

**Plant response to habitat fragmentation: clues from species and functional
diversity in three Cape lowland vegetation types of South Africa**

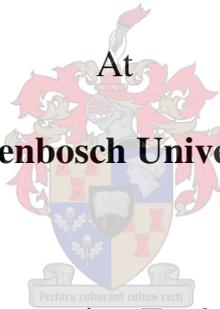
By

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At

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Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.



Date: 23rd March, 2009

Signed: *Raphael Y. Kongor*

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Dedication

I dedicate this dissertation to my beloved son Kongor Etamini Jaden-Ray, whose coming to this world brought back some purpose in my life and to my dear wife Diana Njweipi-Kongor who had to spend some cold winter nights alone while I was busy on the computer.

Abstract

The South African Cape lowlands have been severely transformed and reduced to fragments embedded in matrices of various activities. With the need to prioritise conservation efforts, information on the conservation worthiness and management of these fragments is required. This study aimed to better understand how fragmentation affects the Cape lowland vegetation patterns and dynamics and more specifically, to determine if, and if so to what extent these fragments contribute to regional plant diversity and more importantly their functionality. The novel approach adopted focused on plant functional traits, which are better predictors of ecosystem response to global change than individual species.

Species were sampled at four scales in four sites of decreasing sizes, including: a mainland and three fragments of three Cape lowland vegetation types i.e. Atlantis Sand Fynbos (ASF), Swartland Shale Renosterveld (SSR) and Langebaan Dune Strandveld (LDS). Traits such as dispersal, pollination, breeding mode and longevity were selected based on relevance to species' and plant-functional types' (PFTs) responses to fragmentation. The findings revealed different effects on species richness and PFTs. The effect of reduced patch size on species richness was more evident in ASF where fragments below 600 ha had significantly fewer species than the mainland. This effect was not unequivocal in SSR and LDS due to several confounding factors (notably the grazing history of the sites). The SSR fragment grazed by indigenous herbivores had significantly more species than the ungrazed sites. Also, the largest LDS fragment grazed by livestock had significantly more species than the ungrazed mainland, indicating that grazing rather than fragment size influences species richness, although the smallest fragments of these two vegetation types had significantly fewer species than the larger fragments. Species turnover and complementarity were high for all three vegetation types, reflecting the degree of habitat heterogeneity and high contribution of beta diversity to overall gamma diversity.

The effect of reduced patch size was higher on PFT diversity than on PFT richness, with Langebaan Dune Strandveld where habitat fragmentation was more recent being the least affected of the three vegetation types. This indicates a degree of functional redundancy in the Cape lowlands, which is important for ecosystem resistance and resilience. The ASF mainland and the largest fragment had higher PFT diversity than the medium-sized and the smallest fragments; the mainland had also higher PFT diversity than all the fragments combined. Similarly, the smallest SSR fragment had significantly lower PFT diversity and richness than the other sites. The grazed SSR fragment had higher PFT richness and diversity than the ungrazed mainland and smallest fragment, indicating the role of grazing in maintaining renosterveld vegetation. The PFTs absent from the different sites were mostly short-distance dispersed dioecious and non-dioecious species, and some with highly specialised pollination systems. This suggests that dispersal and pollination are vital functional attributes for the persistence of the studied fragmented ecosystems.

Habitat fragmentation effects plant community composition and ecological functions in the Cape lowlands, a conclusion supported also by the revealed significant trait-convergence and divergence assembly patterns. These communities result from various fragmentation filters that operate at different spatial-temporal scales and selecting species with suitable responses. All three vegetation types are susceptible to fragmentation, albeit at varying degree. The fragmentation effect was confounded by the sampling and temporal scales, the nature of disturbance regime, and the trait-mediated differences in species' response. The role of the surrounding matrix on fragment connectivity and gene flow appears to be of crucial importance, hence mitigation measures focusing on improving connectivity between patches, monitoring threatened taxa, and promoting dispersal and pollination have been recommended.

Opsomming

Suid-Afrika se Kaapse laagland het dramaties verander en weggekwyn tot fragmente wat in matrikse van verskeie bedrywighede veranker is. Gedagtig aan die voorkeuraandag wat bewaringspogings tans geniet, is inligting oor die bewaringswaardigheid en bestuur van hierdie fragmente nodig. Hierdie studie stel dit ten doel om 'n beter begrip te vorm van hoe fragmentasie die plantegroeioptrone en -dinamiek in die Kaapse laagland raak, en meer bepaald om vas te stel óf, en indien wel, in watter mate, hierdie fragmente tot streeksplantdiversiteit en -funksionaliteit bydra. Die ongewone studiebenadering konsentreer op funksionele kenmerke van plante, wat 'n beter aanwyser van ekosisteemreaksie op wêreldwye verandering is as individuele spesies.

Spesiemonsters is op vier skale by vier terreine van wisselende grootte ingesamel, wat insluit 'n moederstrook en drie fragmente van elk van drie plantegroeioptrone in die Kaapse laagland, naamlik Atlantis-sandfynbos (ASF), Swartland-skalierenosterveld (SSR) en Langebaan-duinestrandveld (LDS). Kenmerke soos verspreiding, bestuiwing, voortplantingsmetode en lewensduur is gekies op grond van die tersaaklikheid daarvan vir spesies en plantfunksionele tipes (PFT's) se reaksie op fragmentasie. Die studie bring verskillende uitwerkings op spesie-oorvloed en PFT's aan die lig. Wat spesie-oorvloed betref, was die uitwerking van kleiner strookgrootte ("patch size") duideliker te sien by ASF, waar fragmente kleiner as 600 ha beduidend minder spesies as die moederstrook bevat het. Hierdie uitwerking kon nie so duidelik by SSR en LDS waargeneem word nie weens verskeie strengelingsfaktore, veral die weidingsgeskiedenis van die terreine. Die SSR-fragment waarop inheemse herbivore gewei het, het beduidend meer spesies as die onbeweide terreine bevat. Voorts het die grootste LDS-fragment waarop vee gewei het heelwat meer spesies as die onbeweide moederstrook gehad, wat daarop dui dat weiding eerder as fragmentgrootte spesie-oorvloed beïnvloed, hoewel die kleinste fragmente van hierdie twee plantsoorte steeds aansienlik minder spesies as die groter fragmente bevat het. Spesie-omset en -aanvullendheid was hoog vir ál drie

plantsoorte, wat 'n aanwyser is van die mate van habitat-heterogeniteit en die groot bydrae wat betadiversiteit tot algehele gammadiversiteit lewer.

Die uitwerking van kleiner strookgrootte was duideliker te bespeur op PFT-diversiteit as PFT-oorvloed – in dié verband het LDS, waar habitatfragmentasie mees onlangs plaasgevind het, die ligste van die drie plantsoorte afgekom. Dít dui op 'n mate van funksionele oorbodigheid in die Kaapse laagland wat belangrik is vir ekosisteemweerstandigheid en -gehardheid. Die ASF-moederstrook en die grootste ASF-fragment het hoër PFT-diversiteit getoon as die medium- en kleinste fragmente; die moederstrook het in werklikheid oor hoër PFT-diversiteit as ál die fragmente saam beskik. Insgelyks het die kleinste SSR-fragment beduidend minder PFT-diversiteit en -oorvloed as die ander terreine getoon. Die beweidde SSR-fragment was hoër in PFT-oorvloed én -diversiteit as die onbeweidde moederstrook en die kleinste fragment, wat die rol van weiding in die instandhouding van renosterveldplantegroei beklemtoon. Die PFT's wat nié op die verskillende terreine voorgekom het nie, was meestal tweehuisige en nietweehuisige spesies wat oor kort afstande versprei, en sommige spesies met hoogs gespesialiseerde bestuwingstelsels. Dít dui daarop dat verspreiding en bestuwing noodsaaklike funksionele kenmerke vir die voortbestaan van die bestudeerde gefragmenteerde ekosisteme is.

Habitatfragmentasie raak die samestelling en ekologiese funksies van plantgemeenskappe in die Kaapse laagland. Dié gevolgtrekking word ook gerugsteun deur die bewese patrone van beduidende kenmerkkonvergensie (“trait convergence”) en divergensiesamekoms (“divergence assembly”). Hierdie plantgemeenskappe spruit uit verskeie fragmentasiefilters wat op verskillende ruimte-tydskale funksioneer, en wat spesies met geskikte reaksies kies. Ál drie plantsoorte is ontvanklik vir fragmentasie, hoewel in 'n wisselende mate. Die fragmentasie-uitwerking is beïnvloed deur monsterinsameling- en tydskale, die soort versteuringsbedeling, en die kenmerkbeïnvloede (“trait-mediated”) verskille in spesiereaksie. Die rol van die omringende matriks op

fragmentverbondenheid en geenvloei blyk van die allergrootste belang te wees, en dus word temperingsmaatreëls aanbeveel wat daarop gemik is om verbondenheid tussen stroke te verbeter, bedreigde taksa te moniteer, en verspreiding en bestuiwing aan te help.

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Above all I thank the Almighty God without whom none of these would have been possible.



Photo 1: Typical anthropogenic and fragmented habitats in the Cape lowlands. Top left: Vineyards in the Devon Valley, Stellenbosch (Photo by Dr. C.B. Krug); top right: Wheat field ready for harvest in St. Helena Fonteijn near Rocherpan Nature Reserve, Veldrif District; bottom left: View from Tygerberg Nature Reserve across the Cape Flats towards Tygerberg City; bottom right: *Acacia saligna* encroaching upon sand fynbos in areas adjacent to Riverlands Nature Reserve, Malmesbury District.

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Abbreviations

ASF / F / f :	Atlantis Sand Fynbos
BIOTA :	Biodiversity Monitoring Transect Analysis
C.A.P.E. :	Cape Action for People and the Environment
CF :	Combined fragments
CFR :	Cape Floristic Region
CI(s) :	Confidence Interval(s)
CREW :	Custodians of Rare and Endangered Wildflowers
LDS / S / s :	Langebaan Dune Strandveld
LF / F1 / a :	Largest fragment
ML / m :	Mainland
MF / F2 / b :	Medium-sized fragment
Max L :	Maximum likelihood
MTE :	Mediterranean-type ecosystem
PcoA :	Principal Coordinate Analysis
PFT(s) :	Plant functional type(s)
SAC(s) :	Species accumulation curve(s)
SAR(s) :	Species-area relationship(s)
SF / F3 / c :	Smallest fragment
Std Dev :	Standard Deviation
SSR / R / r :	Swartland Shale Renosterveld
TCAP :	Trait-convergence assembly pattern
TDAP :	Trait-divergence assembly pattern

Structure of the dissertation

The dissertation comprises seven chapters:

Chapter one is the general introduction. It states the rationale, aims and questions addressed and describes the vegetation types and study sites.

Chapter two provides the framework of the study, focusing on key ecological and evolutionary factors as well as the causes and consequences of habitat fragmentation in the Cape lowlands.

The study's field data (Chapters three - six) are presented in the format of scientific articles following the referencing style of the journal *Conservation Biology*.

Chapter three addresses the effect of fragmentation on species diversity.

Chapter four identifies the plant functional types (PFTs) typical of the three Cape lowland vegetation types and formulates predictions on their response to fragmentation.

Chapter five looks into the effect of fragmentation on PFT richness and diversity.

Chapter six assesses the role of habitat fragmentation on trait-convergence and divergence assembly patterns in the region.

Chapter seven is the general conclusion and recommendations. It is dedicated to management issues, and focuses on mitigation measures to curb the negative effects of habitat fragmentation and help promote biodiversity conservation in the Cape lowlands.

Chapter 1

Effects of habitat fragmentation in the Cape lowlands: motivation, aims and questions

1.1 Rationale for the study

Many of the Earth's ecosystems are dominated today by human activities (Vitousek et al. 1997; Sanderson et al. 2002), with almost half of the world now being transformed through large-scale mechanized agriculture and urban developments such as housing, industrial grounds and road building (Chapin et al. 2000). Through globalisation, man has also either intentionally or unintentionally introduced new species from other parts to areas which they would probably never have reached otherwise (Jenkins 1996; French 2000; McNeely 2000). This has left the world dominated by ecosystems with new combinations of species (Hobbs et al. 2006). Such landscape transformations have led to habitat fragmentation whereby "a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original" (Wilcove et al. 1986). The effects of habitat fragmentation are wide-ranging and occur at different levels of biological organisation and spatial scales, changing the spatial patterns of vegetation cover, altering ecological processes and impacting on individuals as well as species' assemblages (Saunders et al. 1991; Debinski & Holt 2000; Fahrig 2003; Henle et al. 2004; Groom et al. 2005; Aguilar et al. 2006; Rebelo et al. 2006; Lindenmayer & Fischer 2006, 2007). Human-induced habitat fragmentation and landscape modification currently constitute the most important threats to biodiversity worldwide (Foley et al. 2005).

Despite the generally perceived pervasive and disruptive effects of habitat fragmentation, the precise implications for the maintenance of biodiversity in fragmented landscapes are largely unknown. This is especially so for plants, due to the limited ability to predict how plant species may respond to fragmentation (Malcolm et al. 2002; Matthies et al. 2004; Bruna & Oli 2005; Vellend et al. 2006). There are manifold reasons for this such as: -

(1) Most studies on the effects of fragmentation on plants have focused on fitness of populations, decreased reproductive rate and genetic diversity of single or few species rather than species assemblages (e.g. Zschokke et al. 2000; Lienert et al. 2002a; Hooftman et al. 2003; Lienert & Fischer 2003; Bruna & Oli 2005; but see for instance Bond et al. 1988; Cowling & Bond 1991; Saunders & Hobbs 1993; Settele et al. 1996; Kemper 1997; Kemper et al. 1999, 2000; Donaldson et al. 2002; Hobbs & Yates 2003; Piessens et al. 2005; Lindenmayer & Fischer 2006).

(2) Developing a general understanding of the mechanisms of how plant species respond to landscape patterns and dynamics is difficult (Freckleton & Watkinson 2002; Ehrlén & Eriksson 2003; Pearson & Dawson 2005; Williams et al. 2005; Zartman & Nascimento 2006). This is mainly due to the challenges of replicating and carrying out fragmentation studies on suitable spatial and temporal scales (Körner & Jeltsch 2008).

(3) Generalisations based on studies of single species are not very reliable (Héroult & Honnay 2005), because conclusions drawn thereof are mostly valid only within phytogeographical boundaries. Species pools vary across regions and variability within species, which is important in some processes, is hardly taken into account in species-based studies (Pillar & Sosinski 2003).

(4) Insufficient attention has been given to the analysis of the matrix habitat, which is critical to the understanding of the patterns and processes within remnant patches (Jules & Shahani 2003; Groom et al. 2005; Wisser & Buxton 2008).

(5) Although some studies show negative effects of habitat fragmentation on plant populations (e.g. Lienert et al. 2002b, 2002c; Byers et al. 2005; Piessens et al. 2005), different species may respond differently to the same processes (e.g. Cunningham 2000; Lindborg et al. 2005; Vellend et al. 2006; Helm et al. 2006) due to different life history traits. These trait differences result in different adaptations to dispersal in time and space and to local habitat conditions (Matthies et al. 2004; Héroult & Honnay 2005; Jongejans & de Kroon 2005; Ewers & Didham 2006).

(6) Despite the growing shift from species-based to plant functional type (PFT) studies (see Steffen et al. 1992; Smith et al. 1997; Steffen & Cramer 1997; Cornelissen et al. 2003) and the fact that

studies have been carried out elsewhere actually linking PFTs to questions relating to habitat fragmentation (see e.g. Fischer & Stöcklin 1997; Stöcklin & Fischer 1999; Higgins et al. 2003; Ozinga et al. 2005; Poschlod et al. 2005; Römermann et al. 2008), there is no study in the Cape region that has actually assessed the effect of habitat fragmentation on both species and plant-functional diversity.

(7) Fragmented landscapes are often altered by other anthropogenic changes (e.g. changes in disturbance regimes, invasion and pollution), which can interact synergistically with habitat fragmentation (Ewers & Didham 2006; Laurance 2008), but are often not investigated.

