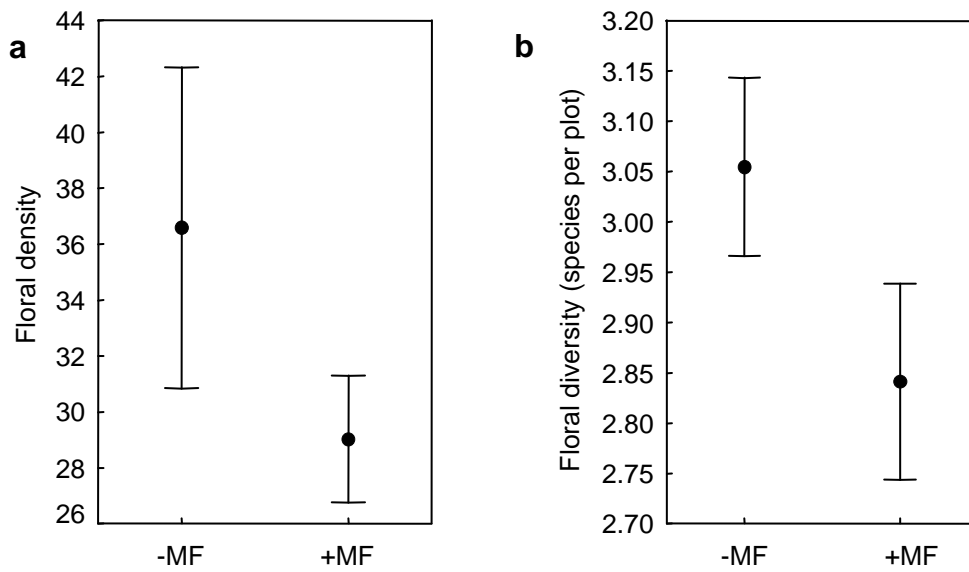


Figure 6.6 – a) Floral density (total area of floral display) and b) diversity (number of flowering species) in plots with (+MF) or without (-MF) the abundant, mass flowering plant species *Relbania fruticosa* and *Salvia chamaeleagnea* in a lowland Renosterveld community. N = 280 (110 non-magnet plots; 170 magnet plots). Mean values for each group shown (\pm S.E.).

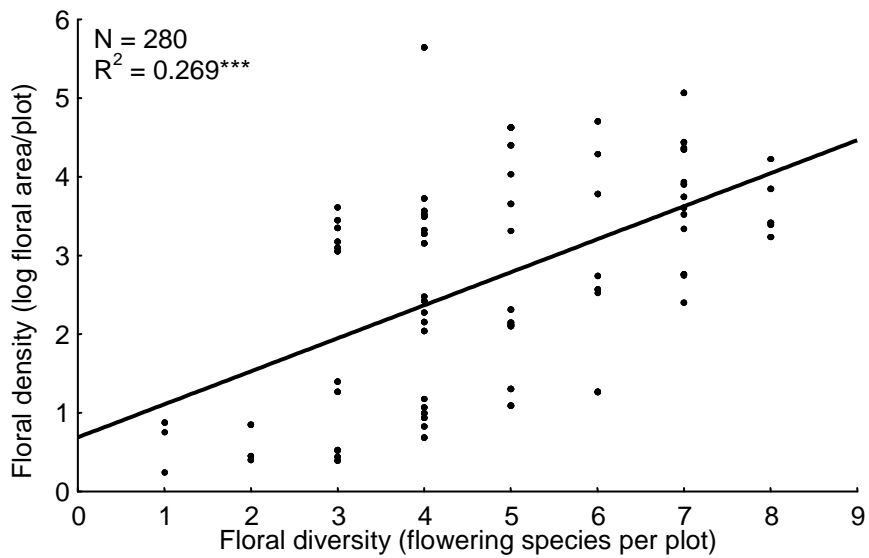


Figure 6.7 - Relationship between floral density and floral diversity in 280 plots in a lowland Renosterveld community. Details of plant species are given in Chapter 5 (Table 5.1).

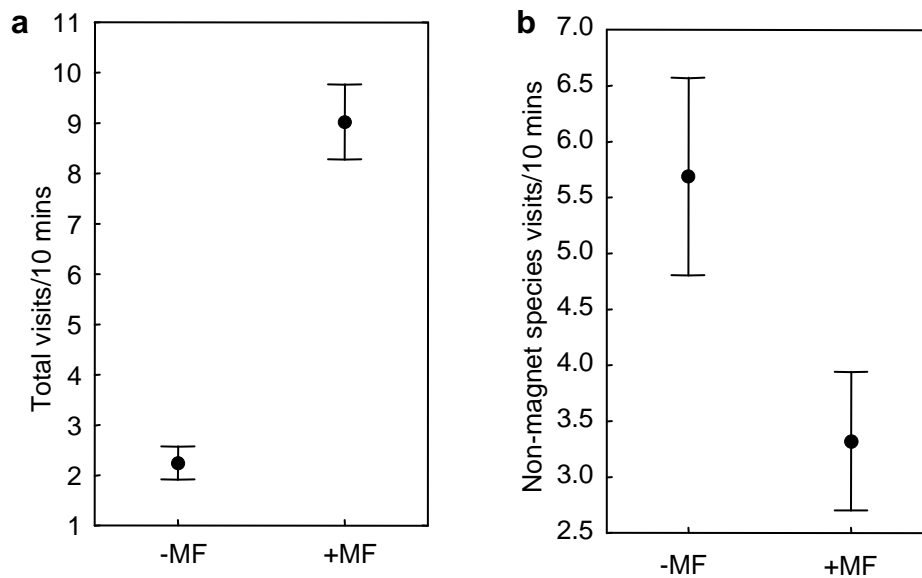


Figure 6.8 - Visitation frequency in plots with (Magnet) or without (Non-magnet) the abundant plant species *Relhania fruticosa* and *Salvia chamaeleagnea* in a lowland Renosterveld community. Mean number of visits per 10 minute visitation period (\pm S.E.) are shown for, a) All plant species in the plot and, b) All other species except *R. fruticosa* and *S. chamaeleagnea*. N = 280 (110 -MF plots; 170 +MF plots)

Pooled visits to all non-MF species per plot was found to be higher in -MF plots ($U = 7970$; $P = 0.037$). However, no significant effects of presence of *S. chamaeleagnea* or *R. fruticosa* (All $P > 0.07$) were detected when the 15 species that co-occurred with MF species were tested individually, but the small, uneven sample sizes greatly lowered the statistical power of these tests (Table 6.3).

Table 6.3 - Differences in visitation frequency and areas of floral display in plots with (+MF plots) and without (-MF plots) the abundant, mass-flowering species *Relbania fruticosa* and *Salvia chamaeleagnea*. Details of plant species are given in Chapter 5, Table 5.1

Variable	U	Z	+MF plots		-MF plots	
			N	Mean (\pm SE)	N	Mean (\pm SE)
Total visits	4675	- 7.064**	170	9.02 (\pm 0.75)	110	2.25 (\pm 0.33)
Non-MF visits	7985	2.062*	170	3.32 (\pm 0.62)	110	5.69 (\pm 0.88)
Total floral density	6716	- 3.979**	170	29.03 (\pm 2.27)	110	36.58 (\pm 5.73)
Non-MF floral density	8629	-1.089	170	19.32 (\pm 2.28)	110	36.58 (\pm 5.73)
Floral diversity	8585	1.155	170	2.84 (\pm 0.08)	110	3.05 (\pm 0.08)
VI by plant species						
All non-MF species	7970		170	1.77 (\pm 0.49)	110	2.66 (\pm 0.43)
<i>Albuca flaccida</i>	45.5	0.0371* 0.458	7		15	0.10 (\pm 0.08)
<i>Aspalathus</i> sp.	110	0.000	17	0.02 (\pm 0.05)	13	0.03 (\pm 0.08)
<i>Babiana angustifolia</i>	1865.5	-0.996	80	0.62 (\pm 0.23)	52	0.95 (\pm 0.26)
<i>Berkheya armata</i>	123	-1.502	27	1.87 (\pm 0.74)	13	4.99 (\pm 2.01)
<i>Cotula turbinata</i>	209	-0.579	11		43	2.94 (\pm 1.37)
<i>Cyanella hyacinthoides</i>	397.5	-0.689	60	0.58 (\pm 0.37)	15	
<i>D. pluvialis</i>	75	0.363	15		11	3.34 (\pm 3.34)
<i>Felicia</i> sp.	405	-0.489	100	0.24 (\pm 0.09)	9	
<i>Heliophila</i> sp.	175.5	-0.215	9		41	0.19 (\pm 0.13)
<i>Moraea lewisae</i>	134	0.017	10	2.70 (\pm 1.8)	27	1.68 (\pm 0.62)
<i>Murhertia heisteria</i>	264	-0.291	13	>0.01 (\pm 0.00)	43	0.01 (\pm 0.01)
<i>Osteospermum tomentosum</i>	256	-0.287	30	2.62 (\pm 0.91)	18	2.71 (\pm 1.31)
<i>Senecio elegans</i>	186	-0.927	30	1.63 (\pm 0.62)	15	0.59 (\pm 0.25)
<i>Senecio</i> sp.	331.5	-0.098	52	0.20 (\pm 0.20)	13	

Mann-Whitney U tests used for differences between magnet and non-magnet plots.

Significant effects are marked (*P < 0.05; **P < 0.01).

For individual species the visitation index (VI = observed visits/area of floral display) was used as a measure of visitation frequency, to account for differences in floral display area.

Discussion

Attractiveness of floral patches

As hypothesised, anthophiles were more likely to occur and be active in areas of high floral density, although the effect of floral density varied between anthophile groups. This relationship may simply be a function of them optimising foraging by selecting areas with a high floral density (Hegland & Boeke 2006) so as to maximise rewards. For some species, plants with larger floral displays have been shown to contain more nectar, offering a greater reward for foragers (Frankie et al. 1983; Herrera 1985; Dafni 1991; Duffield et al. 1993; Inoue et al. 1995). Intraspecific studies have shown that individual plants that have more inflorescences, or those occurring in dense conspecific patches tend to receive more visits from pollinators (Goulson et al. 1998; Totland & Matthews 1998; Pickering 2001). Commonly occurring flowers may also receive more visits through frequency dependent effects (Dupont et al. 2003) which has been found in polymorphic flowers where the commonest morph receives a disproportionately high number of visits (Levin 1970; Levin 1972; Waser & Price 1981; 1983; Cresswell & Galen 1991). Similar patterns have been observed in mixed stands of flowers (Hegland & Totland 2005; Chapter 5, this dissertation; Hegland & Boeke 2006). These relationships may be variable (Grindeland et al. 2005), suggesting that other factors may also affect the attractiveness of floral patches to anthophiles. Assuming that anthophile activity (number of visits per plot) is correlated with anthophile density, it is implied that in the lowland Renosterveld community studied here, anthophiles are more abundant and diverse in areas with a high density and diversity of flowers. However, the effects of these two variables are difficult to separate as they are strongly correlated, as areas of high floral density tended to have more diverse floral resources (Figure 6.7).

The effects of plant community structure (i.e. differences in the relative abundances of different species in mixed floral stands) consistently affected both the likelihood of occurrence and activity of anthophiles in the plots. Although spatially distant plots were likely to have similar density and diversity of flowers (as shown by lack of spatial autocorrelation of these variables), they could be separated on the basis of their floral composition, which in turn affected the composition of the anthophile community observed in these plots (Figure 6.5). Syrphid flies for example, are a group that visits many different flowers (Kevan & Baker 1983), yet have been shown to exhibit constancy (Stanton 1987; Goulson & Wright 1998), as well as having innate preference for certain colours (Kay 1976; Lunau 1993; Lunau & Wacht 1994). If anthophiles were displaying constancy to certain floral forms or colours, even

in the short term, their distribution among floral patches would have been affected by diversity and floral composition, as well as by floral density. Because floral constancy can increase foraging efficiency, many insects focus their attention on one or a few species during a foraging bout (Goulson & Wright 1998; Gegear & Lavery 2001). Anthophile preference for certain flowers could explain the similar grouping of sites by plant community structure and anthophile visitation. This behaviour does not preclude foragers switching among species at low floral densities (Kunin 1993) which would result in a less distinct ordination of sites by anthophile presence in the plots rather than plant community structure as was the case in this study.