More studies focusing on both landscape parameters and PFTs, instead of single species, will hopefully improve our understanding of the phenomenon and ability to make generalised predictions on how plants may respond to habitat fragmentation. Such studies provide opportunities for the systematic evaluation of different aspects of fragmentation and the identification of suitable criteria for grouping species according to their responses (Körner & Jeltsch 2008).

Covering an area of about 90 000 km², the Cape Floristic Region (CFR) of South Africa is home to over 9000 vascular plant species with about 70% being endemic (Goldblatt & Manning 2000). These are distributed among 173 families (5 of them endemic) and 988 genera of which 942 are native seed plant species with 160 (16%) of these being endemic (Goldblatt & Manning 2000). Due to its astounding plant species diversity and endemism, the CFR is recognised as one of the world's biodiversity hotspots (Myers et al. 2000). Most of the plant species (about 7000) in the CFR (Cowling et al. 1996; Cowling 2001), are found in three main vegetation categories of the lowland habitats of the Fynbos Biome i.e. fynbos, renosterveld and strandveld. These lowland habitats are also home to some 1435 of South Africa's Red Data species (Rebelo 1992). Despite this remarkable plant species diversity and endemism, only about 10% of the Fynbos Biome is formally conserved in statutory and non-statutory reserves such as national parks, provincial, local authority and private

nature reserves (Rouget et al. 2006). Most areas under protection are between 1 000 and 10 000 ha and very few being more than 100 000 ha. This does not meet the prescribed target of 23%–36% of the original extent required under conservation to represent 75% of the species in the different vegetation categories (Rouget et al. 2006). Moreover, most of these reserves are located in the less accessible mountain habitats that are under less human influence and therefore, involve little conservation opportunity costs (Pressey 1994; Cowling & Pressey 2003; Rouget et al. 2003a; von Hase et al. 2003).

In contrast, the lowland habitats, particularly those with opportunities for agriculture or urban development, have been severely transformed and fragmented. Most of these lowland habitats are situated on private lands (Rouget et al. 2003a; von Hase et al. 2003), making private landowners the custodians of these unique habitats. With more than 80% transformed and less than 5% protected, renosterveld is considered to be critically endangered (Rouget et al. 2003a, 2003b; 2003c; Rouget et al. 2006). Some figures cited in the literature show that only about 8% of renosterveld (5% for Swartland and Boland Renosterveld) is left, with less than 1% of this under protection (von Hase et al. 2003). Lowland fynbos, with about 40% transformed and less than 5% protected, is considered to be endangered while strandveld is classified as vulnerable, since up to 20% has been transformed and less than 50% is protected (Rouget et al. 2006). Therefore, these lowland habitats are of high conservation value as most of the patches left (especially renosterveld patches) are 100% irreplaceable¹ (Cowling & Pressey 2003; Cowling et al. 2003; Rouget et al. 2006).

However, with limited resources, CapeNature, which is the statutory conservation agency in the Western Cape of South Africa and partnership programmes like C.A.P.E.², as well as some

¹ Irreplaceability is the index calculated by the conservation planning tool C-Plan denoting the contribution of a specific site towards a stated conservation target (see Ferrier et al. 2000; Margules & Pressey 2000). A site with 100% irreplaceability is indispensable for meeting the target because there is no flexibility around the spatial options for conserving the biodiversity contained in it.

² C.A.P.E. = Cape Action for People and the Environment (www.capeaction.org.za/index.php?)

conservation-conscious landowners, wonder whether these fragments are of any conservation value and if so, how best to manage them. Thus, there is a need for fine-scale studies to ascertain the conservation value of these fragments. This study complements others that have been carried out on the effects of habitat fragmentation in the CFR (e.g. Bond et al. 1988; Cowling & Bond 1991; Kemper 1997; Kemper et al. 1999, 2000; Donaldson et al. 2002; Pauw 2004, 2007). Whereas previous studies focused on single vegetation categories, this is the first study that focuses on all the three main Cape lowland vegetation categories with an emphasis on plant functional types, albeit at small but multiple scales. Looking at multiple scales is good for management and also based on the premise that information gathered at one scale may not necessarily answer questions at another.

1.2 Physical and geographical features of the Cape lowlands

The Cape lowlands form part of the Fynbos Biome, which is virtually restricted to South Africa's Western Cape Province with just a small portion occurring in the Eastern and Northern Cape Provinces (Figure 1.1). This biome occupies most of the north-south and east-west mountain chains of the Cape Fold Belt as well as the valleys and lowlands between the mountains and the Atlantic Ocean in the southwest and the Indian Ocean in the south. It is bordered to the north by the Olifants River Valley, to the east by the Albany thickets and inland by the Succulent Karoo (Rebelo et al. 2006). Found roughly below 300 m above sea level and covering some 32 756 km² (Cowling 2001), the Cape lowlands encompass mostly the interior valleys and coastal lowlands of the Fynbos Biome. The entire biome consists of a mosaic of geological substrates such as sandstone, quartzite, granite, gneiss, shale, and limestone that has given rise to a variety of soil types (Goldblatt & Manning 2000; Rebelo et al. 2006). It is drained by five perennial rivers (Olifants, Berg, Breede, Groot-Baviaanskloof-Gamtoos and Olifant-Gourits-Groot), which serve as important migratory routes and opportunities for the exchange of biota between the coastal forelands and the interior basin (Cowling 2001).

The west of the region is characterized by dry summers and wet winters with annual rainfall of between 250 mm to 2000 mm while the east receives more summer precipitation (Cowling et al. 1997). With a characteristically mediterranean-type climate, the Cape lowlands can be classified as a mediterranean-type ecosystem/biome (MTE). The global mediterranean biome consists of five geographically remote areas located on five different continents. These mediterranean regions occur between latitude 30^o and 40^o north or south (Hobbs et al. 1995).

Although they developed only recently during the Pleistocene (Axelrod 1973), MTEs exhibit very high heterogeneity in the composition of their biota, landforms and soil types. This is not only the result of the history of these ecosystems but also a main evolutionary factor for Mediterranean species (Di Castri 1981). The CFR in particular, has experienced quite stable climatic conditions throughout the Quaternary (Goldblatt & Manning 2000; Jansson 2003). Despite the heterogeneity within each region and the evolution of distinctive flora and fauna in isolation and from basically different phylogenetic stocks, MTEs show striking similarities. This is due to their predictable seasonal climate patterns and the role of fire in their ecosystems (Axelrod & Raven 1978; Linder 2003). However, the issue of convergence or non-convergence of MTEs remains contentious (see Di Castri & Mooney 1973; Cody & Mooney 1978; Cowling & Campbell 1980; Cowling & Witkowski 1994; Keeley & Bond 1997; Cowling et al. 2005). It is difficult to give an all-embracing definition of MTEs. Nonetheless, diagnostic features of MTEs are high species richness and endemism (Thiaw & Chouchena-Rojas 1999), frequent fires and an extensive flowering period with seasonal growth patterns that extend into summer (Dodson & Kershaw 1995). MTEs occupy less than 3% of the Earth's surface (Rundel 2004) but account for about 20% of the world's vascular plant species (Cowling et al. 1996). This high floral species richness and high levels of local and regional endemism, qualify MTEs as global biodiversity hotspots, and they are therefore important targets for conservation efforts (Myers et al. 2000).

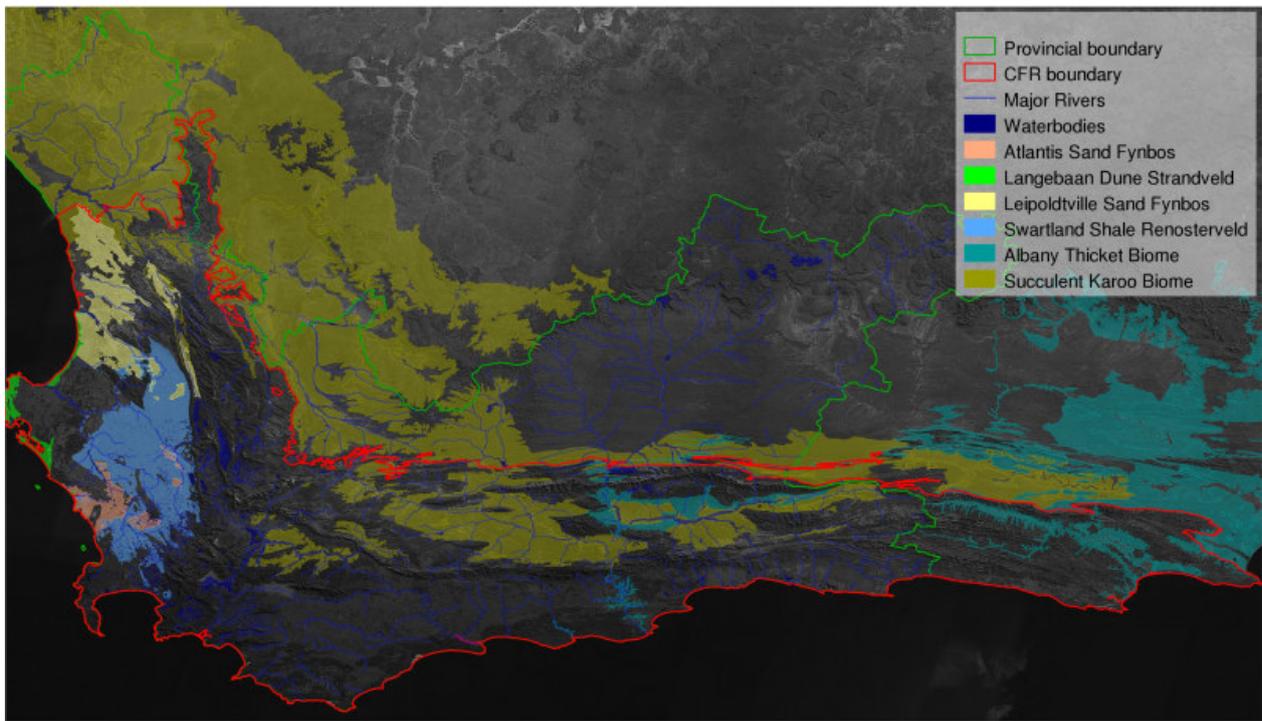


Figure 1.1. Map of the Cape Floristic Region showing the boundary of the Cape Floristic Region (SANBI, 2000), the provincial (Western Cape) boundary (Chief Directorate Surveys & Mapping Western Cape, 2005), the neighbouring Succulent Karoo and Albany Thicket Biomes (Mucina & Rutherford 2006), the three vegetation types studied (Mucina & Rutherford 2006) and the water bodies (Chief Directorate Surveys & Mapping Western Cape, 2005) and major rivers in the Western Cape (from Mucina & Rutherford, 2006). Background: WMS Global Mosaic, pan-sharpened (NASA 1999-2003).

1.3 The vegetation of the Cape lowlands

Like most MTEs, the Cape lowlands are dominated by high-diversity fire-prone ecosystems (some supported by very nutrient-poor soils) characterized by fine-leaved, sclerophyllous and evergreen shrubs (Di Castri 1981; Cowling et al. 1997; Rebelo et al. 2006). The three main vegetation categories are fynbos, renosterveld and strandveld. Fynbos, an evergreen, fire-prone shrubland confined largely to sandy infertile soils is characterised by the presence of Restionaceae (restios), a high cover of fine-leaved ericoid shrubs (belonging to various families such as Ericaceae, Asteraceae, Rhamnaceae, Rutaceae and Thymelaeaceae etc.) and an overstorey dominated by Proteaceae (proteoid) shrubs (Rebelo et al. 2006). Mature fynbos stands are often characterised by high Cyperaceae (sedge) and low Poaceae (grass) cover (Campbell 1986). Renosterveld, which is also an evergreen, fire-prone shrubland/grassland, occurs on relatively more fertile clay-rich shale

and granite derived soils (Boucher & Moll 1981) with rainfall ranging from 250–670 mm (Rebelo et al. 2006). In areas receiving less rainfall, renosterveld is replaced by Karoo vegetation, in those with higher rainfall by fynbos shrublands (Boucher & Moll 1981). Renosterveld is characterised by the presence of cupressoid, leptophyllous, divaricately branched, small-leaved evergreen shrubs mostly of the Asteraceae family (notably *Elytropappus rhinocerotis*, “renosterbos”), and an understorey of grasses and seasonally-active geophytes (Cowling et al. 1997; Rebelo et al. 2006). Other common shrub families are the Boraginaceae, Fabaceae, Malvaceae, Rubiaceae (Goldblatt & Manning 2002) while common geophytes belong to the families Amaryllidaceae, Asphodelaceae, Hyacinthaceae, Iridaceae, Orchidaceae and Oxalidaceae (Procheş et al. 2006). Some proteoids and restios do occur in renosterveld, however at low densities (Taylor 1996). Renosterveld is also characterised by the presence of termitaria (“heuweltjies”) that provide additional micro-habitats for thicket species of the Anacardiaceae, Celastraceae, and Oleaceae families (Boucher & Moll 1981). Strandveld is a short, scrubby, fire-shy shrubland that occurs on calcareous soils along the coast and is dominated by broad-leaved shrubs and many fleshy-fruited ornithochorous species (Cowling et al. 1997; Rebelo et al. 2006). More succulent shrubs are found as aridity increases and geophytes, annuals and restios are common at the transition towards sand fynbos (Rebelo et al. 2006). The exceptionally high level of plant species diversity and endemism found in the Cape lowlands is attributed to the mosaic of sandstone and shale substrates that give rise to a variety of soil types, the extreme climatic variation, the sharp local precipitation gradients, species adaptations to fire as well as factors limiting gene flow (Cowling 1992; Johnson 1996; Johnson & Bond 1997; Goldblatt & Manning 2000; Linder 2003).

1.4 Approach and assumptions

Most studies on fragmented ecosystems have focused mainly on the biogeographic consequences of the creation of habitats of various sizes (i.e. the “island effect”) on species composition and abundance, with little attention given to plant functional type diversity. Most of these studies have

also shown weak and/or inconsistent fragmentation effects with respect to species richness and abundance relative to fragment size. These, coupled with the challenges involved in predicting how plant species may respond to habitat fragmentation as outlined earlier, limit the understanding of the mechanisms behind the community and population-level patterns observed in fragmented ecosystems. Studies within the CFR have shown that plant species continue to persist in very small fragments and that species composition *per se* may not be the best measure of the fragmentation effect. This is probably because, as some researchers observe (see Colwell et al. 2004), species richness is more subject to random variation than other measures of diversity. Furthermore, most species-based studies are restrictive, as the conclusions drawn from these are only valid within phytogeographical boundaries due to the variation in potential species pools across regions. This is in contrast to plant functional traits which are applicable more widely. Therefore, more relevant are changes in community structure as reflected by the frequency of individuals and species with different life history traits than simply changes in species richness.

For this study, both the species- and plant functional type-based approaches were adopted. While focusing on plant functional traits, the effect of fragmentation on species diversity (i.e. richness) was also assessed despite the negative criticisms associated with species richness as a measure of biodiversity. In this way, it was possible to compare the effect of fragmentation on plant functional type and species diversity. Moreover, species remain the simplest and most widely-used concept for quantifying biodiversity and on which most conservation and management interventions are based (see also Chao 2004; Magurran 2004). The shift of emphasis from species to plant functional traits in this study is due to the increasing recognition of the strong predictive power of plant traits on vegetation responses to global change (e.g. Smith et al. 1997; Cornelissen et al. 2003).

Plant communities result from a hierarchy of biotic and abiotic filters that successively select, from the regional species pool, the species that will survive and persist at any given site (Keddy 1992).