Effects of mass-flowering species

The two mass flowering species examined here, *R. fruticosa* and *S. chamaeleagnea*, were shown to be strong determinants of anthophile activity, greatly increasing visitation rates in the plots where they occurred, even though these plots showed, on average, a lower floral density and diversity. Visitation surveys in Chapter 5, found *S. chamaeleagnea* to be highly favoured by monkey beetles (Scarabaeidae: Rutelinae). High visitation rates by scarabs to this species in particular could explain the negative relationship between scarabs and floral diversity (Figure 6.2), as *S. chamaeleagnea* was highly favoured by scarabs in plots despite the relatively lower floral diversity in plots where it occurred. Beetles are often attracted to large or dense floral displays, approaching and landing on them from above (Kevan & Baker 1983), preferring to remain on the display moving but between inflorescences by walking rather than flying (pers. obs.). This behaviour would result in higher abundances on floral displays of this type than other anthophiles, which may only visit briefly.

Although plots where the two MF species occurred had much higher levels of anthophile activity than those without, additional visits were made primarily to whichever MF species was present. Neighbouring plants appeared not to benefit from any kind of magnet species effect, and may have been outcompeted for floral visitors and subsequently lower visitation rates per unit area of non MF-species in these plots. Ratchke (1983) proposed that visitation rates increase with increasing floral resources until anthophiles reach a saturation point, after which visitation decreases due to increased competition between individual plants for anthophiles (Goulson et al. 1998; Goulson 2000; Steven et al. 2003). So although mass flowering species, even as non-native commercial crops (Westphal et al. 2003) can enhance pollinator densities, these effects may not necessarily directly benefit neighbouring plant species through facilitative effects (e.g. Elliott & Irwin 2009) such as those demonstrated in other studies of magnet species effects (Lavery 1992;

Johnson et al. 2003; Ghazoul 2006). Although a significant decrease in visitation to the pooled, non-MF species per plot was shown, rather small sample sizes precluded proper comparison on a per species basis, so it was unfortunately not possible to determine which plant species were most affected.

Implications for conservation

My study shows the effects of short-term, small scale-factors on anthophile activity at the community level. Although these effects differed between various anthophile groups, resource availability plays a consistently important role. As with Hegland & Boeke (2006), there seems to be a general 'hotspot' response (sensu Thomson 1982) by pollinators to patches of favoured resources. This suggests that provided they are species rich and abundantly flowering (Ebeling et al. 2008), maintaining patches of natural or even semi-natural vegetation within the largely transformed lowlands of the CFR is beneficial for maintaining populations of flower visiting insects. Creating conservation headlands, such as wildflower rich field margins has been found to increase local pollinator densities in Europe (Feber et al. 1996; Dover 1997; Pywell et al. 2004; Pywell et al. 2005) and may be an effective means of enhancing habitat for anthophiles at the local scale, although natural remnants are likely to be of greater value than restored habitat (Kohler et al. 2008). On a broader scale efficacy of agri-environment schemes tends to be highly variable depending on their context (Kleijn & Sutherland 2003; Kleijn et al. 2006; Kohler et al. 2007). Patches of high quality habitat may provide useful stepping stones for arthropods in transformed landscapes (Duelli & Obrist 2003) but the scale at which such benefits occur is important. Kohler et al. (2008) found the beneficial effects of high quality habitats within farmland were spatially restricted extending <150 m into the surrounding matrix. This may reflect the very fine scale at which insects respond to environmental and habitat variables.

Landscape management directed approaches to biodiversity conservation operate broadly, at the level of entire communities, however, the conservation of more specialised plants and insects may require more directed efforts (and more directed investigation) given the variable response of different groups of anthophiles, particularly specialist species that may be more susceptible to fragmentation and area effects (Biesmeijer et al. 2006; Pauw 2007). The importance of providing high-quality habitats for pollinators within transformed landscapes is often emphasised, yet it is not always easy to define a 'high quality habitat'. Habitat quality of restored field margins and remnant habitats in agricultural lands is affected by local scale factors such as the density, diversity and community structure of floral resources within

patches (Dicks et al. 2002; Dauber et al. 2010). Landscape level effects such as the context of these patches within the surrounding matrix and the type of landuse on adjacent lands, will also affect the abundance and diversity of both plants and anthophiles in remnant habitats (Dauber et al. 2003; Dauber & Wolters 2004; Asteraki et al. 2004; Pywell et al. 2006; Boutin et al. 2008). My study shows that anthophile activity is affected by several very localised, small-scale factors, namely the density and diversity of flowers and composition of floral resources (community structure), which should be considered in management plans at the landscape scale. The results emphasise the importance of maintaining not only a high abundance, but also a high diversity of floral resources in habitat remnants for the conservation of anthophiles.

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The Cupreous Blue (*Eichochochrysops messapus messapus*) perched on a young renosterbos (*Elytropappus rhinocerotis*) shoot. Although both common species that occur widely across the lowlands of the Cape Floristic Region, they, along with many other species are becoming confined to increasingly transformed and fragmented natural habitats through the expansion and encroachment of agriculture and urban development.

S. Vrdoljak, 2004

7

Synthesis, and implications for conservation

Conservation in biodiversity hotspots is an important challenge facing conservation scientists and practitioners. By their definition, hotspots contain high levels of biodiversity, but have already undergone severe transformation and habitat loss (Myers et al. 2000). This means that, conservation targets are unlikely to be met by the existing coverage, particularly in region with high levels of endemism (Rodrigues & Gaston 2001), and options for expanding this coverage are limited. To meet these challenges we need to be able to integrate biodiversity and agricultural production to create multi-use ecoagricultural landscapes (Fischer et al. 2006; Samways 2007; Scherr & McNeely 2008). This is an outlook that encompasses not only the biodiversity value of protected areas, but also the range of natural and semi-natural remnants of natural habitat that exist within the transformed matrix.

In this dissertation, I have used flower visiting insects, a group which includes many ecologically and economically important pollinator species, to assess the value of these remnants for biodiversity conservation in the Cape Floristic Region (CFR). The body of work contained here covers a range of topics relevant to ecological survey techniques (Chapter 2), landscape and community ecology (Chapter 3), conservation planning and implementation (Chapter 4), and plant-insect interactions (Chapters 5 & 6). Ultimately, these topics share a common theme – a contribution towards insect conservation in the CFR. A summary of the main findings of the dissertation, and their implications for conservation is given in Box 1.

Insect conservation in the CFR is particularly challenging given our limited knowledge of the invertebrates of the region compared to better known groups such the flowering plants (Johnson 1992; Giliomee 2003). Species are the basic currency of biodiversity conservation. They are used to decide where to focus conservation efforts, what action should be taken, and to assess the success (or failure) of these efforts.

The first step in biodiversity conservation, involves assessing biodiversity itself. The limitations of time and resources make it impossible to compile complete species inventories. Much of the basic work upon which biodiversity conservation is built relies upon being able to extract a sample that is representative of the target community (Southwood & Henderson 2000). However, the inherent bias of any collecting technique affects its effectiveness and, subsequently, any ecological measures calculated from the samples.

Overall, pan trapping was an appropriate technique for the comparative studies that I undertook. Although this technique works well for collecting anthophiles among the Cape flora, the effect of colour preferences and the under representation of taxa such as butterflies are two sources of potential bias that would need to be considered when using pan trapping for

other studies. For census and inventory studies, it is advisable to augment pan trapping with other techniques to include rarer species or those excluded from pan traps.

Pan traps are a destructive sampling method that, under favourable conditions, can collect a very large number of individuals in a short time, which could be an important consideration when sampling intensively, over an extended time period or within very small habitat remnants. However, although the deleterious effect of such large-scale trapping on invertebrates is often mentioned, it remains to be properly tested. Nonetheless, it remains an important ethical consideration (Farnsworth & Rosovsky 1993) when undertaking any ecological study.

Given our incomplete knowledge of biodiversity, the concept of surrogacy is widely used in conservation planning. Surrogacy relies on the assumption that we can use one group of organisms to predict the diversity and distributions of another (Rodrigues & Brooks 2007). However, tests of surrogacy often produce contradictory results, leading to considerable debate as to the validity of the concept, with the result that it is unlikely any single taxon can be used as a universal predictor of the species richness of other taxa (Wolters et al. 2006).

The predominant focus of conservation planning in the CFR has been on the floral diversity for which the region is renowned. This is due largely to quality and coverage of botanical data available for the region, whereas other groups such as invertebrates are less well known. My study and others (Wright & Samways 1998; e.g. Proches & Cowling 2006; Proches et al. 2009) suggest that insects are proportionally as diverse as plants in the CFR. Knowledge of the congruence between patterns of plant and insect diversity provides an important basis for refining conservation planning, especially for functionally important groups such as insect pollinators. There is still much room for debate as to whether or not plant diversity is a reliable surrogate for insect diversity in the region. Proches et al. (2009) recently found a direct relationship between plant and insect diversity in certain cases, yet the results of my study suggest that overall, plant diversity was a poor spatial surrogate for anthophile diversity. Although patterns of plant diversity and distribution play a role in shaping pollinator assemblages and species turnover across a range of spatial scales in the CFR, this relationship is not straightforward. In spite of the congruence that can be observed in the patterns of diversity of plants and insects in the CFR, richness of plants does not necessarily imply richness of insects. It may be more productive to examine the factors driving these common patterns rather than attempting to substitute one group for another.

The interactions between plants and animals affect the structure and function of ecosystems at a wide range of spatial scales, affecting species distributions within localised patches all the way up to regional and global distributions. This has important implications for the scale at which conservation and management is applied, in order to maximise the limited resources available for biodiversity conservation. Much of the debate about the efficacy of agri-environment schemes in Europe centres around whether management is most effective at the field or landscape level (Kleijn & Sutherland 2003; Van Buskirk & Willi 2004; Kleijn & Baldi 2005; Kleijn et al. 2006).

We still know relatively little about what constitutes high quality habitat for anthophiles in the CFR, but human influenced changes to the landscape definitely affect plant and anthophile assemblages in the CFR (Donaldson et al. 2002; Colville et al. 2002; Gess & Gess 2004; Mayer 2004; Mayer et al. 2006; Pauw 2007). It seems that anthophile activity can be affected by localised, small scale factors such as the density, diversity and species composition of floral resources. Understanding how insects perceive their environment at a very fine scale can aid understanding of patterns observed at larger scales. Local scale effects can also determine how far the benefits of habitat management might extend into the agricultural matrix (Kohler et al. 2008).

The crux of this dissertation is the value of habitat remnants for biodiversity conservation in the CFR. Systematic conservation planning assigns value to a particular habitat based upon levels of threat and the irreplaceability. All of the field sites in this study were located in endangered or critically endangered vegetation types (Mucina & Rutherford 2006). This would imply that all remnants have value, although we would expect this value to degrade as remnants become smaller, invaded by alien plants and experience more environmental contamination from the transformed matrix. The biodiversity value of the transformed and semi-natural habitats of the CFR has, as yet, seldom been properly assessed. However, a few studies from the region do show that remnants within the matrix (Fabricius et al. 2003; Witt & Samways 2004; Boonzaaier 2006), cultivated botanical gardens (Pryke & Samways 2009) and even to some extent, exotic tree plantations (Ratsirarson et al. 2002) can retain many species. My comparison of sites outside and inside reserve areas shows that remnants and semi-natural habitats within the matrix can make a major contribution to the overall diversity of an area.

Biodiversity, as the number, types and interactions between organisms, determine a range of important ecosystem attributes such as resilience to change, resistance of invasion by alien organisms and how ecosystem properties and processes are maintained over space and time (Loreau et al.

2002). Population dynamics in communities are buffered in both the short and, presumably the long term by their diversity and complexity. These are the essential values of biodiversity that have made it an important currency in conservation. Although there is compelling evidence for the link between biodiversity and ecosystem function, Reiss et al. (2009) postulate that we should focus more on asking how biodiversity matters rather than whether it matters. Conceptually, this links well with the idea of integrating biodiversity conservation and agricultural production. To create functional agroecosystems, management decisions need to be backed by an understanding of underlying processes rather than just pattern. Showing that diversity can be maintained within transformed landscapes is only a starting point. From here we need to ask more fundamental questions about ecosystem function and resilience. Interaction webs of organisms, such as plants and their pollinators, may be more resilient than originally thought (Cane 2001; Memmott et al. 2004) but they still break down in the face of habitat transformation (e.g. Pauw 2007). Even in Europe where much conservation effort has been focused on setting aside land and reducing the effects of intensive agriculture pollinator declines continue. Pollinators are a particularly important component of agricultural biodiversity, both ecologically and economically, given their major role in most terrestrial ecosystems (Kevan 1991; Petanidou & Ellis 1996). In order to integrate sustainability into agricultural production “designer practices” that consider the ecological needs of managed and wild pollinators need to be a central theme in current and future agriculture (Kevan 2003). Ultimately, we need to find ways to soften the effects of transformation in agricultural land, facilitating important ecosystem processes and the movement of individuals and genes through the landscape, moving towards truly integrated ecoagricultural ecosystems.