The effects of habitat fragmentation on these filters occur at different levels of biological organisation and spatial scales, selecting individuals with the appropriate responses that should account for the observed patterns and processes in the region. Focusing on plant traits may elucidate some of the mechanisms affecting plant species responses to habitat fragmentation and the potential for changing responses over time. It is assumed that species that survive and persist in the fragmented Cape lowlands are those with traits conferring a strong persistence ability at the individual, population, community and/or landscape levels, and/or species that have well-developed strategies to respond to the prevalent disturbances in the remnant patches. This could be through avoidance, tolerance and regeneration. Fragmentation in this region is largely responsible for the spatial distributions, sizes, degree of isolation, the type of matrices and the disturbance regimes in the remnant patches. These variables were therefore used in the interpretation of patterns and processes within fragment. Only indigenous species were considered in the analyses in this study.

1.4.1 Study sites and vegetation types

Three areas (Figure 1.2) corresponding to three vegetation types in South Africa's Western Cape Province i.e. Atlantis Sand Fynbos (ASF), Swartland Shale Renosterveld (SSR) and Langebaan Dune Strandveld (LDS) were selected based on the classification of vegetation types by Mucina and Rutherford (2006). In this study, these represent the three main Cape lowland habitats namely fynbos, renosterveld and strandveld. Detailed descriptions of the vegetation types selected are found in Rebelo et al. (2006). One of the largest patches of each of these vegetation types was selected as representative "mainland" and used as reference for comparison with smaller fragments. Fragments were chosen based on availability within a 10 km radius from the corresponding mainland and the landowners' willingness to cooperate. All the sites chosen are below an altitude of 350 m and have a mediterranean-type climate with mild temperatures, wet winters, relatively dry summers, rare frost occurrences, and frequent strong north-westerly winds mostly along the coast in summer and autumn (Table 1.1).

According to Rebelo et al. (2006), ASF is predominantly a restioid and proteoid fynbos vegetation type with asteraceous fynbos and patches of ericaceous fynbos in seepage areas, occurring on acid sands at altitudes of 40–250 m and rainfall of 290–660 mm. Only 6% is formally conserved and about 40% has been transformed by agriculture, urbanization and invasion by alien *Acacia*, *Pinus* and *Eucalyptus* species. SSR occurs mostly in the plains and valleys of the Swartland on the West Coast lowlands, at altitudes of 50–350 m and rainfall of 270–670 mm, and supports low to moderately tall leptophyllous shrubland dominated by renosterbos, with *Athanasia trifurca* and *Otholobium hirtum* dominant in disturbed areas. SSR is considered to be critically endangered because about 90% of it has been transformed, and less than 5% of what is remaining under formal protection. Alien grasses pose a serious threat in this vegetation type. LDS occurs on deep sands and calcrete of marine origin at altitudes of 0–100 m and rainfall of 230–355 mm. Although Mucina and Rutherford (2006) classify the fragments (Modderfontein and St. Helena Fontein 1 & 2) used to complement the LDS mainland under Leipoldtville Sand Fynbos, the plots sampled in these fragments were structurally and floristically similar to those sampled in the mainland (Rocherpan N.R.). Therefore, for the purpose of this study, these sites are grouped under the same broad vegetation type (i.e. Langebaan Dune Strandveld).

Despite the presence of some common families and genera, the floristic affinities between these vegetation types are very low, particularly at species level. Correspondence analysis in Statistica 8.0 (StatSoft 2007) of growth forms of sampled species shows that most geophytic herbs occur in SSR, most graminoids (mainly restios) in ASF and many succulents in LDS (Figure 1.3). Dwarf shrubs tend to occur more in ASF and less so in SSR. Shrubs and herbs occur in all three vegetation types, while climbers are more common in LDS.

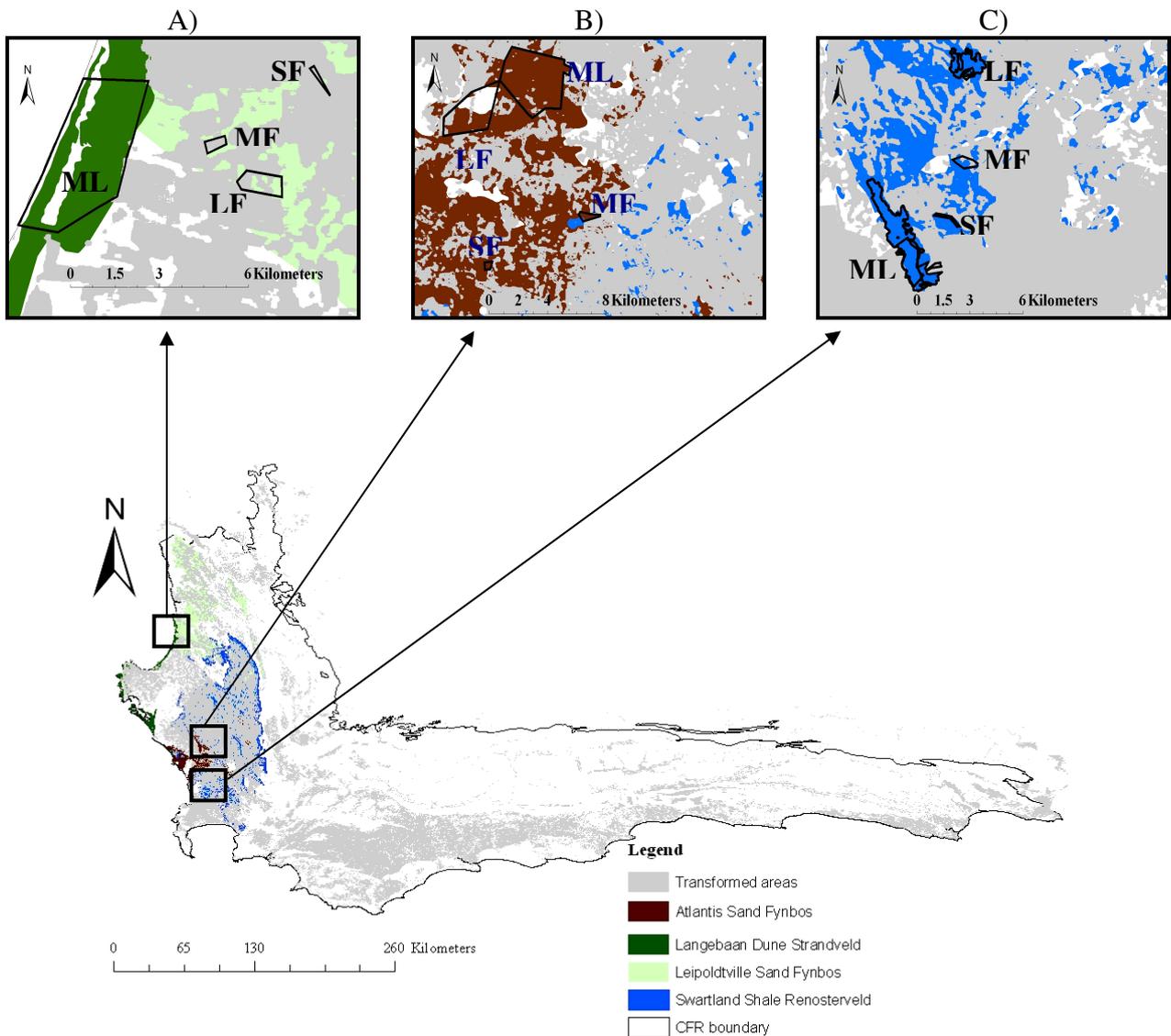


Figure 1.2 Location of the study sites within the transformed (agricultural-urban-invasive alien plant) matrix of the Cape region. ML = mainland, LF = largest fragment, MF = medium-sized fragment and SF = smallest fragment. A) Langebaan Dune Strandveld sites: ML (930 ha) = Rocherpan Nature Reserve (NR), LF (70 ha), MF (18 ha) both situated in the farm St. Helena Fontein, and SF (8 ha) = Modderfontein; B) Atlantis Sand Fynbos sites : ML (1 100 ha) = Riverlands NR, LF (600 ha) = Pella NR, MF (37 ha) = Kalbaskraal NR, and SF (16 ha) = Camphill Private NR (although the ML and the LF appear linked, they are actually separated by a railway line and a Eucalyptus plantation); C) Swartland Shale Renosterveld sites: ML (600 ha) = Tygerberg NR, LF (300 ha) = Meerendal, MF (70 ha) = Clara Anna Fontein Game. Reserve, and SF (15 ha) = Van Riebeeckshof.

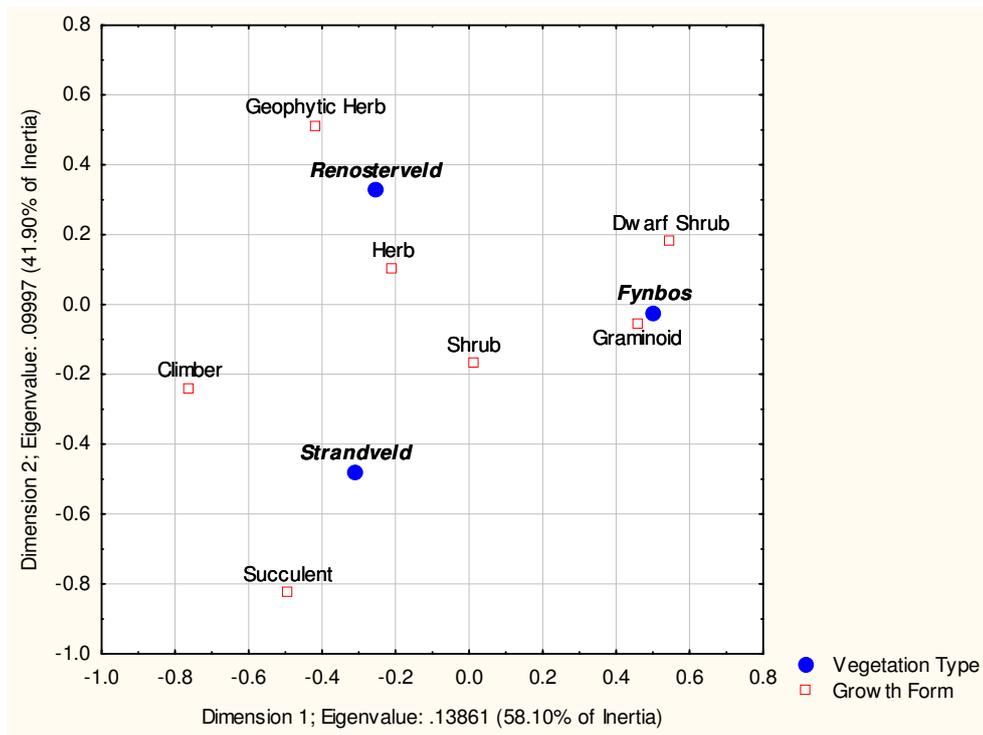


Figure 1.3 Classification Analysis ordination diagram showing the dominant growth forms of the three vegetation types studied.

Table 1.1 Description of study sites with vegetation type, latitude and longitude coordinates, geology/soil type, climate (mean annual rainfall in mm, mean annual minimum and maximum daily temperatures, frost days/year), matrix type (resistance value), fire and grazing history, presence of alien plant species, other land use history and special habitats). Latitude and Longitude coordinates were taken at the middle of the baseline of the three 50 m x 20 m plots sampled in each site. Fragments used to complement the Langebaan Dune Strandveld mainland are classified by Mucina and Rutherford (2006) under Leipoldtville Sand Fynbos but field observations and the relatively low complementarity among these sites showed high floristic affinities with the mainland (Rocherpan), which justifies why they are all grouped under the same vegetation type i.e. Langebaan Dune Strandveld

Fynbos sites (area) [Vegetation ^a type] {Protection status}	Latitude; Longitude	Geology and soil	Climate	Matrix type (resistance value ^f)	Fire history	Grazing history	Presence of alien plant species	Other land use history and special habitats
Riverlands Nature Reserve Mainland (1100 ha) [Atlantis Sand Fynbos] {provincial N.R. managed by CapeNature}	33.49788; 18.58925 33.49066; 18.58388 33.48977; 18.58063	Cambrian Cape granite ^b ; Acidic tertiary grey regic sand ^c (deep-shallow)	Rainfall = 440 ^{c,d} range = (290-660) ^c and (370-580) ^d Temp ^c 7-28 ^o C Frost ^c 3 days	<i>A. saligna</i> (50) Wheat fields (75)	About 2/3 burnt by accident in 2005 and 2006. A small part burnt 7-8 years and another (1/3) burnt 13-18 years ago ^h . Natural fires occur once every seven (min. 4, max. 25) years ^g	No grazing. Mole rat activity in the deep sandy areas	<i>A. saligna</i> . Alien clearing takes place regularly	Patches of seasonally waterlogged areas
Pella NR (600 ha) Largest fragment [Atlantis Sand Fynbos] {provincial N.R. managed by CapeNature}	33.51022; 18.55236 33.50960; 18.54925 33.52011; 18.54766	Cambrian Cape granite ^b ; Acidic tertiary grey regic sand ^c (deep sand and sandy)	Rainfall = 440 ^{c,d} range = (290-660) ^c and (370-580) ^d Temp ^c 7-28 ^o C Frost ^c 3 days	<i>A. saligna</i> (50) <i>Eucalyptus</i> forest and Wheat fields (75)	Part burnt in 2005. A part burnt 7-8 years and another 1/3 burnt 17-27 years ago ^h . Natural fires occur once every seven (min. 4, max. 25) years ^g	Previously grazed by sheep/cattle ^g . Mole rat activity in deep sand	Adjacent to <i>Eucalyptus</i> plantation	Previously used for gravel quarrying ^g
Kalbaskraal N.R. Medium-sized fragment (37 ha) [Atlantis Sand Fynbos] {local council N.R. since 1966}	33.57061; 18.62861 33.57180; 18.62865 33.57133; 18.62773	Cambrian Cape granite ^b ; Acidic tertiary grey regic sand ^c (sandy)	Rainfall = 440 ^{c,d} range = (290-660) ^c and (370-580) ^d Temp ^c 7-28 ^o C Frost ^c 3 days	Settlement (75-100) Minor railway and road (50)	Burnt 10-15 years ago	Some cow dung from stray cattle	Heavily invaded by <i>A. saligna</i> . Alien clearing started in 2006	Patches of coarse sand and deep sand
Camphill Village Private N.R. (16 ha) Smallest fragment [Atlantis Sand Fynbos] {private nature reserve since 1990}	33.59701; 18.56554 33.59787; 18.56433 33.59774; 18.56327	Cambrian Cape granite ^b ; Acidic tertiary grey regic sand ^c (deep sand)	Rainfall = 440 ^{c,d} range = (290-660) ^c and (370-580) ^d Temp ^c 7-28 ^o C Frost ^c 3 days	Settlement (75-100) Minor road and <i>Acacia</i> species (50) <i>Eucalyptus</i> forest (75)	No fire for more than 40 years	No grazing	Surrounded by <i>Acacia</i> and <i>Eucalyptus</i> plantation	Deep sand