Box 1 – Implications and recommendations for insect conservation in the Cape Floristic Region

Ecological survey techniques

Finding - Pan traps are an effective means of sampling major groups of flower visiting insects in the CFR, although the Lepidoptera were found to be underrepresented. The effects of trap colour are an important consideration in the design, implementation and interpretation of pan trap surveys of flower visiting insects among the Cape flora.

Recommendation – For monitoring and comparative studies, the use of at least three colours is recommended encompassing a range of wavelengths is recommended. Census and inventory studies would need to be augmented with other techniques to include taxa excluded from pan traps.

Landscape ecology

Finding - A high degree of spatial turnover at a range of spatial scales (0.5-80km) was apparent for plants and flower-visiting insects. Although there was some congruence between species turnover and assemblage similarity for both groups plant species richness is overall a poor spatial surrogate for flower visiting insects.

Recommendation – Patterns of plant diversity and distribution play a role in shaping assemblages of flower visiting insects but when considered alone, species richness is not reliable predictors and should be used with caution.

Plant-insect interactions

Finding – At the community level, floral visitation in mixed patches of flowers is affected more strongly by community traits such as the density, diversity and composition of floral patches than by traits specific to particular flowers.

Recommendation – Plant insect interactions do not take place in isolation and may be affected by the surrounding community. This can affect habitat quality for flower-visiting insects at a very fine spatial scale, and responses to these factors differ among taxa. The activity of flower visiting insects is affected by very localised, small scale factors that should be considered when managing small patches of habitat for pollinator conservation.

Conservation planning and implementation

Finding - Natural and semi-natural habitat remnants within the landscape mosaic make a major contribution to the overall biodiversity of the CFR, including species that may not be found in local nature reserves.

Recommendation – Successful biodiversity conservation, in the CFR should not take a binary reserves vs. matrix approach, but rather consider the entire landscape as a heterogeneous, ecoagricultural system. Stewardship programs and the conservation of remnants on privately owned land should be actively encouraged and supported.

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Appendices

Appendix 1 - Site descriptions

Study Sites

Table A1.1: Descriptions and locations of study sites used in reserve-remnant complementarity study

Site	Description	Location	Status	Veg Type*
Elandskloofberge – Elandsberg Private Nature Reserve and remnants on neighbouring Bartholomeusklip farm. (All sites within 3 km radius)				
EL1	Remnant adjacent to reserve. Surrounded by wheatfields	33.4482° S, 19.0272° E	Remnant	Swartland Shale Renosterveld ^{CR}
EL2	Old field on border of reserve	33.4438° S, 19.0291° E	Transformed	Swartland Alluvium Fynbos ^{CR}
EL3	Natural vegetation within reserve. BIOTA observatory site	33.448° S, 19.0474° E	Reserve	Swartland Shale Renosterveld ^{CR}
EL4	Remnant surrounded by wheatfields. Some disturbance by feral pigs	33.4536° S, 19.0162° E	Remnant	Swartland Shale Renosterveld ^{CR}
Helderberg Region – Helderberg Municipal Nature Reserve and remnants on nearby wine estates Cordoba and Vergelegen (All sites within 9 km radius)				
HE1	Firebreak on margin of reserve, adjacent to golf estate	34.059° S, 18.8772° E	Disturbed	Lourensford Alluvium Fynbos ^{CR}
HE2	Natural vegetation in within reserve	34.0618° S, 18.8749° E	Reserve	Lourensford Alluvium Fynbos ^{CR}
HE3	Natural vegetation on former plantation area	34.0573° S, 18.8676° E	Reserve	Cape Winelands Shale Fynbos ^{EN}
CO1	Former vineyard, replanted with natural vegetation	34.0334° S, 18.8488° E	Transformed	Cape Winelands Shale Fynbos ^{EN}
CO2	Fragment between current vineyards, moribund, with invasive grasses	34.0313° S, 18.856° E	Remnant	Cape Winelands Shale Fynbos ^{EN}
VG1	60 ha patch of largely intact renosterveld, adjacent to vineyards.	34.0948° S, 18.8974° E	Remnant	Swartland Shale Renosterveld ^{CR}
VG2	Area cleared of IAPs adjacent to vineyard. Recovering vegetation with invasive <i>Echium plantagenium</i> .	34.0886° S, 18.8935° E	Transformed	Swartland Shale Renosterveld ^{CR}
VG3	Old firebreak, 40 m wide with natural vegetation between dense stands of <i>Acacia mearnsii</i> .	34.0763° S, 18.923° E	Disturbed	Boland Granite Fynbos ^{EN}

Site	Description	Location	Status	Veg Type*
Groenlandberg Conservancy – Reserve site in section of the Hottentots Holland Provincial Nature Reserve and remnants on Diepkloof Private Nature Reserve and olive farm. (All sites within a 10 km radius)				
KL1	Large block of relatively undisturbed natural vegetation situated near Theewaterskloof dam	34.0546° S, 19.169° E	Reserve	Elgin Shale Fynbos ^{CR}
GB1	Relatively intact remnant adjacent to fallow wheat field.	34.1017° S, 19.2496° E	Remnant	W. Rûens Shale Renosterveld ^{CR}
GB2	Firebreak in area of moribund, <i>Elytropappus rhinocerotis</i>	34.1035° S, 19.2462° E	Disturbed	W. Rûens Shale Renosterveld ^{CR}
GB3	Disturbed, but recovering area of natural vegetation on ridge above farm.	34.1099° S, 19.2448° E	Transformed	W. Rûens Shale Renosterveld ^{CR}

* Vegetation type conservation status is indicated in superscript CR – Critically Endangered; EN – Endangered (Mucina & Rutherford 2006).

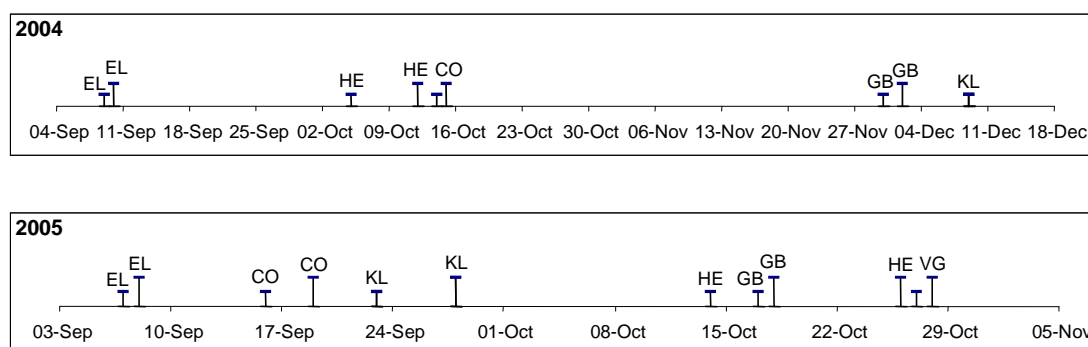


Figure A1.1 – Sampling timeline for the 2004 and 2005 seasons. Codes follow those used in the main text. CO – Cordoba Estate; GB – Groenlandberg Private Nature Reserve; HE – Helderberg Nature Reserve; KL – Klipfontein; VG – Vergelegen (not sampled in 2004).

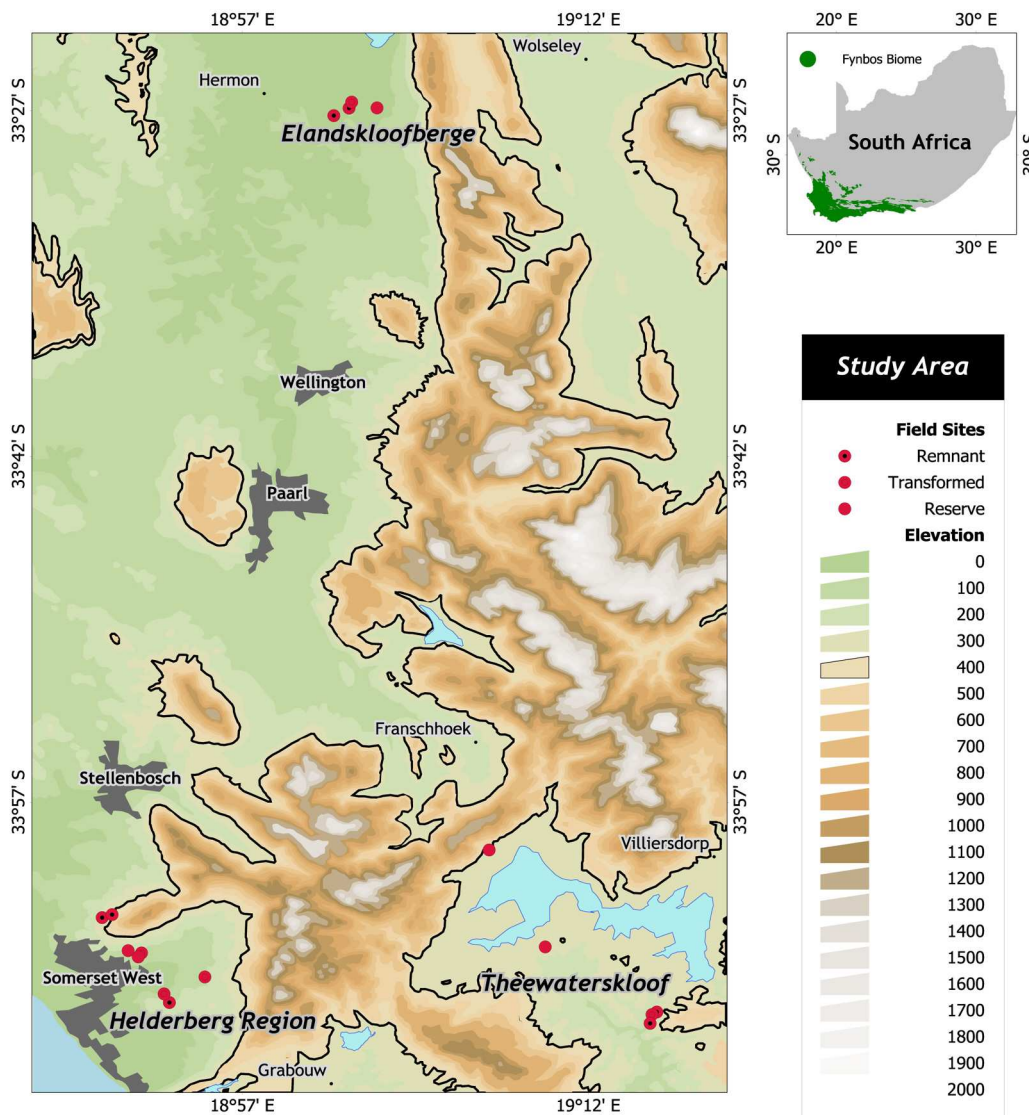


Figure A1.1 - Locations of study sites (red dots) in the lowlands of the CFR. Sites were grouped into three distinct localities, Elandskloofberge, Helderberg Region and Groenlandberg Conservancy, separated by distance or uplands (above 400 m a.s.l.). The 400 m contour line is marked in black.

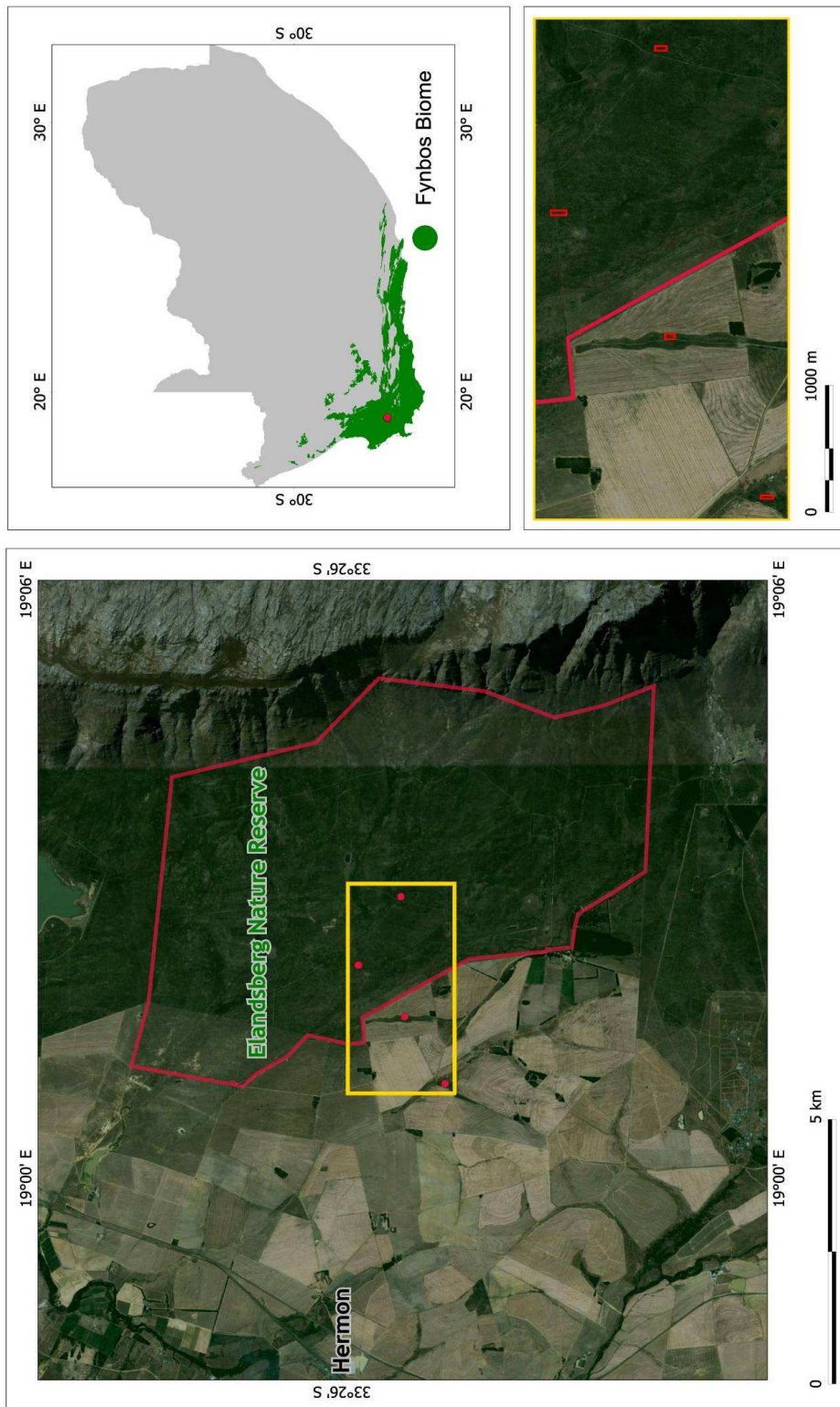


Figure A1.2 – Location of observation plots used for visitation surveys at Elandsberg Nature Reserve. Red dots on the main map show the location of the four study sites, two situated within the reserve and two in habitat remnants outside the reserve. The inset shows the extent of each site. Within each of the red blocks, five 2x2 m plots were placed at least 10 m apart.

Elandskloofberge

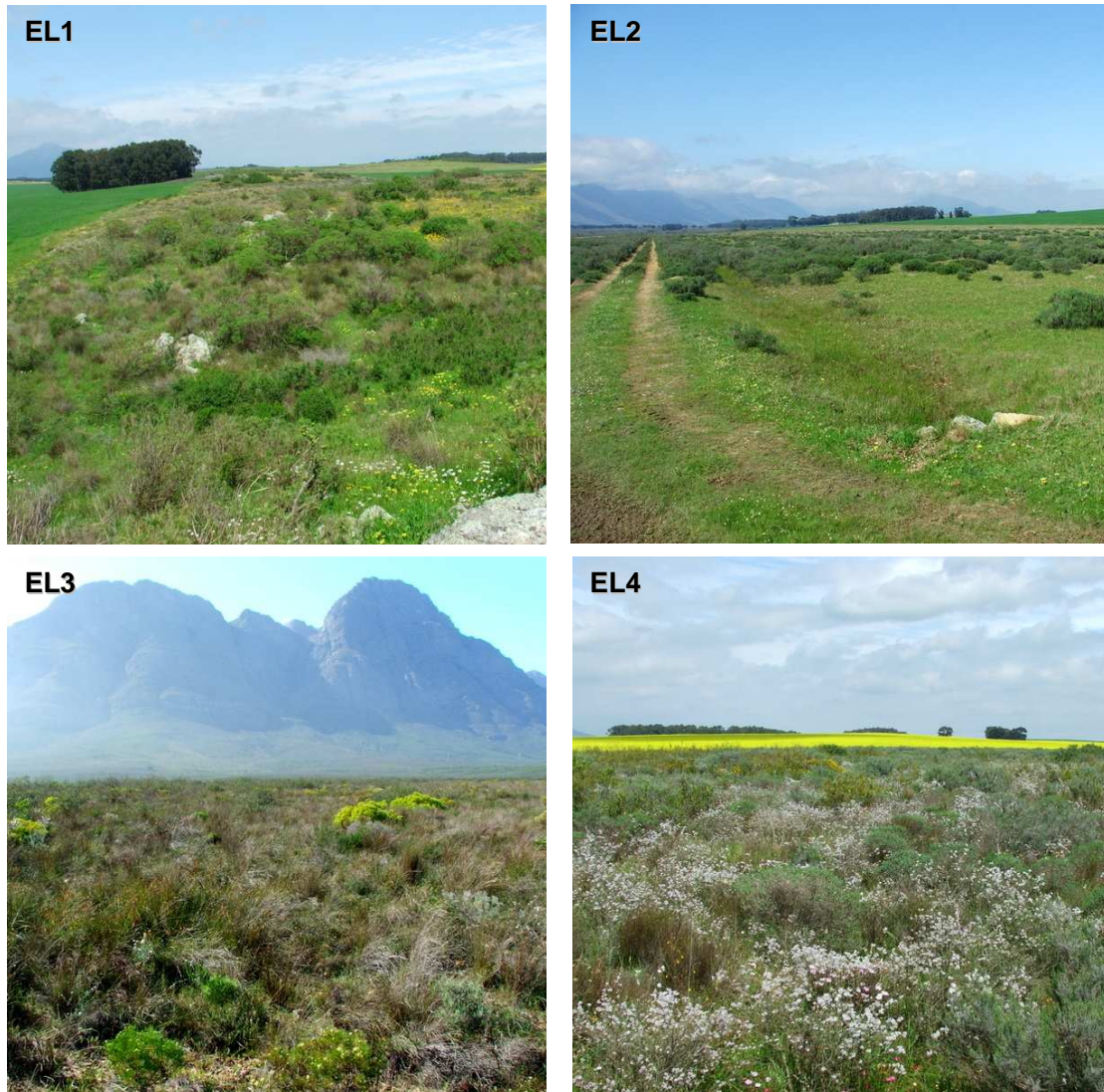


Figure A1.3 – Elandskloofberge study sites. EL1 and EL4 are remnant sites on Bartholomeusklip farm, surrounded by wheat and canola fields. EL2 is a recovering area on the edge of the reserve and EL3 lies within the reserve area.

Helderberg Region

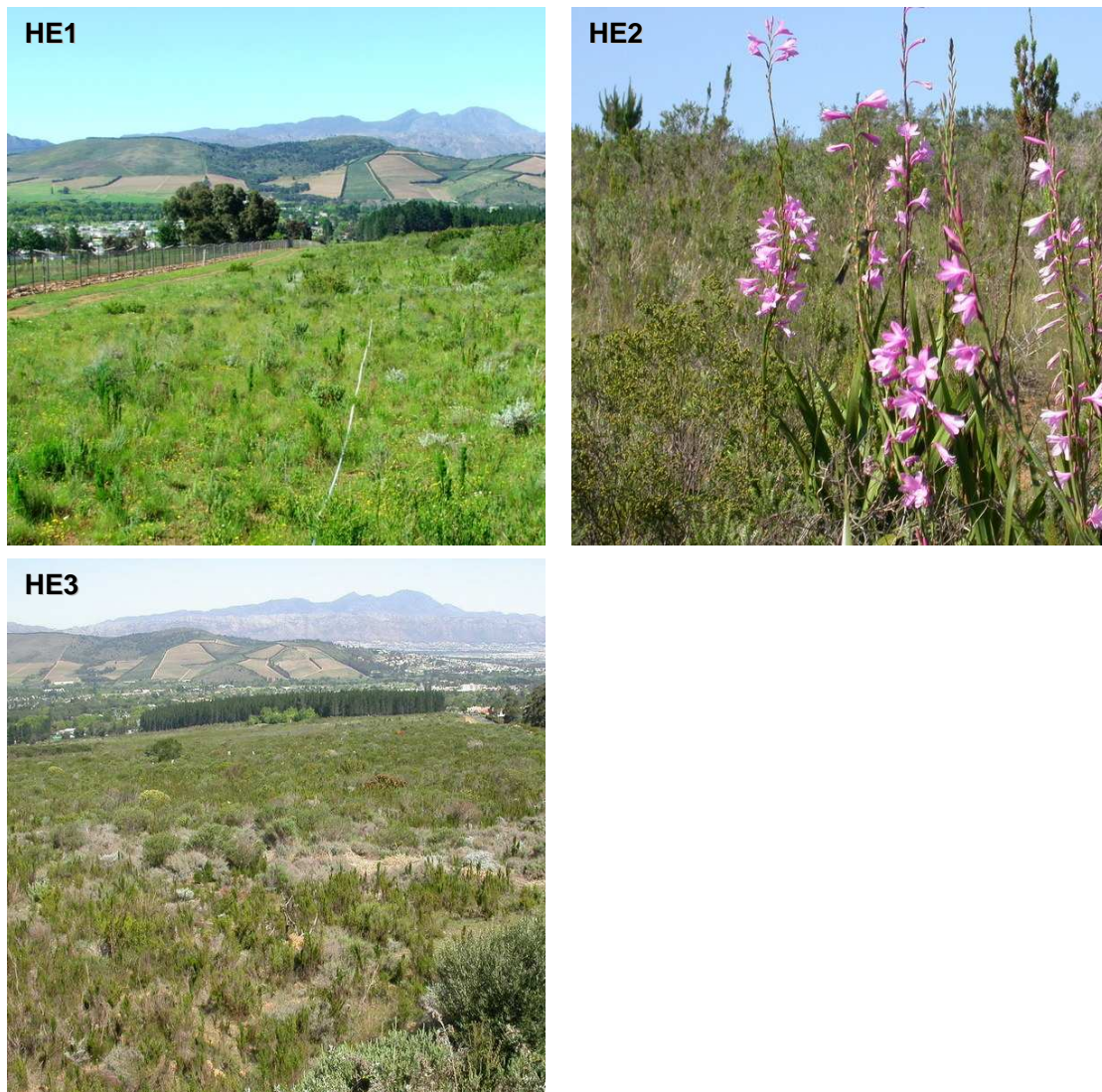


Figure A1.4 – Sites in Helderberg Nature Reserve. HE1 is an annually mowed firebreak on the eastern boundary of the reserve, adjacent to a golf course and housing development. HE2 and HE3 represent more natural areas of the reserve on the lower slopes of Helderberg mountain.

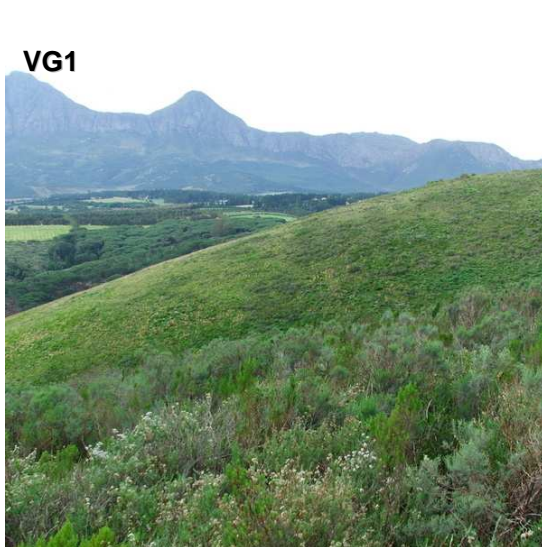


Figure A1.5 – Sites at Cordoba Estate and Vergelegen Estate, outside Helderberg Nature Reserve. CO1 is an abandoned vineyard that has been reseeded with fynbos plants. CO2 is a small fragment of partially transformed natural vegetation situated between vineyards. VG1 is a large patch of relatively undisturbed natural habitat. VG2 is a disturbed area recently cleared of IAPs adjacent to vineyards and VG3 a firebreak between pine plantations.