Renosterveld sites (area) [Vegetation ^a type] {Protection status}	Latitude; Longitude	Geology and soil	Climate	Matrix type (resistance value ^f)	Fire history	Grazing history	Presence of alien plant species	Other land use history and special habitats
Tygerberg N.R. Mainland (600 ha) [Swartland Shale Renosterveld] {local council NR managed by the Tygerberg Council}	33.87411; 18.59930 33.87727; 18.59871 33.87833; 18.59984	Precambrian Malmesbury Group Shale ^{b,c} (sandy clay)	Rainfall = 430 ^c range = (270-670) ^c Temp ^c 6-30 ⁰ C Frost ^c 3-4 days	Settlement (75-100) Vineyards (75)	Part burnt in 1996 and in 2000. But not in areas sampled	Livestock grazing by the Khoi-Khoi people. Introduced 3 rheboks in 1995/6 and 7 bonteboks in 2004	Annual grasses e.g. <i>Briza</i> , <i>Avena barbata</i> , pines and <i>Echium plantagineum</i>	Part of the Loevenstein and Welgemoed farms of the Vrijburgers in the 1700s. Ploughed for over 200 years for grain/grape. Farming ended in 1948 in Welgemoed and in 1963 in Loevenstein (Melville, –pers comm).
Meerendal Estate Largest fragment (300 ha) [Swartland Shale Renosterveld] {Private but part of a conservancy}	33.78627; 18.62378 33.78542; 18.62339 33.78748; 18.61984	Precambrian Malmesbury Group Shale ^{b,c} (clay)	Rainfall = 430 ^c range = (270-670) ^c Temp ^c 6-30 ⁰ C Frost ^c 3-4 days	Vineyards and Wheat fields (75)	No information	Not grazed since the Khoi-Khoi left	Few (<i>Briza minor</i> , <i>Anagallis arvensis</i> , <i>Geranium purpureum</i>)	Granted to J. Meerland in 1702. Bought by the Starkes in 1929. Bought in 2004 by a consortium of South African businessmen who aim to turn it into a conservation-friendly wine estate.
Clara Anna Fontein Private Game Reserve Medium-sized fragment (70 ha) [Swartland Shale Renosterveld] {Managed for tourism by Mr. Basson J.}	33.82700; 18.61697 33.82698; 18.61578 33.82602; 18.61524	Precambrian Malmesbury Group Shale ^{b,c} (sandy clay)	Rainfall = 430 ^c range = (270-670) ^c Temp ^c 6-30 ⁰ C Frost ^c 3-4 days	Vineyards and Wheat fields (75)	No information	Heavily grazed by several herbivores	<i>A. arvensis</i> , <i>Briza</i> , <i>Bromus</i> species, <i>Hypochoeris radicata</i>	Owned by Mr Verwey in the 1700s and later by his daughter Anna. Covers 200 ha with 70 ha of renosterveld with eight red data plant species (Bason J. pers comm.) and old fields. Overstocked with eland, zebra, ostrich, bontebok, blue wildebeest, oryx, rhebok, springbok, steenbok, grysbok, and bat-eared fox).
Van Riebeeckshof Smallest fragment (15 ha). [Swartland Shale Renosterveld] {Rehabilitated by Tygerberg Council}	33.85486; 18.61426 33.85246; 18.61098 33.85196; 18.60743	Precambrian Malmesbury Group Shale ^{b,c} (sandy clay)	Rainfall = 430 ^c range = (270-670) ^c Temp ^c 6-30 ⁰ C Frost ^c 3-4 days	Settlement (75-100) Vineyards (75)	No information	No grazing	<i>Briza</i> , <i>Vicia</i> <i>Bromus</i> species, <i>A. arvensis</i> , <i>Pennisetum clandestinum</i> , <i>Trifolium angustifolium</i>	Part of the Loevenstein farm used for farm workers' houses. Farming ended in 1963.

Strandveld sites (area) [Vegetation ^a type] {Protection status}	Latitude; Longitude	Geology and soil	Climate	Matrix type (resistance value ^f)	Fire history	Grazing history	Presence of alien plant species	Other land use history and special habitats
Rocherpan N.R. Mainland (930 ha) [Langebaan Dune Strandveld] {provincial N.R. managed by CapeNature}	32.60131; 18.31355 32.60672; 18.31566 32.60941; 18.30608	Quaternary superficial sands and limestones ^b (calcareous coastal sand and sandy); Deep tertiary to recent sands and calcrete of marine origin ^c	Rainfall = 212 ^c range = (173-275) ^c and (230-355) ^c Temp ^c 8-26 ⁰ C Frost ^c 3-4 days	Wheat and potato fields (75) Minor road (50)	No fire for over 40 years	Grazed by cattle up to 1967	Insignificant e.g. <i>Bromus diandrus</i> and <i>Avena</i> species.	Named after Pierre Rocher who was in the area in 1839. Expropriated as a reserve in 1967 marking the end of cattle grazing. The major habitat types are: Dunes, seasonal wetland, West Coast Strandveld, Sandy beach and Marine ecosystem.
St Helena Fontein 1 Largest fragment (70 ha) [Leipoldtville Sand Fynbos] {Under rehabilitation since 1990} (A. Coetzee Senior pers. comm.)	32.60356; 18.36715 32.60539; 18.35892 32.60403; 18.36005	Quaternary superficial sands and limestones ^b Deep acid tertiary sands ^c (sandy)	Rainfall = 212 ^c range = (173-275) ^c and 260 range = (130-450) ^c Temp ^c 7-30 ⁰ C Frost ^c 3-4 days	Wheat and potato fields (75)	Burnt 30-40 years ago	Sheep/cattle grazing for over 20 years		Part of the farm St Helena Fontein owned by Mr. A. Coetzee. Strip-ploughed (50 m) and planted with pasture to increase carrying capacity for livestock in 1985. Fifty m of natural vegetation left to prevent wind erosion.
St. Helena Fontein 2 Medium-sized fragment (18 ha) [Leipoldtville Sand Fynbos] {private land}	32.59291; 18.35062 32.59352; 18.34955 32.59446; 18.35166	Quaternary superficial sands and limestones ^b ; Deep acid tertiary sands ^c (sandy)	Rainfall = 212 ^c /260 ^c range = (173-275) ^c and (130-450) ^c Temp ^c 7-30 ⁰ C Frost ^c 3-4 days	Wheat fields (75) and Minor road (50)	Burnt 30-40 years ago	Sheep/cattle grazing over 20 years		Part of the farm St Helena Fontein owned by Mr. A. Coetzee
Modderfontein Smallest fragment (8 ha) [Leipoldtville Sand Fynbos]. {private land}	32.57562; 18.38009 32.57630; 18.38088 32.57673; 18.38105	Quaternary superficial sands and limestones ^b ; Deep acid tertiary sands ^c (sandy)	Rainfall = 212 ^c /260 ^c range = (173-275) ^c and (130-450) ^c Temp ^c 7-30 ⁰ C Frost ^c 3-4 days	Wheat fields (75) Minor road (50)	Burnt 30-40 years ago	Grazed by sheep for over 20 years		Patch forms part of the 200 ha Modderfontein farm owned by the Smits

^a Vegetation types are based on Mucina and Rutherford (2006); ^b Goldblatt and Manning (2000); ^c Rebelo et al. (2006); ^d 2003 to 2006 rainfall data from the Skaapkraal Weather Station; ^e BIOTA South Weather Station data of the Rocherpan Observatory from 2001 to 2005 (courtesy of Ute Schmiedel, Institute of General Botany, University of Hamburg & Klaus Berger, Institute of Soil Science, University of Hamburg); ^f Jonas et al. (2006); ^g Brownlie and Mustart (1988); ^h de Roubaix (2006)

1.5 Objectives and questions

1.5.1 Objectives

The main objective of this study was to assess the impact of habitat loss due to human-induced habitat fragmentation on phytodiversity in three of South Africa's Cape lowland vegetation types. The knowledge and information generated will be useful for the development and promotion of efficient, pragmatic and cost-effective management guidelines for biodiversity conservation and sustainable land use in such a fragmented and mosaic landscape. Specifically, the aims of the study were to:

- a) Investigate the effects of reduced patch size on plant species and plant functional type (PFT) diversity in three selected Cape lowland vegetation types;
- b) Determine if the composition and functioning of plant communities in the Cape lowlands are influenced by site factors (such as patch size, patch distance from nearest neighbour and surrounding matrix type; all associated with fragmentation), disturbance and soil fertility;
- c) Determine whether the fragments of these Cape lowland vegetation types are worth conserving.

1.5.2 Research Questions

To attain the above objectives, the following questions were addressed

- a) Is species richness positively related to fragment size and sampling scale?
- b) What are the PFTs that characterise the three Cape lowland vegetation types and how will the vegetation types respond to and be affected by habitat fragmentation?
- c) Is PFT richness and diversity positively related to fragment size and sampling scale?
- d) Are there any perceived trait-convergence and divergence assembly patterns in these vegetation types related to site factors?
- e) What should be done to promote and ensure the persistence, functionality and conservation worthiness of the Cape lowland fragments?

1.6 Caveats of the study

(1) Like in other parts of the world, habitat fragmentation in the Cape lowlands has resulted in the transformation of once contiguous habitat into numerous smaller patches that are scattered across the landscape and vary (considerably) in size and shape. These patches are isolated from each other by matrices of novel land use types and are often subjected to different disturbance regimes. Researchers on fragmentation usually have no control over these factors. Therefore, replicating and carrying out fragmentation studies on suitable spatial and temporal scales are common challenges faced by most researchers on fragmentation (see Körner & Jeltsch 2008). One of the greatest challenges encountered in this study was to find replicates of fragments with similar parameters (e.g. size, shape, type of matrix and disturbance regime). Moreover, the fragments used in this study were selected based on availability within a 10 km radius of the corresponding mainland and also on the willingness of the landowner to cooperate.

(2) Since the entire Cape region is highly fragmented, the largest remaining patch of each of the vegetation types was used as a “mainland” for comparison with smaller patches. This was done with full recognition of the fact that these are not perfect mainland-island systems.

(3) The main aim of the study was to assess the impact of reduced patch size resulting from habitat fragmentation on the Cape lowland vegetation. To achieve this and also meet one of the objectives of the funders, which was to sample the BIOTA Observatories in the region, all three major habitats in the region (i.e. fynbos, renosterveld and strandveld) had to be investigated. However, due to time constraints and the challenges of identifying plants in the Cape region to species level, only one vegetation type of each of the three major habitats could be included in the study. The patterns revealed apply mainly to the Atlantis Sand Fybos, Swartland Shale Renosterveld and Langebaan Dune Strandveld, but it is assumed that they reflect what may be found in the higher vegetation groups (i.e. fynbos, renosterveld and strandveld).

(4) While acknowledging the shortcomings of the sampling method (i.e the use of replicated relevées), which is considered a pseudoreplication according to Hurlbert (1984), this method was

based on the Standardised BIOTA Monitoring procedure prescribed by the funders in order to facilitate the comparison of the results with those obtained from other BIOTA Observatories elsewhere. However, such detailed and multi-scale sampling is nevertheless useful because it allows for the detection of rare species and takes into consideration the fact that information generated at one scale may not be suitable to answer questions at another scale.

(5) The use of morphological characters and/or categorisation taken from the literature to assign species particular traits, especially related to dispersal distance has been criticised (see e.g. Poschlod et al. 2005). However, the paucity of information on traits of most species in the Cape region meant that I had to rely on these methods as well as on expert knowledge to assign plant species to the traits selected. Besides, the traits selected were “soft” traits which are considered realistic surrogates for more functional, but difficult to measure “hard” traits (McIntyre et al. 1999).

(6) Despite the fact that experts in the field have reached an agreement on a set of plant traits with standardized, easy and universally applicable measurement protocols for trait-based community descriptions (Cornelissen et al. 2003), there is no generally accepted method for classifying plant species into types (see e.g. Petchey & Gaston 2006; Wright et al. 2006). Therefore, assessing how plant species in the Cape lowlands will respond to habitat fragmentation, posed two major challenges. First, the relevant traits had to be chosen. Secondly, an appropriate method had to be applied to classify the plant species into functional types. Trait selection was done using expert knowledge, and based on considerations of which traits are most likely to be sensitive to fragmentation. Plant functional types (trait combinations) were defined using two approaches (a subjective and an objective one), which yielded similar results in the end.

(7) The very strong synergetic relationships between habitat fragmentation and other biotic factors, such as ecosystem processes, land use, disturbance regime and alien plant species infestation, makes it difficult distinguish between true fragmentation (in this case, fragment size) effects, and effects the other confounding factors may have on species and species assemblages.

With all these constraints in mind, extrapolating the results found in this study to infer that the same patterns will be found in the entire Cape lowlands fynbos, renosterveld and strandevld or that they are only linked to habitat fragmentation (fragment size) is done with caution.

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Chapter 2

Ecosystem processes and threats to biodiversity in the Cape lowlands

Abstract

The Cape lowlands of South Africa and share the same evolutionary and ecological features that shaped the flora of the Fynbos Biome. These include a mediterranean-type climate, generally nutrient-poor soils, recurrent natural fires (particularly in fynbos and renosterveld) and intricate plant-animal interactions involving grazing, pollination and dispersal. In response to these, the plant species in the region have developed several adaptive features such as sclerophylly, serotiny, myrmecochory, obligate reseedling and resprouting abilities and highly specialised pollination systems. While the less accessible mountain habitats have remained almost intact, the lowland habitats have been severely transformed by human activities. Consequently, vast areas of natural lowland habitats that were once contiguous have been drastically reduced to several smaller patches that are isolated from one another by matrices of novel land-use types. Habitat fragmentation in the Cape lowlands has many effects that occur at different levels of biological organisation and spatial scales. All of these affect species numbers and composition in remnant patches. A detailed knowledge of species' behaviour and demography is necessary to predict their responses to habitat fragmentation. This is due to the fact that plant species are likely to respond differently to fragmentation because of differences in life history traits related to dispersal, establishment and persistence. Consequently, emphasis should be placed on research related to plant functional traits in order to better understand the long-term effects of habitat fragmentation.

Keywords: Habitat fragmentation, Cape Floristic Region, Fynbos Biome, plant adaptive features, plant species assembly patterns; plant functional types.

2.1 Introduction

For decades, the Cape Floristic Region (CFR) of South Africa has attracted the attention of botanists due to its floristic, ecological and evolutionary peculiarities (e.g. Campbell 1986; Cowling et al. 1997; Goldblatt 1997; Goldblatt & Manning 2000a, 2002a; Linder 2003; Pressey et al. 2003; Rebelo et al. 2006). Adding to the existing botanical and ecological studies, this study investigated the role of human-induced habitat fragmentation in the patterns and dynamics of three Cape lowland vegetation types namely Atlantis Sand Fynbos, Langebaan Dune Strandveld and Renosterveld Shale Renosterveld. The aim was to better understand the ecology of plant communities in a fragmented landscape and to propose mitigation measures to counteract the negative effects, thus contributing towards successful conservation planning and management in the region. This chapter provides the framework within which the study was conducted. It outlines some of the major ecological and evolutionary processes that have helped to shape the Cape lowlands flora and describes the impact of habitat fragmentation on these processes.

2.2 Ecological and evolutionary phenomena of the Cape lowlands flora

The Cape lowlands share the same evolutionary and ecological features that have contributed to shaping the flora of the Fynbos Biome. These include:

(1) The typical mediterranean climate with cool, wet winters and dry summers mainly in the west, since the east has more summer rainfall. As a result of this, the vegetation is dominated by sclerophyllous shrubs adapted to seasonal drought by their small leaf size and low transpiration rates (Rebelo et al. 2006). Native trees are conspicuously absent (Rebelo et al. 2006) even though many alien tree species are well established in the region. There is also an abundance of geophytes, especially in renosterveld (Esler et al. 1999; Goldblatt & Manning 2000a; Procheş et al. 2006).

(2) The soils are generally nutrient-poor, posing serious ecological challenges to the plant species. In response to this, the species have developed adaptive features such as serotiny (Le Maitre & Midgley 1992), myrmecochory (Bond & Slingsby 1984; Johnson 1992), and obligate reseeding and

resprouting abilities (Bond & Midgley 2003). In the absence of mycorrhiza, some species (mostly in fynbos) have developed cluster roots to facilitate nutrient uptake (Lamont 2003). There are few annuals, especially in fynbos, because the nutrient-poor soil does not permit them to complete their life cycles and produce seeds in one growing season (Wisheu et al. 2000). In addition to this, there is a low biomass of herbivores, especially in fynbos, where many plant species are low in nitrogen-to-carbon ratios and are therefore unpalatable (Le Maitre & Midgley 1992).