Groenlandberg Conservancy

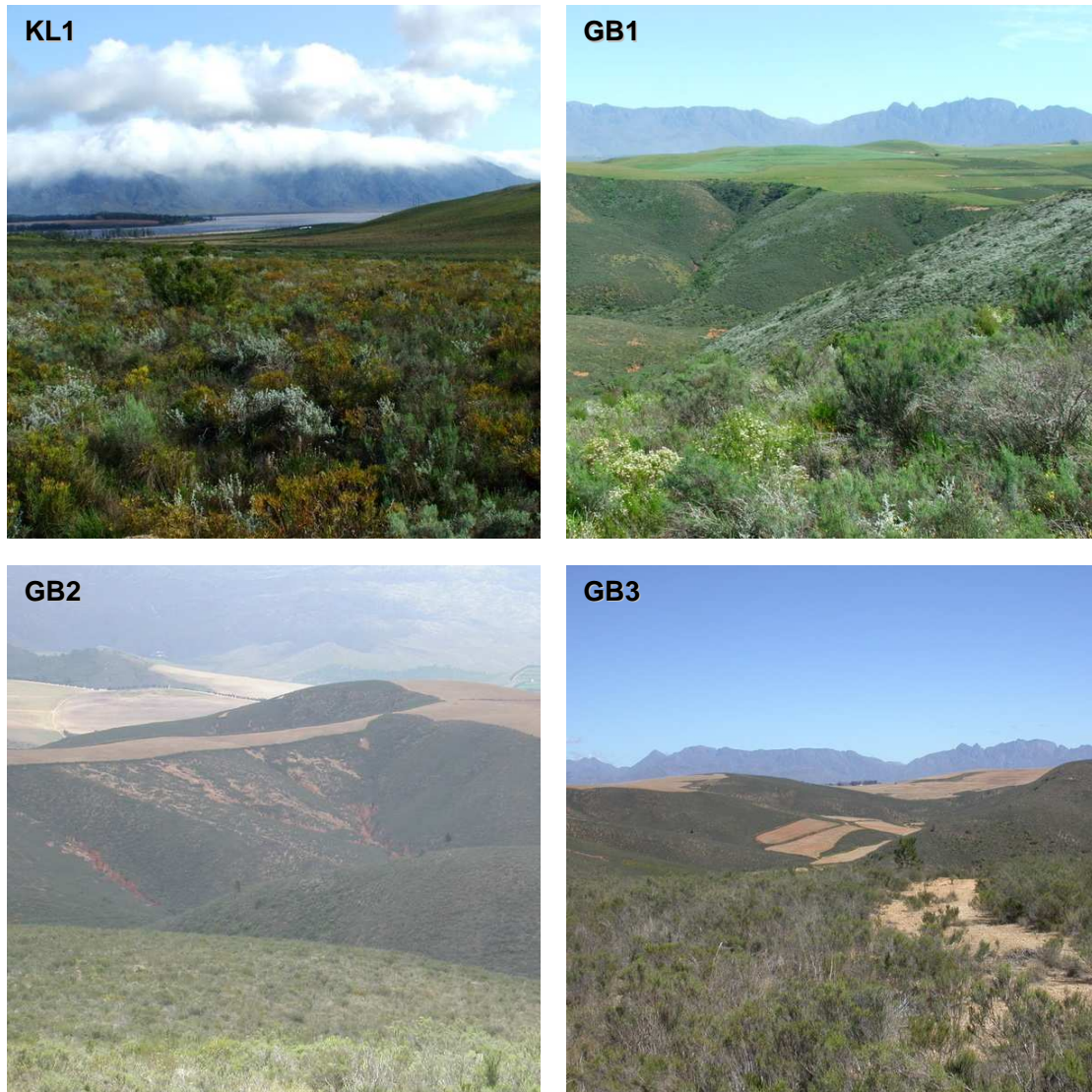


Figure A1.6 – Sites in the Groenlandberg region. KL1 is a portion of the Hottentotsholland Nature Reserve. GB1 is a relatively intact area of natural vegetation adjacent to a fallow field in the Diepklowe Private Nature Reserve. GB2 and GB3 are areas within the same reserve with more moribund, disturbed vegetation. In 2005, a firebreak was mowed in GB2, with plans for a controlled burn of a portion of the reserve, although it was unburnt at the time of sampling.

Appendix 2 - List of flower visiting insects recorded

Flower-visiting insects

Table A2.1 – List of flower-visiting insects recorded in pan-trap surveys of six sites in the lowlands of the Cape Floristic region. Further details of the sites can be found in the main text and Appendix 3.1. Colours indicate the colour pan-traps in which species were recorded (R = red; O = orange; Y = yellow; W = white; B = blue; V = violet). Arrangement of families follows that of Scholtz & Holm (2008).

Species/morphospecies	Sites	Colours					
		R	O	Y	W	B	V
DERMAPTERA							
Labiduridae							
Dermapteran sp.I	HE		•				
HEMIPTERA							
Reduviidae							
Reduviid	EL				•		•
<i>Rhinocoris</i> sp.	HE GB	•			•		
Coreidae							
<i>Acanthoria</i> cf. <i>muricata</i>	HE						•
Lygaeidae							
<i>Dieuches</i> sp.	CO HE GB VG	•	•	•	•	•	•
Lygaeid sp.I	HE GB	•					
<i>Pachygrontha</i> sp.	EL						•
Cydnidae							
<i>Plonisa plagiata</i>	HE			•			
Scutelleridae							
<i>Solenstethium lilligerum</i>	CO HE GB VG	•	•	•	•	•	•
Pentatomidae							
Pentatomid sp.I	EL VG	•	•				•
Cercopidae							
Cercopid sp.II	CO		•				
THYSANOPTERA							
Phlaeothripidae							
Phlaeothripid sp.I	CO EL HE KL GB VG	•	•	•	•	•	•
Thripidae							
Thripid sp.I	CO EL HE KL GB VG	•	•	•	•	•	•
COLEOPTERA							
Indet. Beetle							
Indet. Beetle sp.I	HE		•				
Indet. Beetle sp.II	EL					•	•
Carabidae							
<i>Abacetus minutus</i>	VG			•			
<i>Abacetus perturbator</i>	EL HE			•		•	•

	Species/morphospecies	Sites	Colours					
			R	O	Y	W	B	V
	<i>Cophosomorpha</i> sp.I	EL HE			•		•	•
Staphylinidae								
	Staphylinid sp.I	CO EL HE VG	•	•	•	•	•	•
Scarabaeidae								
	<i>Anisochelus inornatus</i>	EL	•	•	•	•	•	•
	<i>Anisonyx</i> sp.I	EL RU	•	•	•	•	•	•
	<i>Anisonyx ursus</i>	EL KL RU	•	•	•	•	•	•
	<i>Campulipis limbatus</i>	EL				•	•	•
	<i>Dichelus</i> sp.I							
	<i>Dichelus</i> sp.II	HE GB	•	•	•		•	
	<i>Dichelus</i> sp.III	HE			•			
	<i>Pachynema</i> sp.	GB VG		•	•	•		•
	<i>Cyrtothyrea marginalis</i>	HE RU	•	•	•	•		
	<i>Diaplochelus</i> sp.	CO HE GB VG	•	•	•	•		
	<i>Dichelus (Heterochelus) arthriticus</i>	CO HE KL GB VG	•	•	•	•	•	•
	<i>Dichelus (Heterochelus) ditus</i>	CO EL HE	•	•	•			
	<i>Dichelus (Heterochelus) forcipatus</i>	HE KL	•	•	•	•		
	<i>Dichelus (Heterochelus) hybridus</i>	GB	•		•			
	<i>Dichelus (Heterochelus) insignis</i>	VG					•	
	<i>Dichelus (Heterochelus) rufimanus</i>	HE GB VG	•	•	•	•	•	
	<i>Dichelus (Heterochelus) sp.</i>	GB RU			•	•	•	•
	<i>Dichelus (Ischnochelus) sulcatus</i>	EL	•	•		•	•	•
	<i>Dichelus cf. acanthropus</i>	CO EL HE RU	•	•	•	•		•
	<i>Dichelus cf. denticeps</i>	CO EL HE GB	•	•	•	•		•
	<i>Dichelus cf. detritus</i>	GB		•				
	<i>Dichelus</i> sp.I	CO EL HE KL VG	•	•	•	•	•	•
	<i>Dichelus</i> sp.II	CO EL HE KL VG	•	•	•	•	•	•
	<i>Dichelus</i> sp.III	CO EL HE KL RU	•	•	•	•	•	•
	<i>Dichelus villosus</i>	CO EL HE KL RU	•	•	•	•	•	•
	<i>Idutywa cf. collaris</i>	CO EL HE		•	•	•		
	<i>Kubousa axillaris</i>	CO EL GB VG	•	•	•	•	•	•
	<i>Kubousa gentilis</i>	EL VG	•	•			•	•
	<i>Lepithrix cf. ornatella</i>	CO EL HE VG	•	•	•	•	•	•
	<i>Lepithrix modesta</i>	EL KL	•	•		•		
	<i>Lepithrix</i> sp.I	EL HE KL			•	•		•
	<i>Lepithrix</i> sp.II	KL RU	•	•	•	•		•
	<i>Macrodicranocnemus andreaei</i>	EL KL	•	•	•	•	•	•
	<i>Monochelus elandsbergensis</i>	CO EL	•	•	•	•		
	<i>Omoctrates cf. cylindricus</i>	CO EL KL VG	•	•	•	•	•	
	<i>Omoctrates</i> sp.	CO EL KL VG	•	•	•	•	•	
	<i>Pachynema crassipes</i>	EL	•	•	•	•	•	•

Species/morphospecies	Sites	Colours					
		R	O	Y	W	B	V
<i>Pachynema saga</i>	GB	•	•	•	•		
<i>Peritrichia abdominalis</i>	CO EL HE KL VG	•	•	•	•	•	•
<i>Peritrichia cf. pistinaria</i>	CO HE KL GB VG	•	•	•	•	•	•
<i>Peritrichia pulchella</i>	EL KL	•	•	•	•	•	•
<i>Peritrichia sp.</i>	RU				•		
<i>Platychelus cf. caffer</i>	CO EL HE	•	•	•	•		
<i>Platychelus cf. karrooensis</i>	EL VG	•	•	•	•		
<i>Platychelus pyropygus</i>	CO EL HE	•	•	•	•	•	•
Rutelinid sp.I	EL HE GB	•	•	•		•	
Rutelinid II	EL VG	•	•	•	•		
Rutelinid sp.III	CO EL HE KL GB VG	•	•	•	•	•	•
Rutelinid sp.IV	GB RU			•	•	•	•
Rutelinid V	CO KL GB RU	•	•	•	•	•	•
Scarabaeid sp.I	HE				•	•	
Scarabaeid sp.II	EL					•	
<i>Trichostetha capensis</i>	HE				•		
<i>Trichostetha signata</i>	KL RU	•	•	•	•		•
Byrrhidae							
Byrrhid sp.I	EL HE KL VG	•	•	•	•	•	•
Byrrhid sp.II	HE GB				•	•	
Byrrhid sp.III	HE KL VG	•	•	•	•		
Byrrhid sp.IV	KL GB RU	•	•	•	•		
Buprestidae							
<i>Acmaeodera sp.I</i>	CO HE KL GB	•	•	•	•	•	•
<i>Acmaeodera sp.sp.II</i>	HE GB	•	•	•	•	•	
<i>Acmaeodera sp.III</i>	KL RU	•	•	•	•		
<i>Acmaeodera sp.IV</i>	EL HE	•	•				
<i>Acmaeodera sp.V</i>	CO EL HE VG	•	•	•	•	•	•
<i>Anthaxia barkeri</i>	HE RU	•	•	•	•		
<i>Anthaxia hilaris</i>	CO EL HE	•		•	•		
<i>Anthaxia holubi</i>	CO HE VG	•	•	•			
<i>Anthaxia tristis</i>	CO EL HE GB VG	•	•	•	•	•	•
<i>Nothomorpha sp.</i>	GB VG	•	•	•		•	•
<i>Sphenoptera sp.</i>	HE	•					
Elateridae							
<i>Aliteus adspersus</i>	EL			•			
Dermestidae							
Dermestid sp.I							
Dermestid sp.II	CO EL HE VG	•	•	•	•	•	•
Cleridae							
Cleriid sp.I	EL VG	•	•	•			

	Species/morphospecies	Sites	Colours					
			R	O	Y	W	B	V
	Cleriid sp.II	GB	•					
Melyridae								
	<i>Condylops aulicus</i>	CO EL HE KL VG	•	•	•	•	•	•
	<i>Dasytes costatipennis</i>	CO EL KL	•	•	•	•	•	•
	<i>Dasytes plumbeicolor</i>	EL HE GB VG	•	•	•	•	•	•
	<i>Dasytes rubrocupreus</i>	EL HE KL GB	•	•	•	•	•	•
	Melyrid sp.I	EL RU		•	•	•		
	<i>Melyris limbata</i>	GB				•		
	<i>Melyris nigra</i>	EL HE KL VG		•	•	•	•	•
	<i>Necrobia rufipes</i>	EL HE	•		•			
Coccinellidae								
	<i>Epilachna</i> sp.	CO			•			
	<i>Hippodamia variegata</i>	CO GB VG	•	•	•			
	<i>Liodalia flavomaculata</i>	HE			•			
Meloidae								
	<i>Ceroctis capensis</i>	CO EL HE KL RU	•	•	•	•	•	•
	<i>Ceroctis</i> cf. <i>capensis</i>	CO KL GB RU	•	•	•	•	•	•
	<i>Iselma</i> sp.I	EL			•			
	<i>Iselma</i> sp.II	EL			•			
	<i>Lytta nitidula</i>	CO HE	•	•	•	•	•	•
	Meloid sp.I	KL			•	•		
	Meloid sp.II							
	<i>Mylabris (Decatopoma) lunata</i>	CO HE VG	•	•	•		•	
	<i>Mylabris (Decatopoma)</i> sp.	GB					•	
	<i>Pagurodactylus angustulus</i>	EL VG						•
Cerambycidae								
	<i>Cerambycid</i>	EL HE			•	•	•	•
	<i>Promeces longiceps</i>	CO EL HE	•	•	•			
Chrysomelidae								
	Chrysomelid sp.I	CO EL HE	•	•	•	•		•
	Chrysomelid sp.II	CO EL HE GB	•	•	•	•	•	•
	Chrysomelid sp.III	CO EL HE GB	•	•		•	•	•
	Chrysomelid sp.IV	HE	•		•	•		
	Chrysomelid sp.V	CO EL	•	•	•	•	•	•
	<i>Creorane erythrocephala</i>	EL HE VG	•	•	•	•	•	
	<i>Eurysthenes</i> sp.	CO				•		
	<i>Exora</i> cf. <i>testacea</i>	CO VG				•		•
	<i>Exora</i> sp.	CO HE VG	•	•	•	•		
	<i>Pagurodactylus angustissimus</i>	CO EL HE KL GB VG	•	•	•	•	•	•
Curculionidae								
	Curculionid sp.I	EL HE	•		•	•		

	Species/morphospecies	Sites	Colours					
			R	O	Y	W	B	V
	Curculionid sp.II	CO HE KL VG			•	•	•	•
	Curculionid sp.III	HE			•			
DIPTERA								
	Indet. Dipteran	HE KL GB		•	•			
Bibionidae								
	<i>Bibio breviceps</i>	CO EL VG	•	•	•	•	•	•
	<i>Bibio</i> sp.	CO HE VG	•	•	•	•	•	•
	<i>Bibio turneri</i>	CO HE KL RU		•	•	•	•	•
	<i>Dilophus</i> sp.I	CO HE GB	•	•	•	•	•	•
	<i>Dilophus</i> sp.II	CO HE GB	•	•	•	•	•	•
Tabanidae								
	<i>Philoliche atricornis</i>	CO EL HE KL GB VG	•	•	•	•	•	•
Asilidae								
	Asilid sp.I	HE GB	•		•	•		
	Asilid sp.II	GB	•	•	•	•		
	<i>Neolophonotus</i> sp.	EL HE VG	•	•	•	•	•	•
Bombyliidae								
	<i>Austrolechus</i> cf. <i>hirtus</i>	KL			•			
	Bombyliid sp.I	EL						•
	Bombyliid sp.II	CO EL HE	•	•	•	•		
	Bombyliid sp.III	EL	•	•		•		
	Bombyliid sp.IV	EL	•	•	•	•		•
	<i>Parisus</i> sp.	CO				•		
	<i>Pthiria</i> sp.	KL GB		•	•	•	•	•
	<i>Systoechus</i> sp.I	EL RU	•	•	•	•		
	<i>Systoechus</i> sp.II	RU			•	•	•	
	<i>Systoechus</i> sp.III	EL RU	•		•	•		
	<i>Systoechus</i> sp.IV	EL RU	•	•	•	•		
Empididae								
	Empidid sp.I	CO		•	•	•		
	Empidid sp.II	CO EL		•	•	•	•	•
Dolichopodidae								
	Dolichopodid sp.I	VG	•	•			•	
Syrphidae								
	<i>Allograpta fuscotibialis</i>	CO EL		•	•	•		•
	<i>Eristalis</i> sp.							
	Syrphid sp.I	HE GB		•	•	•		
Tephritidae								
	Tephritid sp.I	EL HE			•	•		
	Tephritid sp.II	CO EL HE KL GB VG	•	•	•	•	•	•
Heleomyzidae								

Species/morphospecies	Sites	Colours					
		R	O	Y	W	B	V
Drosophilidae							
Heleomyzid sp.III	CO EL KL GB VG	•	•	•	•	•	•
Drosophilid sp.I	CO EL HE KL GB VG	•	•	•	•		•
Drosophilid sp.II	CO	•	•	•	•	•	
Scathophagidae							
<i>Scathophaga sercoraria soror</i>	CO EL HE KL GB VG	•	•	•	•	•	•
<i>Scathophaga</i> sp.	HE GB			•	•		
<i>Scathophaga stercoraria soror</i>	CO EL HE KL GB VG	•	•	•	•	•	•
Muscidae							
Muscid sp.I	GB		•				
Muscid sp.II	GB					•	•
<i>Phumosia</i> sp.	CO EL HE KL GB VG	•	•	•	•	•	•
Calliphoridae							
<i>Chrysoma albiceps</i>	GB		•	•	•	•	•
<i>Chrysomya chloropyga</i>	EL HE KL GB VG		•	•	•	•	•
<i>Cosmina</i> sp.	CO EL HE KL GB RU	•	•	•	•	•	•
<i>Phumosia</i> sp.	CO EL HE GB VG	•	•	•	•	•	•
Tachinidae							
<i>Gonia</i> cf. <i>bimaculata</i>	EL HE	•	•	•	•	•	•
<i>Linnaemya</i> sp.	VG						•
<i>Zygobothria</i> sp.	CO				•		
HYMENOPTERA							
Parasitoid wasp sp.I	RU			•			
Parasitoid wasp sp.II	EL HE GB			•	•	•	
Parasitoid wasp sp.III	CO			•	•		
Parasitoid wasp sp.IV	HE KL GB	•	•	•	•	•	•
Parasitoid wasp sp.V	CO EL HE KL GB VG	•	•	•	•	•	•
Parasitoid wasp sp.VI	HE KL			•			•
Tenthredinidae							
Tenthredinid sp.I	HE				•		
Tenthredinid sp.II	HE			•			
Ichneumonidae							
<i>Anomalon</i> sp.	RU	•					
Banchinaeid I	GB		•				
Campopleginaeid	GB						•
Creastinaeid	GB			•			
Cryptinaeid sp.I	HE			•			
Tersilochinaeid sp.I	CO	•					
Braconidae							
Braconid sp.I	CO HE				•		•

	Species/morphospecies	Sites	Colours					
			R	O	Y	W	B	V
	Braconid sp.II	EL				•		•
	Braconid sp.IV	GB			•			
	Braconid sp.V	HE	•					
	Microgasterinaeid	GB			•			
Scelionidae								
	Scelionid sp.I	RU		•				•
	Scelionid sp.II	CO EL HE VG	•	•	•	•	•	•
Megaspilidae								
	Megaspilid	EL						•
Platygasteridae								
	Platygasterid sp.I	KL GB	•		•	•	•	•
	Platygasterid sp.II	EL KL					•	•
	Platygasterid sp.III	CO EL HE KL GB RU	•	•	•	•	•	•
Figitidae								
	Charipinaeid							
	Eucoilinaeid sp.I	CO	•					
	Eucoilinaeid sp.II	HE						•
Chalcidae								
	Chalcid sp.I	HE			•			
Ormyridae								
	<i>Ormyrus</i> sp.	CO EL HE KL GB VG	•	•	•	•	•	•
Pteromalidae								
	Pteromalid sp.I	CO EL	•			•		
Eulophidae								
	Eulophid sp.I	EL HE GB	•			•	•	
Encyrtidae								
	Encyrtid sp.I	CO		•				
Bethylidae								
	Bethylid sp.I	KL			•	•		
	Bethylid sp.II	CO			•			
Tiphiidae								
	<i>Tiphia</i> sp.	KL GB	•	•	•	•		•
	Tiphiid sp.I	KL				•		•
	Tiphiid sp.II	EL GB	•	•	•	•		•
Pompilidae								
	Pompilid sp.I	CO HE GB		•	•	•		•
	<i>Pompiloides</i> cf. <i>decipens</i>	RU	•	•				
	<i>Pompiloides</i> sp.	GB		•				
	<i>Tachypompilus ignitus</i>							

	Species/morphospecies	Sites	Colours					
			R	O	Y	W	B	V
Vespidae								
	Masarinaeid sp.I	HE KL RU	•	•	•			
	Masarinaeid sp.II	GB	•					
	Masarinaeid sp.III							
Eumenidae								
	<i>Delta hottentotum</i>	VG					•	•
Sphecidae								
	<i>Podalonia</i> sp.							
Megachilidae								
	<i>Immanthium</i> cf. <i>junadi</i>	HE GB VG	•	•	•	•		
	Megachilid sp.I	GB VG				•	•	•
	Megachilid sp.II	CO HE				•	•	
	Megachilid sp.III	CO RU			•			•
Apidae								
	<i>Allodape</i> sp.	HE						•
	<i>Anthophora</i> cf. <i>diversipes</i>	EL KL GB VG	•	•	•	•	•	•
	<i>Anthophora</i> cf. <i>labrosa</i>	CO HE KL GB VG	•	•	•	•	•	•
	Apid sp.I	GB				•		
	Apid sp.II	GB						•
	Apid sp.III	CO EL HE	•	•	•	•		•
	Apid sp.IV	CO HE KL VG				•	•	•
	<i>Apis mellifera</i>	CO EL HE GB VG	•	•	•	•	•	•
	<i>Ceratina</i> cf. <i>aloës</i>	HE						•
	<i>Ctenoceratina</i> sp.	EL VG	•	•	•	•	•	•
	<i>Sphécodopsis</i> sp.	HE KL GB	•	•	•	•		
	<i>Sphécodopsis</i> sp.	CO HE GB	•	•		•		
Colletidae								
	<i>Scrapter</i> sp.	EL KL	•	•				
	Colletid sp.I	HE RU				•		•
	Colletid sp.II	GB						•
	<i>Polyglossa peringueyi</i>	EL				•		
Halictidae								
	<i>Ceratina</i> cf. <i>subquadrata</i>	CO HE KL			•	•	•	•
	cf. <i>Patellapis</i> sp.I	GB	•	•	•	•	•	•
	cf. <i>Patellapis</i> sp.II	HE KL GB RU	•		•	•	•	•
	Halictid sp.I	CO HE VG			•	•	•	•
	Halictid sp.II	EL			•			
	Halictid sp.III	KL GB				•	•	
	<i>Halictus andreniformis</i>	CO HE KL				•	•	•
	<i>Halictus</i> cf. <i>deceptus</i>	CO EL HE KL GB VG	•	•	•	•	•	•
	<i>Halictus</i> cf. <i>hotoni</i>	CO HE KL GB VG	•	•	•	•	•	•

	Species/morphospecies	Sites	Colours					
			R	O	Y	W	B	V
	<i>Halictus jucundus</i>	CO EL HE GB VG	•	•	•	•	•	•
	<i>Halictus vittatus</i>	CO GB	•		•	•	•	•
Melittidae								
	<i>Redivivoides</i> sp.	CO VG						•
	<i>Rediva</i> sp.	CO EL HE KL			•	•	•	•
Formicidae								
	<i>Formicid</i> sp.I	CO GB	•	•				
	<i>Formicid</i> sp.II	HE	•					

Appendix 3 - List of plant species recorded

Plants from sites in the lowlands of the Cape Floristic region. Further details of the sites can be found in the main text and Appendix 1. Aliens, are non-native plants, (indicated by ●). Threat status uses IUCN threatened species categories (CR – critically endangered, EN – Endangered, VU – vulnerable). All information is derived from SANBI online databases (South African National Biodiversity Institute 2007; 2009). Arrangement of families follows that of Germishuizen & Meyer (2003)

	Species	Sites	Alien	Threat Status
PTERIDOPHYTA				
Anemiaceae				
	<i>Mohria caffrorum</i> (L.) Desv.	HE		
GYMNOSPERMS				
Pinaceae				
	<i>Pinus pinea</i> L.	HE	●	
DICOTYLEDONS				
Aizoaceae				
	<i>Aizoon paniculatum</i> L.	EL		
	<i>Aizoon</i> sp.	VG		
Anacardiaceae				
	<i>Rhus angustifolia</i> L.	HE		
	<i>Rhus laevigata sensu</i> Thunb.	HE		
	<i>Rhus rosmarinifolia</i> Vahl	VG		
	<i>Rhus tomentosa</i> L.	CO		
Apiaceae				
	<i>Annesorhiza</i> sp	PH VG		
	<i>Arctopus echinatus</i> L.	CO KL PH VG		
	<i>Centella</i> sp	EL HE RU		
	<i>Itasina filifolia</i> (Thunb.) Raf.	EL		
	<i>Lichtensteinia</i> sp.	EL PH		
	<i>Torilis arvensis</i> (Huds.) Link	PH VG	●	
Apocynaceae				
	<i>Microlooma tenuifolium</i> (L.) K.Schum.	HE		
Asteraceae				
	<i>Arctotheca calendula</i> (L.) Levyns	EL HE		
	<i>Arctotheca</i> sp.	EL		
	<i>Arctotis incisa</i> Thunb.	EL		
	<i>Arctotis</i> sp.	KL		
	<i>Athanasia crenata</i> (L.) L.	HE		EN
	<i>Athanasia crithmifolia</i> (L.) L.	HE		
	<i>Athanasia trifurcata</i> (L.) L.	EL HE KL PH VG		
	<i>Berkheya armata</i> (Vahl) Druce	EL KL		