(3) The region is characterised by recurrent natural fires caused by lightning and/or rock falls which occur mainly in late summer and early autumn, particularly in fynbos and renosterveld (Rebelo et al. 2006), to which the plant species are well adapted (Bond & van Wilgen 1996). Fires occur at intervals of 5–50 years in fynbos, while in renosterveld, they occur at intervals of 2–10 years (Rebelo et al. 2006) or 3–40 years (Rebelo 1992a), depending on the grazing intensity. In strandveld, fires are rare due to the abundance of succulent shrubs and occur at intervals of 50–200 years (Rebelo et al. 2006). Man-made fires are frequent nowadays due to increased human population and are also increasingly being used as management options. The fire regime is influenced by the age of the vegetation, the fuel load and environmental factors such as moisture content, season, and temperature, time of day, wind and aspect. This also plays a vital role in species composition (van Wilgen et al. 1992). Smoke-induced seed germination, which for some taxa is the only means of breaking dormancy, is a typical plant species adaptation to fire in fynbos and renosterveld (De Lange & Boucher 1990; Dixon et al. 1995).

(4) The region is also characterised by intricate plant-animal interactions involving grazing, pollination and dispersal. It is believed that several large indigenous herbivores once roamed the Cape lowlands (Boshoff & Kerley 2001). These included *Loxodonta africana* (African elephant), *Diceros bicornis* (black rhino), *Hippopotamus amphibius* (hippo), *Syncerus caffer* (Cape buffalo), *Taurotragus oryx* (eland), *Equis burchelli quagga* (quagga), *Alcephalus buselaphus* (red hartebeest), *Damaliscus pygargus pygargus* (bontebok) and several species of antelope, which were associated with large carnivores such as the Cape lion (*Panthera leo*), leopard (*Panthera pardus*),

cheetah (*Acinonyx jubatus*), wild dog (*Lycaon pictus*), spotted hyena (*Crocuta crocuta*) and brown hyaena (*Hyaena brunnea*) (Rebelo et al. 2006). Although the indigenous Khoekhoen used to practise nomadic livestock farming (mainly sheep and cattle) with less impact on the ecosystem, livestock grazing was intensified with the arrival of the Dutch some 350 years ago (Deacon 1992; Krug et al. 2004). These animals preferred renosterveld on the more nutrient-rich soils (which might have been grassier in the past compared to fynbos and strandveld sites, Rebelo et al. 2006) rather than fynbos (Bigalke 1979; Johnson 1992; Owen-Smith & Danckwerts 1997). Through their feeding modes and physical disturbances, large herbivores change the structure, biomass, production and species composition of vegetation, thus altering ecosystem properties and causing long-term changes in ecosystems (Hobbs 1996; Owen-Smith & Danckwerts 1997; Archibald et al. 2005). Although grazing and fire intervals are implicated in the fluctuation between the shrub and grass states in renosterveld, the actual mechanisms involved are still unclear (Rebelo et al. 2006). Most of these animals were virtually driven to extinction through hunting for game and meat or the elimination of predators, scavengers and problem animals, which is why there are currently very few herbivores in the Cape lowlands, particularly in fynbos (Rebelo 1992a; Krug et al. 2004). Insect diversity is high (Le Maitre & Midgley 1992; Procheş & Cowling 2006) and there is also an exceptional diversity of pollination systems (Rebelo 1987; Johnson 1992, 1996), some of which are highly specialised (Johnson & Steiner 2000, 2003; Johnson 2004). These include: ornithophily (Rebelo et al. 1984; Goldblatt et al. 1999), therophily (Weins et al. 1983; Johnson et al. 2001), pollination by long-proboscid flies (Goldblatt & Manning 2000b), pollination by oil-collecting bees (Manning & Goldblatt 2002; Steiner & Whitehead 2002; Pauw 2004), beetle pollination (Picker & Midgley 1996), pollination by butterflies and moths (Goldblatt & Manning 2002b), and pollination by the Cape honeybee (*Apis mellifera capensis*), which is specifically adapted to survive the cold wet winters of this region (Hepburn & Crewe 1990; Hepburn & Guillardmod 1991). Ornithochory is another interesting animal-plant interaction that is common in strandveld where there are many fleshy-fruited plant species and frugivorous birds (Knight 1988); it is also frequent in renosterveld,

especially in fire-safe areas such as termitaria which harbour thicket species (Le Maitre & Midgley 1992). Ornithochory is virtually absent from fynbos due to the lack of a regeneration niche as the fruit and seedlings are killed by fire (Rebelo et al. 2006).

2.3 Causes of habitat fragmentation in the Cape lowlands

The large-scale influence of man on the natural habitats in the Fynbos Biome of South Africa (especially in fynbos shrublands as well as renosterveld shrublands and possibly also grassland), dates back to the arrival of European settlers more than 350 years ago (Deacon 1992). This resulted in the extensive habitat transformation (fragmentation and degradation) that prevails in the region today. The magnitude of such human-induced habitat transformation is strongly associated with topography and geographical location, with vegetation types on shale, granite, young alluvial sediments and ferricrete being the most heavily transformed (Rebelo et al. 2006). While the less accessible mountain habitats have remained virtually undamaged, the lowlands have been severely transformed by agriculture, urbanization, mining and invasion by mostly woody alien species

Lowland fynbos has been transformed by urbanization (Rebelo 1992b), alien plant species invasions (Macdonald & Richardson 1986; Richardson et al. 1992) and agriculture (Rouget et al. 2006). Agriculture and afforestation with mostly alien *Eucalyptus* and *Pinus* species account for 49%, while invasive alien plant species account for 36% of the area transformed (Rebelo et al. 2006). The transformation of renosterveld started at a small scale in pre-historical times with the indigenous Khoekhoen herders, who used fire to obtain additional grazing pastures for their livestock and has continued until today with transformation through mechanized agriculture and urbanization (Krug et al. 2004). Renosterveld, with its relatively-fertile soils, has been transformed to less than 10% of the original area since the arrival of the European settlers. It was and is still used for the cultivation of mainly cereals, grape and livestock farming, and is today considered the most endangered habitat in South Africa (Kemper 1997; Rouget et al. 2003a, 2003b; von Hase et al.

2003; Rouget et al. 2006). Unlike in renosterveld and fynbos, the transformation of strandveld is relatively recent and happened mainly due to invasion by alien *Acacia* species, agricultural exploitation, overgrazing (Liengme 1987) as well as urban development, mostly along the West Coast. Since all lowland habitat patches that are left are required to meet the conservation target of about 30% to represent $\frac{3}{4}$ of the species in the different vegetation types, most of them are of high conservation value and are even considered to be 100% irreplaceable (Rouget et al. 2006).

2.4 Consequences of habitat fragmentation in the Cape lowlands

Habitat transformation in the Cape lowlands has severely reduced once contiguous natural habitats into several smaller patches of various sizes and shapes scattered across the landscape and isolated from one another by different land uses (Kemper 1997; Rouget et al. 2003a, 2003b; von Hase et al. 2003). The surrounding matrices often harbour activities with by-products that directly threaten biodiversity in the remnant patches (Rebelo et al. 2006). Most of the patches are located on private property (von Hase et al. 2003) and the much sought after interior valleys and coastal lowlands of the Fynbos Biome and thus, remain vulnerable to further transformation (Jonas et al. 2006).

Habitat fragmentation has many effects. These include an increase in the number of remaining patches, the reduction in size and further isolation of remnant patches from each other, the alteration of the microclimate within and around remnant patches, as well as the change in the surrounding matrix (Saunders et al. 1991; Hobbs & Yates 2003; Groom et al. 2005; Lindenmayer & Fischer 2006). All these processes apply to the Cape lowlands and impact on biodiversity at different levels and spatial scales, ultimately affecting species numbers in and composition of remnant patches (see Figure 2.1). The main focus of this study was the effect of reduced patch size, but other aspects which were not explicitly measured, such as patch distance from nearest neighbour and matrix type (which influence patch isolation), disturbance regime (fire and grazing) and alien infestation, were used as explanatory variables of within-patch dynamics.

Since the consequences of habitat fragmentation are wide ranging and occur at different levels of biological organisation and spatial scales, their full impact may be confounded by several factors (Laurance 2008). The spatial scale may influence the extent of the fragmentation effect since most ecological phenomena vary with scale (Palmer & White 1994; Crawley & Harral 2001). The temporal scale of the fragmentation event may also mask the magnitude of its effect through short term crowding (Debinski & Holt 2000; Ewers & Didham 2006). Plant species may also respond differently to fragmentation due to trait differences (Ewers & Didham 2006; Laurance 2008). The matrix influences fragment connectivity, and thus plays a vital role in how different species respond to fragmentation (Fahrig 2001; Jules & Shahani 2003; Jonas et al. 2006; Wiser & Buxton 2008).

2.4.1 Reduced patch size and increased isolation

Fragmentation leads to the loss of habitat and changes in the spatial configuration of remnant patches, which in turn alter species numbers, composition and interactions (Saunders et al. 1991; Fahrig 2003; Hobbs & Yates 2003). Small patches often support small populations, which are more susceptible to stochastic events (demographic, genetic and environmental), putting them at higher risk of extinction (Pimm et al. 1988; Lindenmayer & Fischer 2006). This situation is further compounded by the ‘isolation effect’ resulting from the reduced connectivity between remnant patches that may prevent gene flow due to the breakdown of plant-pollinator and plant-disperser relationships. This will most likely affect re-colonisation (the “rescue effect”) from other patches (Brown & Kodric-Brown 1977; Cole 1981; Burkey 1989) and may lead to altered fecundity and genetic deterioration. This in turn renders species in isolated patches more prone to demographic and environmental changes (Hobbs & Yates 2003; Lindenmayer & Fischer 2006). Thus, the dispersal behaviour and demography of a species will determine its response to fragmentation.

Since colonising ability is related to dispersal mode, long-distance dispersed species are more likely to arrive at isolated patches than short-distance dispersed species (Bond 1994; Hobbs & Yates 2003; Harris & Johnson 2004; Aguilar et al. 2006). However, the arrival of a species in a patch is no

guarantee of its continued existence there. Successful reproduction and recruitment, which depend on physical and biotic factors such as nutrient availability and competitive interactions, are required (Hobbs & Yates 2003). The increased isolation of remnant patches from one another is also more likely to affect obligate reseeders, specialist-pollinated and bird-dispersed species than resprouters, geophytes and generalist-pollinated species (Bond et al. 1988; Pauw 2004; Rebelo et al. 2006). In addition, an isolated patch may have more species than it can maintain and so, species will eventually be lost as the changes brought about by fragmentation take effect (Debinski & Holt 2000; Ewers & Didham 2006; Helm et al. 2006).

2.4.2 Effects on microclimate

Habitat fragmentation causes changes in the physical and biogeographic environments. This can lead to significant alteration of fluxes of radiation, wind, water and nutrients across the landscape, especially near the edges. This results in what is commonly referred to as the “edge effect” and has numerous consequences on the biodiversity within remnant patches (see Saunders et al. 1991; Hobbs & Yates 2003; Lindenmayer & Fischer 2006). Replacing natural vegetation with crop species that differ in architecture alters the radiation balance by increasing sunlight reaching the ground. This increased soil heating may affect nutrient cycling processes such as litter decomposition, soil moisture retention, and resource availability, through its effects on soil microorganisms and invertebrate numbers and activities (Saunders et al. 1991; Hobbs & Yates 2003; Lindenmayer & Fischer 2006). In addition, the entire pattern of wind fluxes over the landscape is altered. This has serious implications for plant gas exchange as there is increased exposure, which may result in physical damage to plants and increased evapotranspiration (Saunders et al. 1991). Wind increase may result in reduced soil moisture and may affect the regeneration of species requiring high soil moisture (Saunders et al. 1991). The transfer of particulate matter (e.g. dust, seeds, nutrients and farm chemicals) from the surrounding matrix also

increases, while gaps created through clearing of natural vegetation favour invasive and pioneer species (Saunders et al. 1991; Groom et al 2005; Rebelo et al. 2006).

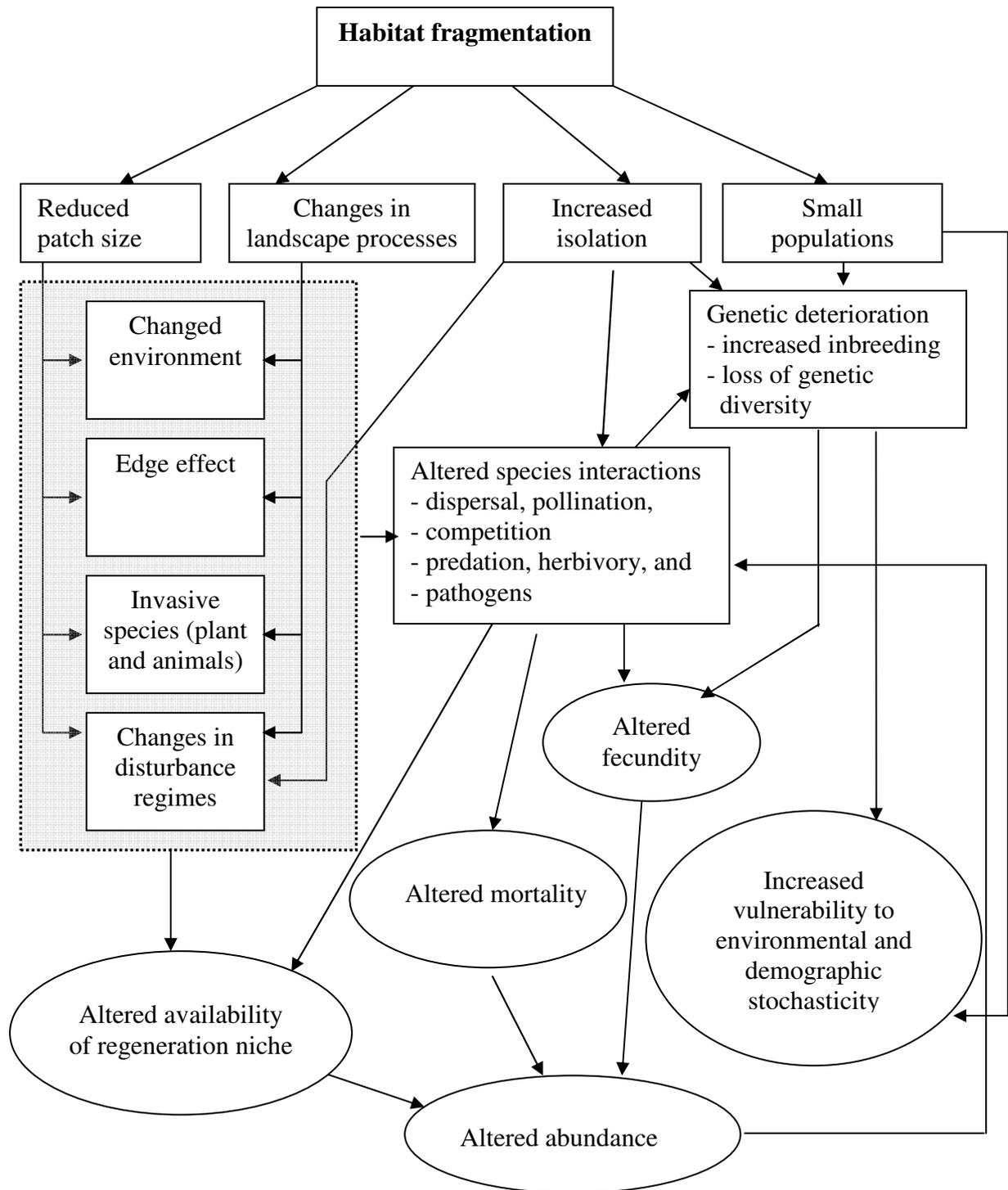


Figure 2.1 Conceptual model on the effects of habitat fragmentation on plants reproduced from Lindenmayer and Fischer (2006), based on that of Hobbs and Yates (2003)

2.4.3 Changes in the surrounding landscape

Dynamics within remnant patches are often driven by factors originating from and temporal changes in the surrounding matrix (Fahrig 2001; Jules & Shahani 2003; Wisser & Buxton 2008). In the case of the Cape lowlands, most of the remnants of natural vegetation are in matrices of habited environments, cultivated, degraded and pasture lands and/or invasive alien plant species. These matrices are often subject to different disturbances such as trampling, farm chemicals, grazing, frequent or infrequent fires etc, which may inhibit the establishment and regeneration of some native species in remnant patches (Bond et al. 1988; Kemper 1997; Rouget et al. 2006). For example, grazing by livestock may help in propagule dispersal, reducing isolation between remnants and therefore restoring and preserving metacommunities (Pueyo et al. 2008). However, grazing may also have negative synergistic effects on fragmentation by facilitating invasions of alien plant species that compete with native species (Kemper et al. 1999; Hobbs 2001). The physical damage caused by grazing animals can change the structure and species composition of the vegetation, leading to further habitat degradation with severe ramifications for ecosystem functioning (Owen-Smith & Danckwerts 1997; Archibald et al. 2005).