Species	Sites	Alien	Threat Status
<i>Berkheya barbata</i> (L.f.) Hutch.	VG		
<i>Berkheya herbacea</i> (L.f.) Druce	KL		
<i>Carduus</i> sp.	CO		
<i>Chrysanthemoides monilifera</i> L. (Norl.)	HE		
<i>Chrysocoma</i> sp.	PH		
<i>Conyza canadensis</i> (L.) Cronquist	CO HE VG	•	
<i>Corymbium</i> sp.	EL KL RU		
<i>Cotula</i> sp.	PH		
<i>Cotula turbinata</i> L.	EL HE PH VG		
<i>Dimorphotheca nudicaulis</i> (L.) DC.	VG		
<i>Dimorphotheca pluvialis</i> (L.) Moench	EL HE VG		
<i>Elytropappus rhinocerotis</i> (L.f.) Less	CO EL HE KL PH VG		
<i>Eriocephalus africanus</i> L.	EL PH VG		
<i>Euryops</i> sp.	RU		
<i>Felicia amoena</i> (Sch.Bip.) Levyns	EL		
<i>Felicia filifolia</i> (Vent.) Burtt Davy	PH VG		
<i>Felicia tenella</i> (L.) Nees	EL		
<i>Gazania serrata</i> DC.	EL		
<i>Gazania</i> sp.	KL VG		
<i>Gerbera</i> sp.	VG		
<i>Gorteria personata</i> L.	PH		
<i>Helichrysum asperum</i> (Thunb.) Hilliard & B.L.Burtt	EL PH VG		
<i>Helichrysum cymosum</i> (L.) D.Don	CO HE PH VG		
<i>Helichrysum dasyanthum</i> (Willd.) Sweet	CO HE		
<i>Helichrysum patulum</i> (L.) D.Don	CO HE KL PH VG		
<i>Helichrysum</i> sp.	EL HE KL PH VG		
<i>Helichrysum teretifolium</i> (L.) D.Don	KL VG		
<i>Hypochaeris radicata</i> L.	CO EL HE KL VG	•	
<i>Inuloides tomentosa</i> (L.f.) B.Nord.			
<i>Leysera gnaphalodes</i> (L.) L.	EL		
<i>Metalasia</i> sp.I	CO EL HE KL RU		
<i>Metalasia</i> sp.II	CO		
<i>Oedera</i> sp. L.	RU		
<i>Othonna</i> sp.	EL VG		
<i>Picris echioides</i> L.	CO		
<i>Printzia polifolia</i> (L.) Hutch.	PH		
<i>Pseudognaphalium luteo-album</i> (L.) Hilliard & B.L.Burtt	VG	•	
<i>Relhania fruticosa</i> (L.) K.Bremer	EL		

	Species	Sites	Alien	Threat Status
	<i>Relhania</i> sp.	PH		
	<i>Senecio elegans</i> L.	EL		
	<i>Senecio hastatus</i> L.	HE VG		
	<i>Senecio pterophorus</i> DC.	CO VG		
	<i>Senecio puberulus</i> DC.	CO		
	<i>Senecio pubigerus</i> L.	CO HE KL PH VG		
	<i>Senecio</i> sp.	PH		
	<i>Senecio</i> sp.	EL PH		
	<i>Senecio thunbergii</i> Harv.	EL		
	<i>Sonchus asper</i> (L.) Hill	CO	•	
	<i>Sonchus oleraceus</i> L.	CO PH	•	
	<i>Sonchus</i> sp.	VG	•	
	<i>Stoebe capitata</i> P.J.Bergius	EL		
	<i>Stoebe cinerea</i> Thunb.	CO		
	<i>Stoebe plumosa</i> (L.) Thunb.	CO EL HE KL VG		
	<i>Stoebe</i> sp.	HE KL RU VG		
	<i>Tripteris clandestina</i> Less.	EL		
	<i>Tripteris tomentosa</i> (L.f.) Less	EL		
	<i>Ursinia anthemoides</i> Poir.	EL HE KL PH VG		
	<i>Ursinia discolor</i> (Less.) N.E.Br.	VG		
	<i>Ursinia</i> sp.	PH		
	<i>Ursinia</i> sp.	HE		
Boraginaceae	<i>Echiostachys incanus</i> (Thunb.) Levyns	EL		VU
	<i>Echium plantagineum</i> L.	VG		
	<i>Lobostemon argenteus</i> (P.J.Bergius) H.Beuk	EL VG		
	<i>Lobostemon glaber</i> (Vahl) H.Beuk	EL		
Brassicaceae	<i>Heliophila macrosperma</i> Burch. Ex DC.	EL		
	<i>Heliophila</i> sp. L.	PH		
Campanulaceae	<i>Merciera</i> sp.	KL VG		
	<i>Microcodon</i> sp.	KL		
	<i>Wahlenbergia capensis</i> (L.) A.DC.	EL HE VG		
Caryophyllaceae	<i>Cerastium capense</i> Sond.	EL		
	<i>Petrorhagia prolifera</i> (L.) Ball & Heywood	VG		
	<i>Polycarpon tetraphyllum</i> (L.) L.	EL	•	
	<i>Silene gallica</i> L.	CO EL	•	
Chenopodiaceae	<i>Atriplex semibaccata</i> R.Br.	PH		
Convolvulaceae				

	Species	Sites	Alien	Threat Status
	<i>Convolvulus capensis</i> Burm.f.	EL		
Crassulaceae				
	<i>Crassula capensis</i> (L.) Baill.	KL PH		
	<i>Crassula ciliata</i> L.	PH		
	<i>Crassula fascicularis</i> Lam.	VG		
	<i>Crassula glomerata</i> P.J.Bergius	EL		
	<i>Crassula</i> sp.	KL		
Dipsacaceae				
	<i>Scabiosa</i> sp.	PH		
Droseraceae				
	<i>Drosera cistiflora</i> L.	EL KL		
	<i>Drosera pauciflora</i> Banks. Ex DC.	EL KL		
	<i>Drosera trinervia</i> Spreng.	EL HE		
Ebenaceae				
	<i>Diospyros glabra</i> (L.) De Winter	KL		
Ericaceae				
	<i>Erica imbricata</i> L.	HE RU		
	<i>Erica paniculata</i> L.	KL		
	<i>Erica parviflora</i> L.	HE		
	<i>Erica plukenetii</i> L.	HE		
	<i>Erica</i> sp.I	HE RU		
	<i>Erica</i> sp.II	KL RU		
	<i>Erica sphaeroidea</i> Dulfer	HE		
Euphorbiaceae				
	<i>Clutia</i> sp.	PH VG		
	<i>Euphorbia erythrina</i> Link	EL VG		
	<i>Euphorbia</i> sp.	CO EL PH VG		
Fabaceae				
	<i>Acacia mearnsii</i> De Wild	VG	•	
	<i>Acacia saligna</i> (Labil.) H.L.Wendl.	CO	•	
	<i>Aspalathus aculeata</i> Thunb.	EL		
	<i>Aspalathus attenuata</i> R.Dahlgren	EL		EN
	<i>Aspalathus cephalotes</i> Thunb.	PH VG		
	<i>Aspalathus cordata</i> R.Dahlgren	VG		
	<i>Aspalathus ericifolia</i> L.	VG		
	<i>Aspalathus hispida</i> Thunb.	HE		
	<i>Aspalathus</i> sp.I	EL KL PH VG		
	<i>Aspalathus</i> sp.II	HE		
	<i>Aspalathus spinosa</i> L.	VG		
	<i>Aspalathus tridentata</i> L.	EL		
	<i>Indigofera</i> sp.I	PH		
	<i>Indigofera</i> sp.II	CO PH VG		
	<i>Lotononis involucrata</i> s. <i>involucrata</i> (P.J.Bergius) Benth.	VG		VU
	<i>Lotus</i> sp.	CO HE		

	Species	Sites	Alien	Threat Status
	<i>Medicago sativa</i> L.	EL		
	<i>Medicago</i> sp.	HE VG		
	<i>Otholobium decumbens</i> (Aiton) C.H.Stirt.	HE		
	<i>Otholobium hirtum</i> (L.) C.H.Stirt	CO		
	<i>Podalyria biflora</i> Lam.	VG		
	<i>Priestleya</i> sp.	KL		
	<i>Psoralea laxa</i> T.M.Salter	HE		
	<i>Rafnia</i> sp. Thunb.	VG		
	<i>Sutherlandia frutescens</i> (L.) R.Br.	PH		
	<i>Trifolium angustifolium</i> L.	CO	•	
	<i>Vicia</i> sp.	HE PH	•	
Gentianaceae				
	<i>Chironia baccifera</i> L.	CO HE PH		
	<i>Sebaea albens</i> (L.f.) Roem. & Schult.	EL		
	<i>Sebaea exacoides</i> (L.) Schinz	KL PH VG		
	<i>Sebaea</i> sp. Sol. Ex R.Br.	CO HE PH VG		
Geraniaceae				
	<i>Erodium botrys</i> (Cav.) Bertol.	EL		
	<i>Geranium</i> sp.	CO		
	<i>Monsonia speciosa</i> L.	VG		EN
	<i>Pelargonium chamaedryfolium</i> Jacq.	HE PH		
	<i>Pelargonium elongatum</i> (Cav.) Salsib.	CO KL PH VG		
	<i>Pelargonium myrrhifolium</i> (L.) L'Hér.	CO KL VG		
	<i>Pelargonium pinnatum</i> (L.) L'Hér.	VG		
	<i>Pelargonium rapaceum</i> (L.) L'Hér.	VG		
	<i>Pelargonium</i> sp.	EL KL		
	<i>Pelargonium triste</i> (L.) L'Hér.	KL VG		
Lamiaceae				
	<i>Salvia chamelaeagnea</i> P.J.Bergius	EL		
Lauraceae				
	<i>Cassytha ciliolata</i> Nees	EL		
Lobeliaceae				
	<i>Cyphia bulbosa</i> (L.) P.J.Bergius	EL		
	<i>Cyphia phyteuma</i> (L.) Willd.	HE KL		
	<i>Cyphia</i> sp.	PH		
	<i>Cyphia volubilis</i> (Burm.f.) Willd.	EL HE KL PH		
	<i>Lobelia erinus</i> L.	HE VG		
Malvaceae				
	<i>Hermannia cuneifolia</i> Jacq.	PH		
	<i>Hibiscus aethiopicus</i> L.	VG		
Mesembryanthemaceae				
	<i>Antimima</i> sp.	EL		
	<i>Dorotheanthus bellidiformis</i> (Burm.f.) N.E.Br.	EL		
	<i>Erepsia</i> sp.	EL		
	<i>Lampranthus elegans</i> (Jacq.) Schwantes	EL		

	Species	Sites	Alien	Threat Status
	<i>Lampranthus scaber</i> (L.) N.E.Br.	EL		EN
	<i>Lampranthus</i> sp.	VG		
	<i>Lampranthus spiniformis</i> (Haw.) N.E.Br.	EL		
	<i>Phyllobolus</i> sp.	PH		
	<i>Ruschia</i> sp.	PH		
Molluginaceae				
	<i>Adenogramma</i> sp.	EL		
	<i>Limeum africanum</i> L.	EL		
	<i>Polypoda stipulacea</i> (F.M.Leight.) Adamson	EL		
Montinaceae				
	<i>Montinia caryophyllacea</i> Thunb.	HE KL		
Orobanchaceae				
	<i>Orobanche ramosa</i> L.	VG	•	
Oxalidaceae				
	<i>Oxalis adspersa</i> Eckl. & Zeyh.	EL		
	<i>Oxalis commutata</i> Sond.	EL KL RU		
	<i>Oxalis flava</i> L.	KL PH		
	<i>Oxalis glabra</i> Thunb.	EL HE KL		
	<i>Oxalis hirta</i> L.	EL		
	<i>Oxalis lanata</i> L.f.	HE		
	<i>Oxalis livida</i> Jacq.	EL KL PH		
	<i>Oxalis monophylla</i> L.	EL		
	<i>Oxalis obtusa</i> Jacq.	EL KL PH		
	<i>Oxalis pes-caprae</i> L.	EL HE VG		
	<i>Oxalis polyphylla</i> Jacq.	EL KL		
	<i>Oxalis purpurea</i> L.	EL HE KL PH		
		VG		
	<i>Oxalis</i> sp.	EL RU		
	<i>Oxalis tenuifolia</i> Jacq.	VG		
Plantaginaceae				
	<i>Plantago lanceolata</i> L.	CO HE VG		
Polygalaceae				
	<i>Muraltia heisteria</i> (L.) DC.	EL		
	<i>Muraltia</i> sp.	HE		
	<i>Muraltia trinervia</i> (L.f.) DC.	EL PH		
	<i>Polygala bracteolata</i> L.	VG		
	<i>Polygala scabra</i> L.	PH		
Polygonaceae				
	<i>Rumex cordatus</i> Poir.	EL		
Primulaceae				
	<i>Anagallis arvensis</i> L.	CO HE PH VG		