Patches surrounded by alien plant species are more likely to be invaded (Haila et al. 1993; Hobbs & Yates 2003; Lindenmayer & Fischer 2006). Invaders (especially woody species) can significantly alter the fuel structure and hence the fire regime. This in turn can inhibit the regeneration of some native species in remnant patches (Macdonald & Richardson 1986; Rebelo et al. 2006). The change in fire regime occurs through increased biomass and fuel loads, which increases fire hazards. Some alien plant species change the nutrient status of the soil as well as the faunal community (Rebelo et al. 2006). Altered feeding behaviour of native generalist birds that disperse seeds is likely to have detrimental effects on native plant species. This has been reported in strandveld (Richardson & Van Wilgen 2004). Alien annuals (mostly grasses) are also becoming invasive in the Cape lowlands, and

although the extent and impact of such invasions are largely unknown, they are thought to severely affect geophytes (Vlok 1988; Musil et al. 2005; Rebelo et al. 2006).

The type of matrix also determines its resistance i.e. the difficulty of species to cross it (Nikolakaki 2004) and can disrupt plant-animal mutualisms (Bond 1994). Based on how difficult it is for species to cross the different matrices, Jonas et al. (2006) allocated resistance values ranging from 0 (very low) to 100 (high) in the Fynbos Biome. The different matrices and their resistance values are: 0 for indigenous forests and woodlands, thicket/bushveld, grassland, and wetlands; 25 for water bodies; 50 for minor roads and degraded land; 75 for cultivated land and alien forest plantations; and less than 75–100 for mines and quarries, major roads, urban and built-up land. Using the matrix resistance values, average fragment size and connectivity, Jonas et al. (2006) also calculated habitat fragmentation indices for different vegetation types and showed that Swartland Shale Renosterveld had the highest fragmentation index of about 62, thus making it the most threatened of all the Cape lowland vegetation types.

2.5 Predictors of ecosystem response to global change

Biodiversity has been variously defined to include the number and composition of genotypes, individuals, demes, populations, metapopulations, species, functional types, communities, ecosystems and landscapes in a given area (e.g. Noss 1990; Franklin 1993; Begon et al. 1996; Díaz & Cabido 2001). Biodiversity therefore occurs at several hierarchical levels, each having links to the response of ecosystems to global change (Risser 1994; Díaz & Cabido 2001). However, ecologists have long used species to describe plant communities while other components such as functional diversity have often been underestimated (Díaz & Cabido 2001) or neglected. Although phylogenetic classifications will remain the backbone of systematic and evolutionary studies, their application in ecology has limitations. Since the potential species pool differs from region to region, results from species-based studies may only apply to the particular region where the study was

conducted. Moreover, species-based classifications often do not consider within-species variability, which may be crucial for some ecological processes (Pillar & Sosinski 2003).

The response of plant species to global changes such as habitat fragmentation depends on plant life history traits like dispersal ability, perturbation tolerance, and habitat specificity (Kolb & Diekmann 2005; Cagnolo et al. 2006). Therefore, to better understand the effects of global change on terrestrial ecosystems, more attention should be given to easily measured, universally-applicable predictors. Studies from different parts of the world now show that classifying plant species into functional types using sets of co-occurring plant traits is more useful in predicting the response of an ecosystem to global change (Díaz & Cabido 1997; Lavorel et al. 1997; Smith et al. 1997; Steffen & Cramer 1997; McIntyre et al. 1999; Cornelissen et al. 2003).

Plant functional type (PFT) is defined as a group of plant species that, irrespective of phylogeny, are similar in a given set of traits and similar in their responses to environmental factors and/or their roles in ecosystems (Gitay & Noble 1997). Therefore, the focus of this study was on plant functional traits that were deemed relevant to species' responses to habitat fragmentation, although species were not ignored. After all, species remain the most tangible component of biodiversity and continue to play a vital role in biodiversity conservation since most management interventions are based on species.

2.6 Formation of plant communities

Plant communities result from a series of biotic and abiotic filters that successively (both on short-term and long-term time scales) select from a regional species pool, those species and traits that can endure the conditions prevalent in a particular site (Woodward & Diament 1991; Keddy 1992; Weiher & Keddy 1995, 1999). Thus, the composition and functioning of a plant community is the ultimate outcome of the operation of these filters that act at different spatial and temporal scales to

select individuals with suitable responses, resulting in assemblages with varying trait compositions (Lavorel & Garnier 2002). This implies that a plant community is not just a random group of species with traits that enable the species to cope with the prevalent abiotic and biotic conditions, but that also enable them to coexist (Pillar et al. 2009). Therefore, there is likely to be trait-convergence assembly patterns (TCAP) among species within a community if they are very similar in their ecological requirements. On the other hand, trait-divergence assembly patterns (TDAP) will be found when the coexistence of species is restricted by their trait similarity (Pillar et al. 2009). TDAP is expressed when communities contain species with less similar traits. Since both TCAP and TDAP can be found in species composition of communities along ecological gradients, these assembly patterns should be revealed within the plant communities sampled in relation to various site factors associated with habitat fragmentation. This will indicate that the composition and functioning of the plant communities in the Cape lowlands are influenced by factors related to habitat fragmentation such as patch size, patch distance from nearest neighbour, surrounding matrix type, disturbance (e.g. grazing, fire and alien infestation) and soil fertility (vegetation type). These factors operate at different spatial and temporal scales and select from the regional species pool, those species with appropriate responses that can persist at any given site, resulting in assemblages with varying trait compositions. For instance, if the communities in the small and less connected fragments are predominantly composed of species with similar traits such as long distance dispersed and generalist-pollinated species, it would imply that they are responding in a similar way to factors such as patch distance and /or surrounding matrix type, thus expressing TCAP. On the other hand, TDAP or dissimilarities in trait composition can be expected if the factors impacting on the sites are different. For example one would expect more resprouters in grazed than in ungrazed sites and fewer annuals in the less fertile (fynbos) than in the more fertile (renosterveld and strandveld) fragments.

2.7 Implications of habitat fragmentation for the Cape lowlands

Fragmentation in the Cape lowlands, while relatively recent in evolutionary time, has severely reduced natural habitats that were once contiguous into tiny fragments embedded in agricultural fields, urban development, and alien vegetation, and which are often subjected to changes in natural disturbance regimes. These fragments are scattered across the landscape and on different soil types; possess different vegetation types, and vary in size, shape and degree of isolation. Assuming that plant communities result from the selection of species and traits that can persist at a particular site from the regional species pool through biotic and abiotic filters, one can expect that habitat fragmentation in the Cape lowlands will lead to the following:

- (1) Loss of species, the magnitude thereof being proportional to patch size and sampling scale;
- (2) Loss of plants functional types (PFTs), the magnitude thereof being proportional to the fragment size, sampling scale, connectivity and the resistance value of the surrounding matrix (i.e. the difficulty of species to cross the matrix) of the remnant patch;
- (3) If the disruption of dispersal, pollination and insularisation, which are linked to small population size, are the main drivers of pattern, then in smaller and less connected patches (i.e. patches furthest from the nearest neighbour), one would expect to find:

- an over-representation of PFTs with traits conferring persistence at the individual, local and landscape scales (such as perennials, long distance dispersal ability, generalist-pollinated and resprouting ability); conversely, one would expect to find fewer annuals, short-distance dispersed, specialist-pollinated and dioecious species in smaller, farther-removed patches;

- (4) If selective processes determine pattern, then one would expect the fragmentation effect to be confounded by site factors such as disturbance regime (e.g. grazing, fire, and alien invasion). Thus one would expect a higher representation of PFTs with traits reflecting species' abilities to cope with the prevalent disturbance regime in a particular site. Consequently, one would expect to find:

- In areas prone to grazing, a high representation of PFTs with traits such as resprouting ability and spinescence;

- In areas subject to fire, one would expect to find a predominance of short- and long-distance dispersed perennial resprouters that require fire to regenerate (fire gap exploiters) or can persist without fire, as well as annual seeders that require fire to stimulate germination;
- In areas invaded by aliens, one would expect a low proportion of slow growing resprouters (i.e. poor competitors);

(5) Plant species with traits that confer high persistence ability at the individual, population, community/local and regional/landscape levels will be the least threatened and therefore the most widely distributed across the Cape lowlands;

(6) If the composition and functioning of plant communities in the Cape lowlands are influenced by factors related to fragmentation such as patch size, patch distance from nearest neighbour, surrounding matrix type and other site factors such as disturbance regime and soil fertility, then species with similar traits and similar responses to these site factors will be expected to coexist, thus expressing TCAP whereas TDAP will be found if the plant communities contain species with less similar traits due to differences in the prevalent site factors;

(7) Given that fragmentation in the Cape lowlands is relatively recent compared to evolutionary time, the effects may be masked by the relatively-short time lag of the fragmentation event.

2.8 Synthesis and recommendations

Although the Cape lowland habitats are severely transformed, the remnant patches are still important for biodiversity conservation. This is so because most of them are 100 per cent irreplaceable. Biodiversity conservation in this region has to take place within the present context of global changes such as habitat fragmentation, invasion by alien plant species and climate change.

Given that very little funds are available for conservation, there is an urgent need to develop appropriate means of prioritising conservation efforts. Therefore, successful conservation of the unique biodiversity of the Cape lowlands requires the use of appropriate measures of ecosystem

status to identify the most threatened and least protected vegetation types. These should then be given urgent conservation priority. Such areas should be mapped and equipped with management plans that mimic the natural disturbance regimes in the different vegetation types. These could be controlled burning in fynbos and the reintroduction of large herbivores in renosterveld and strandveld. Considering that most of these patches are on private property and may not be strictly subjected to the implementation of formal reserve regulations, conservation through protected areas may not always be the solution. Instead, a concerted effort must be made to encourage all stakeholders (government, local councils, NGOs, civil society, private individuals and industries) to prevent further habitat destruction. One way of doing this is through the initiation and careful implementation of large-scale restoration programmes to link fragments. In addition, local council and provincial governments should incorporate spatial biodiversity priorities and environmental assessment processes into their land-use planning.

Although the Fynbos Biome has been studied for decades, many gaps still exist in the knowledge about it. To bridge this knowledge gap and to gain a better understanding of how this ecosystem functions, there is need for more detailed studies in the region. For instance, research is largely insufficient and is required on systematic primary taxonomy and vegetation inventories. There is also a need for more detailed studies on the long-term effects of habitat fragmentation and the role of corridors. Such studies should identify the patches and links that are indispensable from those that are expendable.

Emphasis should be placed on research related to plant functional types (PFTs). This is because plant species are likely to respond differently to the creation of sub-populations and may have differential susceptibility to habitat fragmentation due to differences in life history traits related to dispersal, establishment and persistence. This means that detailed knowledge of species' behaviour and demography is necessary to predict their responses to habitat fragmentation. Despite the

existing commendable efforts toward controlling and managing alien plant species invasion, there is still need for more research on the impact and control of all alien invasive plants including alien grasses, considering that they seem to affect native species. Moreover, since these lowlands are highly-fragmented and are often altered by other anthropogenic changes such as changes in disturbance regime, alien plant species invasion and pollution, there is need for detailed studies of the synergistic interactions between fragmentation and these changes, which may confound the fragmentation effect. With the effect of global climate change in the region, there is also need for studies that focus on the magnitude of habitat transformation expected to result from climate change. Such studies should help to identify the taxa and vegetation types that will be most affected and should propose mitigation measures.

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Chapter 3

Effects of fragment size and sampling scale on species richness in three Cape lowland vegetation types

Abstract

Habitat loss due to fragmentation is considered the main threat to biodiversity worldwide because of its disruptive impact on species and ecological processes. In South Africa, the Cape lowlands have been heavily transformed by human activities, leading to the reduction of once-adjointing natural habitats into fragments embedded in novel land-use types. Conservationists doubt whether these fragments are worth conserving and if so, how best to do so. This study investigated the effect of fragment size on plant diversity by comparing species richness from incidence data at four scales (0.1, 1, 50, and 100 m²). Species were sampled within modified Whittaker plots in representative mainlands and three different-sized fragments of three Cape lowland vegetation types (Atlantis Sand Fynbos - ASF, Swartland Shale Renosterveld - SSR and Langebaan Dune Strandveld - LDS). Overall, species accumulation curves showed weak and inconsistent fragment size effects at different sampling scales, indicating an area rather than a fragmentation effect *per se*. However, fragment size effect was evident in fynbos, with fragments < 600 ha having significantly fewer species than the mainland at all scales. This fragment size effect was not very evident in SSR and LDS. Possible confounding factors of the fragment size effect are: - (1) the sample size and number, (2) the time lag since fragmentation, (3) trait-mediated differences in plant species responses to fragmentation, (4) the high degree of habitat diversity and endemism in the region, and (5) site factors (notably fire and grazing). The higher species numbers recorded in the fragments combined, compared to the mainlands, the high species turnover (β -diversity) and the high complementarities among sites for the three vegetation types indicate that the fragments do contribute to overall regional species diversity.

Keywords: complementarity, fragmentation, fynbos, patch size, renosterveld, spatial scale, species accumulation curves, strandveld

3.1 Introduction

Habitat fragmentation affects species abundances, composition, and interactions within and between habitat patches through habitat loss; changes in landscape processes; increased isolation; changes in the spatial configuration; and reduced populations in remnant patches (Saunders et al. 1991; Hobbs & Yates 2003; Lindenmayer & Fischer 2006). Due to its disruptive impacts, habitat fragmentation is regarded today as one of the greatest threat to biodiversity worldwide (see Wilcove et al. 1986, 1998; Debinski & Holt 2000; Fahrig 2002, 2003; Henle et al. 2004; Groom et al. 2005; Rebelo et al. 2006; Rouget et al. 2006).

Due to their size, the small patches often harbour small populations that are more sensitive to stochasticity and therefore, are at greater risk of extinction (MacArthur & Wilson 1967; Pimm et al. 1988; Lindenmayer & Fischer 2006). This state of affairs is further aggravated by the ‘isolation effect’ that prevents gene flow and re-colonisation from other patches (the “rescue effect”, Brown & Kodric-Brown 1977). What happens within remnant patches is often influenced by factors originating from the surroundings (Fahrig 2001, Jules & Shahani 2003; Wisser & Buxton 2008). Consequently, the invasibility of remnant patches is likely to increase (Hobbs & Yates 2003; Lindenmayer & Fischer 2006) depending on its surroundings. Alien plants change the disturbance regimes in remnant patches for instance through fire, thus affecting the regeneration of some native species (Macdonald & Richardson 1986; Haila et al. 1993; Rebelo et al. 2006).

Habitat fragmentation has many feedback effects that occur at different levels of biological organization and spatial scales, affecting individual species as well as species assemblages (Hobbs & Yates 2003; Lindenmayer & Fischer 2006, 2007). In addition to the fact that species in remnant patches are under a modified environment of reduced area, increased isolation and novel ecological boundaries, the fragments are often altered by other anthropogenic changes such as pollution. The synergistic interactions between fragmentation and these human-induced changes may confound the

full impact of fragmentation when coupled with trait-mediated differences in species responses and time lag in the manifestation of fragmentation effects (Ewers & Didham 2006; Laurance 2008).