	Species	Sites	Alien	Threat Status
Proteaceae	<i>Leucadendron corymbosum</i> P.J.Bergius	EL		VU
	<i>Leucadendron lanigerum</i> H.Beuk. ex Meisn.	EL		EN
	<i>Leucadendron salignum</i> P.J.Bergius	HE KL VG		
	<i>Leucadendron</i> sp.	RU		
	<i>Leucospermum gueinzii</i> Meisn.	CO		EN
Rosaceae	<i>Cliffortia polygonifolia</i> L.	CO HE		
	<i>Cliffortia ruscifolia</i> L.	HE		
	<i>Cliffortia</i> sp.	RU		
Rubiaceae	<i>Anthospermum aethiopicum</i> L.	VG		
	<i>Anthospermum galioides</i> Rchb.	HE		
	<i>Anthospermum spathulata</i> Spreng.	EL HE PH VG		
	<i>Galium</i> sp.	KL PH RU		
Rutaceae	<i>Agathosma betulina</i> (P.J.Bergius) Pillans	HE		VU
	<i>Agathosma</i> sp. Willd.	PH		
	<i>Diosma hirsuta</i> L.	HE VG		
	<i>Diosma pedicellata</i> I.Williams	EL		
	<i>Diosma</i> sp.	RU		
Santalaceae	<i>Thesium</i> sp.	HE KL VG		
Scrophulariaceae	<i>Diascia elongata</i> Benth.	PH VG		
	<i>Dischisma arenarium</i> E.Mey.	EL		
	<i>Dischisma capitatum</i> (Thunb.) Choisy	EL		
	<i>Dischisma</i> sp.	VG		
	<i>Nemesia</i> sp.	PH VG		
	<i>Polycarena galioides</i> Benth.	EL		
	<i>Selago fruticosa</i> L.	PH		
	<i>Selago</i> sp.	RU		
	<i>Zaluzianskya divaricata</i> (Thunb.) Walp.	PH VG		
Thymelaeaceae	<i>Gnidia laxa</i> (L.f.) Gilg	HE		
	<i>Gnidia</i> sp.	PH		
	<i>Gnidia</i> sp.	HE KL VG		
	<i>Passerina vulgaris</i> (Meisn.) Thoday	HE		
	<i>Struthiola dodecandra</i> (L.) Druce	VG		
	<i>Struthiola</i> sp.	RU		
Zygophyllaceae	<i>Zygophyllum sessilifolium</i> L.	EL VG		
MONOCTYLEDONS				

	Species	Sites	Alien	Threat Status
Amaryllidaceae	<i>Gethyllis</i> sp.	VG		
Anthericaceae	<i>Chlorophytum undulatum</i> (Jacq.) Oberm.	EL		
Asparagaceae	<i>Asparagus capensis</i> L.	PH		
Asphodelaceae	<i>Bulbine praemorsa</i> (Jacq.) Spreng.	VG		
	<i>Bulbinella</i> sp. Kunth	RU		
	<i>Trachyandra flexifolia</i> (L.f.) Kunth	EL		
	<i>Trachyandra hirsuta</i> (Thunb.) Kunth	HE		
	<i>Trachyandra muricata</i> (L.f.) Kunth	VG		
	<i>Trachyandra revoluta</i> (L.) Kunth	EL		
	<i>Trachyandra</i> sp.	VG		
Colchicaceae	<i>Androcymbium</i> sp.	PH		
	<i>Baeometra uniflora</i> (Jacq.) G.J.Lewis	HE VG		
	<i>Wurmbea recurva</i> B.Nord.	EL VG		
Cyperaceae	<i>Ficinia indica</i> (Lam.) Pfeiff.	EL KL VG		
	<i>Ficinia nigrescens</i> (Schrad.) J.Raynal	VG		
	<i>Ficinia</i> sp.I	HE		
	<i>Ficinia</i> sp.II.	CO EL HE KL PH RU		
	<i>Isolepis</i> sp.	CO HE		
	<i>Isolepis verrucosula</i> (Steud.) Nees	EL		
	<i>Tetraria</i> sp.	RU		
	<i>Tetraria ustulata</i> (L.) C.B.Clarke	HE VG		
Eriospermaceae	<i>Eriospermum capense</i> (L.) Thunb.	VG		
	<i>Eriospermum</i> sp. Jacq. Ex Willd	EL VG		
Haemodoraceae	<i>Wachendorfia paniculata</i> Burm.	EL KL		
	<i>Wachendorfia</i> sp.	EL		
Hyacinthaceae	<i>Albuca juncifolia</i> (Hilliard & B.L.Burtt)	EL		
	<i>Albuca</i> sp.	EL VG		
	<i>Drimia capensis</i> (Burm.f.) Wijnlands	PH		
	<i>Drimia physodes</i> (Jacq.) Jessop	EL		
	<i>Lachenalia contaminata</i> Aiton	EL		
	<i>Lachenalia pallida</i> Aiton	EL		
	<i>Lachenalia polyphylla</i> Baker	EL		
	<i>Lachenalia</i> sp.	EL VG		
	<i>Lachenalia unifolia</i> Jacq.	EL		

	Species	Sites	Alien	Threat Status
	<i>Ornithogalum hispidum</i> Hornem	KL RU		
	<i>Ornithogalum</i> sp.	PH		
	<i>Ornithogalum thyrsoides</i> Jacq.	EL PH VG		
Hypoxidaceae				
	<i>Empodium plicatum</i> (Thunb.) Garside	EL		
	<i>Empodium</i> sp.	VG		
	<i>Spiloxene capensis</i> (L.) Garside	EL		
	<i>Spiloxene</i> sp.	HE PH		
Iridaceae				
	<i>Babiana</i> sp.	EL KL VG		
	<i>Bobartia</i> sp.	HE RU VG		
	<i>Ferraria</i> sp. Burm. ex Mill.	EL		
	<i>Geissorhiza aspera</i> Goldblatt	EL HE KL PH		
	<i>Geissorhiza imbricata</i> (D.Delaroche) Ker Gawl.	EL		
	<i>Geissorhiza</i> sp.	EL PH RU		
	<i>Gladiolus alatus</i> L.	EL		
	<i>Gladiolus carneus</i> D.Delaroche	VG		
	<i>Gladiolus</i> sp.	KL RU		
	<i>Hesperantha falcata</i> (L.f.) Ker Gawl.	HE VG		
	<i>Hesperantha pilosa</i> (L.f.) Ker Gawl.	EL		
	<i>Hesperantha radiata</i> (Jacq.) Ker Gawl.	PH		
	<i>Hesperantha</i> sp.	RU		
	<i>Ixia lutea</i> Eckl.	EL		
	<i>Ixia</i> sp.	PH VG		
	<i>Lapeirousia azurea</i> (Eckl. ex Baker) Goldblatt	EL		
	<i>Lapeirousia</i> sp.	VG		
	<i>Micranthus alopecuroides</i> (L.) Rothm.	HE VG		
	<i>Micranthus junceus</i> (Baker) N.E.Br.	KL		
	<i>Micranthus tubulosus</i> (Burm.) N.E.Br.	EL KL VG		
	<i>Moraea angusta</i> (Thunb.) Ker Gawl.	VG		
	<i>Moraea bituminosa</i> (L.f.) Ker Gawl.	VG		
	<i>Moraea galaxia</i> (L.f.) Goldblatt & J.C.Manning	EL KL PH VG		
	<i>Moraea inconspicua</i> Goldblatt	PH VG		
	<i>Moraea lewisiae</i> (Goldblatt) Goldblatt	EL		
	<i>Moraea</i> sp.	EL HE KL PH RU VG		
	<i>Moraea tricuspida</i> (L.f.) G.J.Lewis	HE		
	<i>Moraea tripetala</i> (L.f.) Ker Gawl.	RU		
	<i>Moraea umbellata umbellata</i>	EL		
	<i>Moraea villosa</i> s. <i>villosa</i> (Ker Gawl.) Ker Gawl.	EL		
	<i>Romulea</i> sp.	EL RU		

	Species	Sites	Alien	Threat Status
	<i>Sparaxis</i> sp.	KL PH		
	<i>Tritonia crispera</i> (L.f.) Ker Gawl.	VG		
	<i>Tritonia</i> sp.	PH VG		
	<i>Watsonia</i> sp.	HE VG		
Juncaceae				
	<i>Juncus cephalotes</i> Thunb.	EL		
Orchidaceae				
	<i>Corycium orobanchoides</i> (L.f.) Sw.	VG		
	<i>Disa bracteata</i> Sw.	HE		
	<i>Disperis</i> sp.	PH		
	<i>Disperis villosa</i> (L.f.)	EL		
	<i>Holothrix</i> sp. Rich. Ex Lindl.	PH VG		
	<i>Holothrix villosa</i> Lindl.	RU		
	<i>Pterygodium alatum</i> (Thunb.) Sw.	EL KL		
	<i>Pterygodium catholicum</i> (L.) Sw.	HE KL PH		
	<i>Satyrium</i> sp.	RU		
Poaceae				
	<i>Aira cupaniana</i> Guss.	KL PH VG		
	<i>Avena barbata</i> Pott ex Link	HE		
	<i>Avena</i> sp.	CO		
	<i>Brachypodium distachyon</i> (L.) P.Beauv.	HE PH		
	<i>Briza maxima</i> L.	CO EL HE PH VG	•	
	<i>Briza minor</i> L.	EL HE VG	•	
	<i>Bromus molliformis</i>	CO HE	•	
	<i>Bromus pectinatus</i> Thunb.	HE PH		
	<i>Bromus rigidus</i> Roth.	HE	•	
	<i>Bromus</i> sp.	HE		
	<i>Cymbopogon marginatus</i> (Steud.) Stapf ex Burt Davy	EL HE VG		
	<i>Cynodon dactylon</i> (L.) Pers	EL		
	<i>Ehrharta calycina</i> Sm.	EL HE PH VG		
	<i>Ehrharta capensis</i> Thunb.	EL KL PH VG		
	<i>Ehrharta</i> sp.	PH		
	<i>Eragrostis curvula</i> (Schrad.) Nees	EL VG		
	<i>Eragrostis</i> sp.	VG		
	<i>Heteropogon contortus</i> Pers.	VG		
	<i>Lolium perenne</i> L.	CO EL	•	
	<i>Merxmuellera</i> sp.	KL		
	<i>Merxmuellera stricta</i> (Schrad.) Conert	HE PH VG		
	<i>Pennisetum clandestinum</i> Hochst. ex Chiov	CO	•	
	<i>Pentaschistis airoides</i> s. <i>airoides</i> (Nees) Stapf	HE VG		
	<i>Pentaschistis</i> sp.I	KL		
	<i>Pentaschistis</i> sp.I	KL PH RU VG		
	<i>Setaria</i> sp.	VG		
	<i>Stipagrostis zeyheri</i> subsp. <i>zeyheri</i> (Nees) De Winter	EL		

	Species	Sites	Alien	Threat Status
	<i>Themeda triandra</i> Forssk.	EL VG		
	<i>Tribolium hispidum</i> (Thunb.) Desv.	EL VG		
	<i>Tribolium</i> sp. Desv.	PH		
	<i>Tribolium uniolae</i> (L.f.) Renvoize	EL HE KL VG		
	<i>Vulpia myuros</i> (L.) C.C.Gmel.	CO EL HE PH VG	•	
Restionaceae				
	<i>Elegia</i> sp.	EL RU		
	<i>Hypodiscus</i> sp.	RU		
	<i>Ischyrolepis capensis</i> (L.) H.P.Linder	EL KL VG		
	<i>Ischyrolepis</i> sp.	EL KL RU		
	<i>Ischyrolepis</i> sp.	RU		
	<i>Restio</i> sp.	KL RU VG		
	<i>Thamnochortus</i> sp.	EL KL RU		
	<i>Willdenowia</i> sp.	RU		
Tecophilaeaceae				
	<i>Cyanella hyacinthoides</i> L.	EL HE PH VG		
	<i>Cyanella lutea</i> L.f.	KL PH		

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