The species-area relationship (SAR), which stipulates that species numbers increase with increase in the area sampled, is a general characteristic of ecological communities that has attracted much attention and that continues to play a major role in conservation biology (Holt 1992; Rosenzweig 1995; Arita & Rodríguez 2002; Cam et al. 2002; Arita & Rodríguez 2004). The species-area relationship is described using species-area curves (McGuinness 1984) and deals with the number of species in areas of different sizes irrespective of their identity. SARs were used to estimate species extinction rates due to land-use change (Pimm et al. 1995) and became important tools for quantifying changes in species richness across different spatial scales (Rosenzweig 1995; Lomolino 2000; Drakare et al. 2006). Species accumulation curves (SACs) are appropriate for estimating and comparing species richness between sites when only presence-absence data are collected (Gotelli & Colwell 2001; Colwell et al. 2004) and feature the rates of accumulation of new species over a pooled set of equal-sized samples (Ugland et al. 2003).

The Cape lowlands form part of the Fynbos Biome and host most of the plant species in the Cape Floristic Region (CFR). Having a predominantly mediterranean-type climate, these lowlands are dominated by species-rich ecosystems characterised by fine-leafed, sclerophyllous and evergreen shrubs forming fire-prone fynbos and renosterveld as well as fire-shy strandveld (see Chapter 1). Being more productive and more accessible than mountain habitats, these lowlands have been severely transformed by agriculture, urbanization, mining, and by invasion of alien plant species (Rebelo et al. 2006). Although they form part of a biodiversity hotspot (the CFR) and are recognised as regional conservation priority areas (Cowling & Pressey 2003; Cowling et al. 2003), most of these lowland habitats are found outside formally protected areas. Renosterveld is the most highly transformed and least conserved of the three Cape lowland habitats (see Chapter 1). In

contrast, the high-altitude regions are better conserved because of lower conservation opportunity costs involved (Pressey 1994; Cowling & Pressey 2003; Rouget et al. 2003a; von Hase et al. 2003).

Despite the extensive habitat transformation (fragmentation and degradation) in the CFR, and in the Cape lowlands in particular, relatively few studies have been carried out to investigate the impact fragmentation on plant species diversity (e.g. Bond et al. 1988; Cowling & Bond 1991; Kemper 1997; Kemper et al. 1999, 2000). These studies, like similar ones elsewhere (e.g. Simberloff & Gotelli 1984; Debinski & Holt 2000; Fahrig 2003), revealed rather weak and/or conflicting fragmentation effects, especially with respect to species richness relative to fragment size. Most of the remnant patches in the Cape lowlands are located on private properties, they are scattered across the landscape, and vary in size, shape and degree of isolation (Rouget et al. 2003b; von Hase et al. 2003). These patches are also often surrounded by new land-use types (such as vineyards, orchards, cereal and pasture lands, invasive alien species, settlement and urban development) that are subjected to farm chemicals, grazing, changes in fire regime, and trampling (Kemper 1997; Rebelo et al. 2006).

This situation, coupled with limited resources, has left CapeNature (the statutory conservation body of the region), conservationists and conservation-conscious landowners doubting whether these fragments are worth conserving, and if so, how best to do so. Therefore, fine-scale studies are necessary to ascertain the conservation value of these remnant patches. Whereas previous studies focused on single vegetation categories, this study is the first to focus on all three Cape lowland vegetation types. Fragmentation effects in strandveld are studied here for the first time ever.

I investigated the effect of reduced patch size on species richness and complementarity at different spatial scales in three Cape lowland vegetation types namely, Atlantis Sand Fynbos (ASF), Swartland Shale Renosterveld (SSR) and Langebaan Dune Strandveld (LDS). The aim was to

determine whether, and to what extent, the fragments contribute to overall regional plant species diversity. It is expected that habitat fragmentation would lead to the loss of species and the magnitude thereof is expected to be proportional to patch size and sampling scale. However, if patterns are determined by selective processes, then the effect of reduced patch size on species richness would be confounded by site factors such as disturbance regime (e.g. grazing, fire, and alien invasion). Since habitat fragmentation in the Cape lowlands is relatively recent compared to evolutionary time, the effects on species richness may also be masked by the relatively-short time lag of the fragmentation event.

3.2 Methods

3.2.1 Study sites

The vegetation types and sites selected for the study are as described in Chapter 1 (section 1.4.1).

3.2.2 Sampling

Species inventories were carried out in three plots per site using a modified 50 m x 20 m Whittaker plot design (Stohlgren et al. 1995), between September and December (i.e. in spring and summer) of 2004 and 2005, when most species were flowering. In total, 12 plots were sampled for each vegetation type, each 50 m x 20 m having ten 0.1 m², ten 1 m², three 5 m² and three 100 m² subplots (Appendix 1). This design allows for detailed sampling and the detection of rare and important species or habitats (Colwell & Coddington 1994; Stohlgren et al. 1997) and also recognises that information collected at one scale may not be appropriate to answer questions at another scale. In each sub-plot, presence-absence and Braun-Blanquet cover-abundance data of plant taxa were recorded and herbarium specimens were collected and identified in the Compton Herbarium, Kirstenbosch, using the nomenclature and taxonomic concepts in Goldblatt and Manning (2000).

3.2.3 Estimation of species richness

Only indigenous species were included in all data analyses since only very few alien species were found in the sites sampled. In sites where alien plant species were present, the occurrence of these alien plants was used as one of the explanatory variables for within-patch patterns and dynamics. In order to estimate species richness, the presence-absence data for indigenous species in the different sub-plots (0.1, 1, 50 and 100 m²) were pooled into a species-by-sample incidence matrix and imported into EstimateS version 7.5 (Colwell 2005) for the computation of closed-form expressions of expected species richness with approximate upper and lower 95% confidence intervals (CIs). The Mao Tau expected richness function and its 95% confidence intervals are computed analytically (Colwell et al. 2004; Mao et al. 2005) and do not need any resampling runs in EstimateS (Colwell 2005). These were used to construct and compare species accumulation or “sample-based rarefaction” (Gotelli & Colwell 2001) curves. The 95% CIs allowed for direct statistical comparisons of richness of different sites for the different scales (Colwell et al. 2004). The accumulation curve of species richness in samples is the average number of species under all possible permutations of the samples. Thus, samples are independent and may occur anywhere in the random permutation (Ugland et al. 2003).

Apart from being the most appropriate method for the kind of data collected (i.e. incidence data), accumulation curves are also useful for assessing the completeness of inventories, and the estimated asymptote is used as species richness estimate (Colwell & Coddington 1994; Gotelli & Colwell 2001; Colwell et al. 2004). Using rarefaction curves is one way of avoiding some of the common pitfalls in quantifying and comparing biodiversity (Gotelli & Colwell 2001). Sample-based rarefaction curves implicitly reflect empirical levels of within-species aggregation of individuals by considering only incidence, thus providing a realistic estimate of species numbers to be found in sets of real-world samples (Colwell & Coddington 1994; Gotelli & Colwell 2001). Alpha, beta and gamma diversities were also estimated, with α -diversity being the first point on the SAC, β -

diversity is the difference in species richness between the last and first points on the SAC, and γ -diversity is the total cumulative species richness in a pooled set of samples (Crist & Veech 2006).

Given that the asymptotic 95% CIs computed by EstimateS are approximate, and that the Mao Tau richness estimator is normally distributed (Colwell et al. 2004), a maximum likelihood ratio was used to derive a test statistic Chi-square = $-2\ln\lambda$ (where λ = likelihood ratio), which was used to complement the test for the null hypothesis (H_0) in addition to comparing 95% CIs of SACs. The maximum likelihood test was particularly useful for cases with marginal overlap of the SACs' CIs. As a result of reduced patch size due to fragmentation, the following predictions were made:

- (1) There will be significant difference in species accumulation (theta) with increasing sampling effort among the four sites, i.e. theta mainland (ML) > theta largest fragment (LF) > theta medium-sized fragment (MF) > theta smallest fragment (SF) and;
- (2) There will be significant difference in species accumulation (theta) with increasing sampling effort between the mainland and the combined fragments (i.e. theta ML > theta combined fragments (CF)). The null hypotheses were rejected in favour of the alternative hypotheses if there were no overlaps in the 95% CIs of the SACs and/or the p-value of the maximum likelihood test $< \alpha$ (0.05).

3.2.4 Estimation of complementarity

Complementarity (C) was used as a measure of distinctness or dissimilarity between species assemblages of the respective “mainlands” and their corresponding fragments. Incidence matrices for each site were constructed by pooling data for all sub-plots for the three 50 m x 20 m plots and complementarity between sites calculated using the formula of Colwell and Coddington (1994):

$$C_{jk} = \frac{\sum_{i=1}^{S_{jk}} |X_{ij} - X_{ik}|}{\sum_{i=1}^{S_{jk}} \max(X_{ij}, X_{ik})}$$

(where X_{ij} and X_{ik} are the incidence values (1, 0) for species i in list j and list k)

3.3 Results

3.3.1 Fragment size and sampling scale effects

Only the general trends (Figure 3.1), the box plots (Figures 3.2 – 3.4) of mean species accumulation (richness) per site for the three vegetation types, as well as the significance (effect size) of the confidence intervals (CIs) and the maximum likelihood (Max L) Chi-square tests (Table 3.1) are presented here. Comparisons between sites for all three vegetation types at the four different scales (i.e. 0.1, 1, 50 and 100 m²), respectively, are in Appendices 2, 3, 4, and 5 (for ASF), 6, 7, 8, and 9 (for SSR) and 10, 11, 12, and 13 (for LDS).

The ASF SACs did not approach asymptote at all sampling scales (Figure 3.1 A-D), indicating that the sample scales and number were not sufficient for a full species representation. There was a general positive relationship between species richness and fragment size in ASF, with more species recorded per unit area sampled in the mainland than in the fragments, as well as in larger fragments than smaller ones. The only exception was at the 0.1 m² scale where slightly more species were recorded in the smallest, than in the medium-sized fragment (Figure 3.1 A-D). More species were recorded with increasing sampling effort in the mainland than in the medium-sized fragment at all sampling scales (Figure 3.2), despite the marginal overlap of the CIs at the 0.1 and 50 m² (Table 3.1). Species richness was also much higher in the mainland than in the smallest fragment at all but the 0.1 m² scale (Figure 3.2 A and Table 3.1). The maximum likelihood test also showed that species richness was higher in the largest than in the smallest fragment at the 1 and 50 m² scales, although there was a slight overlap of their CIs (Table 3.1, see also Figure 3.2 B and C). At the 50 and 100 m² scales, species richness was higher in the fragments combined (653 ha) than in the mainland (Figure 3.2 C and D, and Table 3.1). Species richness did not differ much between the other sites at all the scales (Figure 3.2 A-D and Table 3.1).

All SSR curves did not approach asymptote, indicating that sampling was not sufficient at all scales. Although there was no clear positive relationship between species richness and fragment size in SSR, the smallest fragment was lowest in species richness at all scales (Figure 3.1 E-H and Figure 3.3 A-D). The medium-sized fragment was consistently much richer in species than the other sites at all four scales (Figure 3.1 E-H and Figure 3.3 A-D), despite the marginal overlap of CIs between this and the largest fragment at the 0.1 and 1 m² scales (Table 3.1). Species richness was also much higher in the largest fragment than in the smallest one at all scales (Figure 3.3 A-D and Table 3.1). More species were also found in the mainland than in the smallest fragment at the 50 and 100 m² scales (Figure 3.3 C and D), despite the slight overlap of their CIs (Table 3.1). Fewer species were recorded in the mainland than in the largest fragment at all but the 0.1 m² scale (Figure 3.3), despite the marginal overlap of the CIs at the 1 and 100 m² scales (Table 3.1). Species richness was much higher in all the fragments combined (385 ha) than in the mainland at all scales (Figure 3.3). Species richness did not differ much between the other sites at all scales (Figure 3.3 and Table 3.1).

As for SSR, trends in LDS showed no clear positive relationship between fragment size and species richness at all sampling scales (Figure 3.1 I-M and Figure 3.4 A-D). Asymptote was again not reached, an indication that the sampling was not enough for a full species representation. More species were recorded in the medium-sized fragment at the smaller scales (Figure 3.1 I and K, and Figure 3.4 A and B) and in the largest fragment at the larger scales (Figure 3.1 L and M, and Figure 3.4 C and D), which indicates a scale effect. Species richness was slightly higher in the largest fragment than in the mainland and much higher in the largest fragment than in the smallest one fragment at the 50 and 100 m² scales (Figure 3.4 C and D, and Table 3.1). The medium-sized fragment was slightly richer in species than the smallest one at the 1 and 50 m² scales (Figure 3.4 B and C, and Table 3.1). Species richness for all LDS fragments combined (96 ha) was higher than in the mainland (Table 3.1) and much more at the bigger scales (Figure 3.4 A-D).

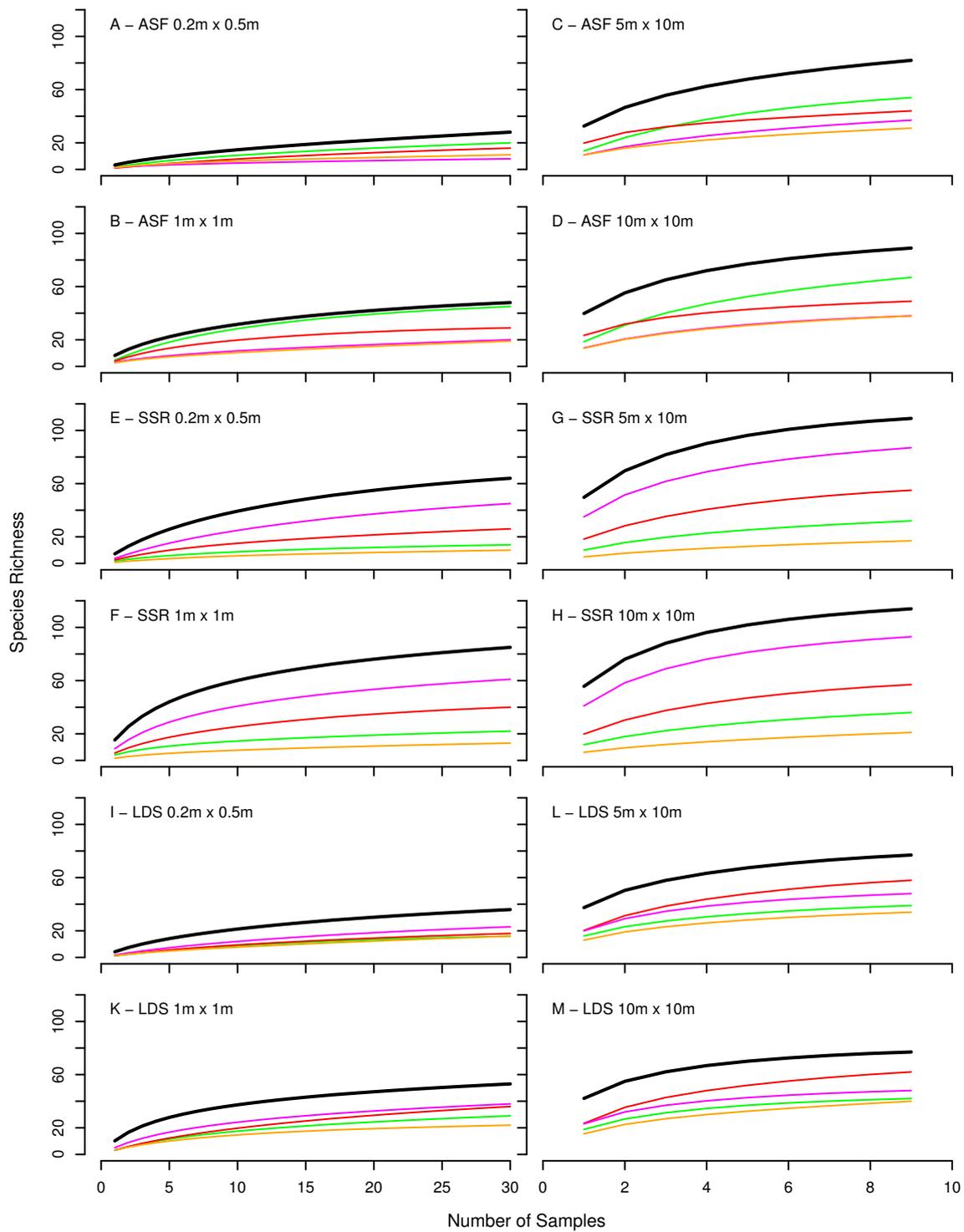


Figure 3.1 Species accumulation curves for the mainland and fragments at 0.1, 1, 50, and 100 m² in: **ASF** (A-D), **SSR** (E-H) and **LDS** (I-M). Species richness is based on the Mao Tau moment-based estimator computed using EstimateS (Colwell 2005). **Mainland**, **Largest fragment**, **Medium-sized fragment**, **Smallest fragment** and **Combined fragments**.

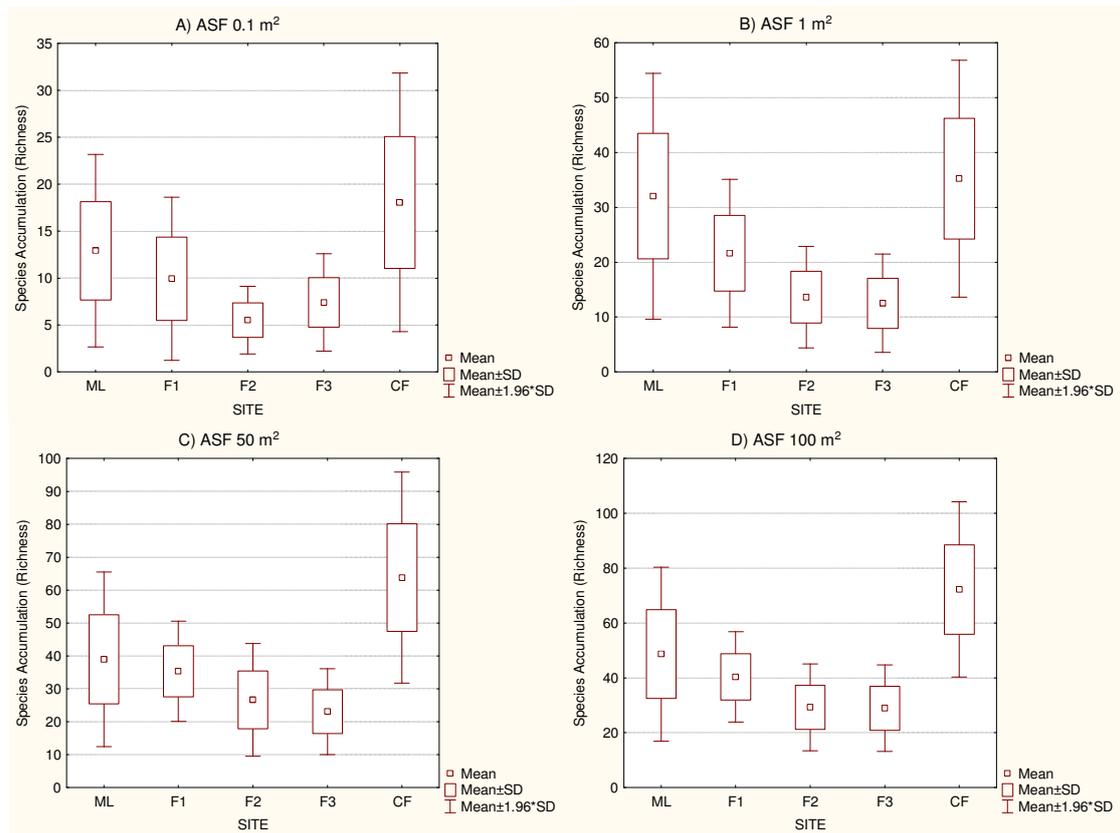


Figure 3.2 Mean species accumulation (richness) in the Atlantis Sand Fynbos (ASF) mainland (ML), Largest fragment (F1) Medium-sized fragment (F2), Smallest Fragment (F3) and Combined fragments (CF), for the four sampling scales.

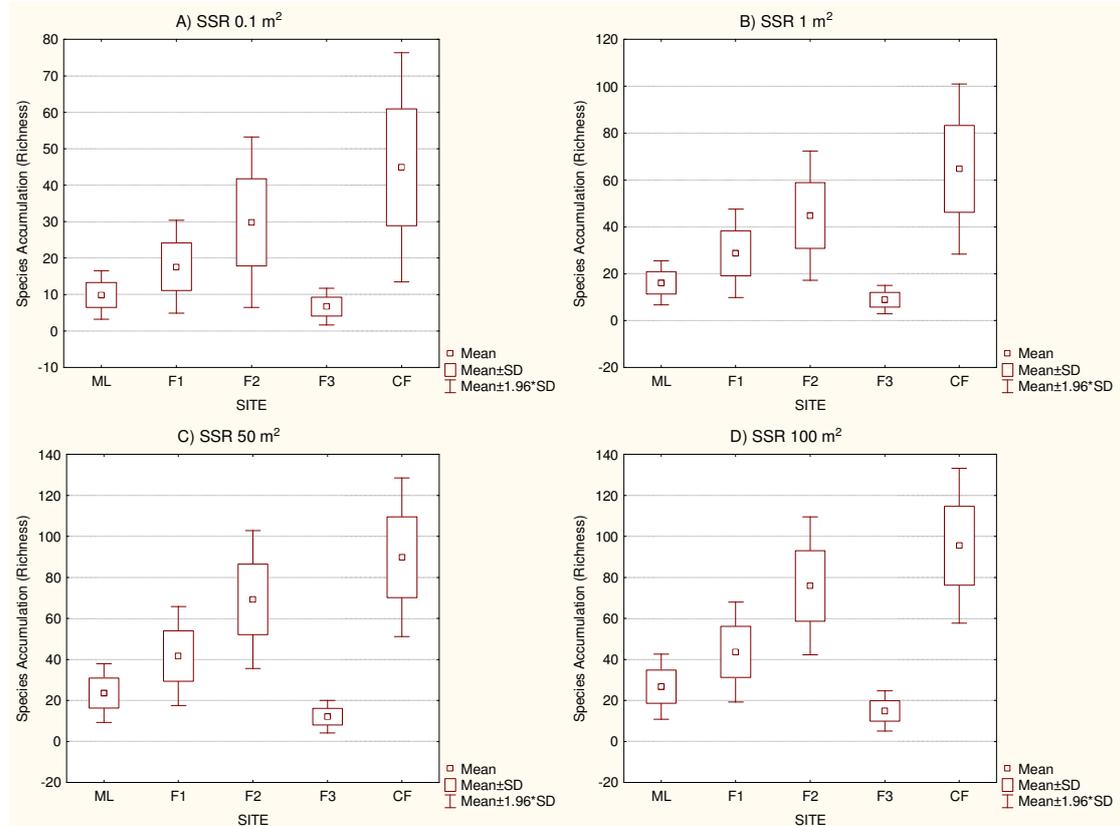


Figure 3.3 Mean species accumulation (richness) in the Swartland Shale Renostervled (SSR) mainland (ML), Largest fragment (F1), Medium-sized fragment (F2), Smallest Fragment (F3) and Combined fragments (CF), for the four sampling scales.

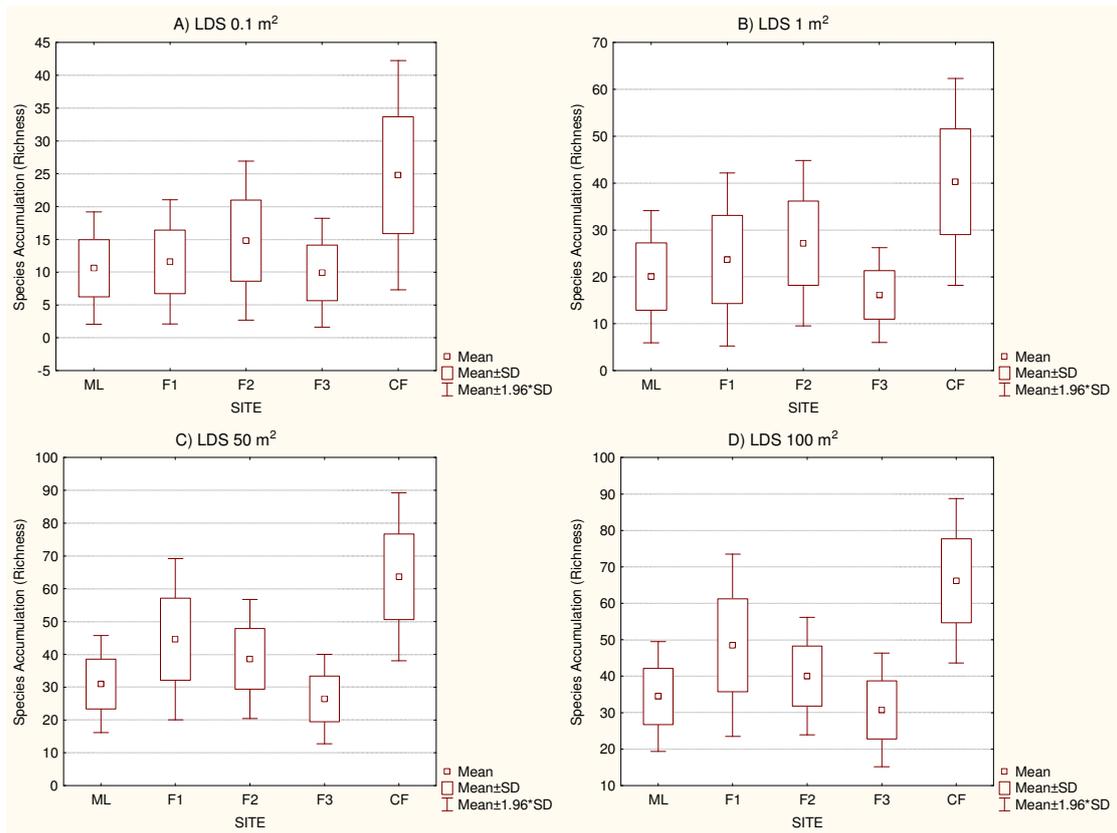


Figure 3.4 Mean species accumulation (richness) in the Langebaan Dune Strandveld (LDS) mainland (ML), Largest fragment (F1), Medium-sized fragment (F2), Smallest Fragment (F3) and Combined fragments (CF), for the four sampling scales.

Table 3.1 Significance of 95% confidence intervals (CI) of species accumulation curves and maximum likelihood (Max L) tests between sites of the three Cape lowland vegetation types at the four sampling scales. The Max L test result is based on the median for all samples (ns = no significant, * = very small, ** = small, *** = large, **** = very large difference and marginal = slight overlap of CI).

	Scale	Site	ML		LF		MF	
			CI	Max L	CI	Max L	CI	Max L
Atlantis Sand Fynbos	0.1 m ²	CF	ns	ns				
		LF	ns	ns				
		MF	marginal	*	ns	ns	ns	ns
		SF	ns	ns	ns	ns	ns	ns
	1 m ²	CF	ns	ns				
		LF	ns	ns				
		MF	*	****	ns	ns		
		SF	*	****	marginal	*	ns	ns
	50 m ²	CF	*	****				
		LF	ns	ns				
		MF	marginal	*	ns	ns		
		SF	*	**	marginal	*	ns	ns
100 m ²	CF	*	****					
	LF	ns	ns					
	MF	*	**	ns	ns	ns	ns	
	SF	*	****	ns	ns	ns	ns	
Swartland Shale Renosterveld	0.1 m ²	CF	*	****				
		LF	ns	ns				
		MF	*	****	marginal	*		
		SF	ns	ns	*	**	*	****
	1 m ²	CF	*	****				
		LF	marginal	*				
		MF	*	****	marginal	*		
		SF	ns	ns	*	****	*	****
	50 m ²	CF	*	****				
		LF	*	**				
		MF	*	****	*	****		
		SF	marginal	*	*	****	*	****
100 m ²	CF	*	****					
	LF	marginal	**					
	MF	*	****	*	****			
	SF	marginal	*	*	****	*	****	
Langebaan Dune Strandveld	0.1 m ²	CF	*	**				
		LF	ns	ns				
		MF	ns	ns	ns	ns	ns	ns
		SF	ns	ns	ns	ns	ns	ns
	1 m ²	CF	*	****				
		LF	ns	ns				
		MF	ns	ns	ns	ns	marginal	*
		SF	ns	ns	ns	ns		
	50 m ²	CF	*	****				
		LF	marginal	*				
		MF	ns	ns	ns	ns		
		SF	ns	ns	*	***	marginal	*
100 m ²	CF	*	****					
	LF	marginal	*					
	MF	ns	ns	ns	ns			
	SF	ns	ns	*	**	ns	ns	

3.3.2 Diversity partitioning and sampling scale effects

The contribution of α -diversity to total γ -diversity at the two smaller scales (0.1 and 1 m²) in all three Cape lowlands vegetation types was less than 20% (6–19%), with β -diversity contributing more than 80% (81–94%) of total γ -diversity (Table 3.2). At the larger (50 and 100 m²) scales, the contribution of α -diversity to overall γ -diversity almost tripled to between 26% and 55% with β -diversity contributing between 45 and 74%.

Table 3.2 Diversity partitions for the mainland and fragments of the Cape lowland **ASF**, **SSR** and **LDS** at four scales: α = mean species richness per sample corresponding to the first point (rounded up) on each SAC; β = difference (rounded up) in species richness between the last and first point on each SAC; and γ = total cumulative species richness in all samples pooled for each site corresponding to last point on each SAC.

Scale	0.1 m ²			1 m ²			50 m ²			100 m ²		
	α	β	γ	α	β	γ	α	β	γ	α	β	γ
ASF												
ML	2	18	20	4	41	45	14	40	54	19	48	67
LF	1	15	16	4	25	29	20	24	44	23	26	49
MF	1	7	8	3	17	20	11	26	37	14	24	38
SF	1	10	11	3	16	19	11	20	31	14	24	38
CF	3	25	28	8	40	48	33	49	82	40	49	89
SSR												
ML	2	12	14	4	18	22	10	22	32	12	14	36
LF	3	23	26	6	34	40	18	37	55	20	38	57
MF	4	41	45	9	52	61	35	52	87	41	52	93
SF	1	9	10	2	11	13	5	12	17	6	15	21
CF	7	57	64	15	70	85	50	59	109	56	58	114
LDS												
ML	1	15	16	3	26	29	16	23	39	19	23	42
LF	1	17	18	3	33	36	20	38	58	23	39	62
MF	2	21	23	5	33	38	20	28	48	23	25	48
SF	1	15	16	3	19	22	13	21	34	16	24	40
CF	4	32	36	10	43	53	37	40	77	42	35	77

3.3.3 Complementarity

Average percentage complementary (C) and standard deviation (Table 3.3), was $76 \pm 4\%$ for ASF (71–81%) and $76 \pm 7\%$ for SSR (63–84%) sites, indicating a high degree of distinctness among sites, and a high number of species unique to any one site. LDS sites were more similar to one another with an average percentage complementarity of $57 \pm 8\%$ (45%–66%), with fewer numbers of unique species occurring at each site (Table 3.3).

Table 3.3 Percentage Complementarity (C) between sites of three Cape lowland vegetation types: **ASF**, **SSR** and **LD**
Matrix entries: species richness per site (S), {species unique to each site}; **percentage complementarity**, (species common to both sites), [species unique to either site].

ASF	ML	LF	MF	SF	CF	Mean \pm Std Dev
Richness (S)	74 {36}	53 {20}	41 {12}	41 {14}	95 {57}	S = 52 \pm 16
CF	71 (38) [93]					
LF	78 (23) [81]					
MF	78 (21) [73]	71 (21) [52]				
SF	78 (21) [73]	78 (17) [60]	81 (13) [56]			C = 76 \pm 4
SSR						
Richness (S)	46 {13}	67 {18}	101 {39}	25 {3}	126 {93}	S = 60 \pm 33
CF	76 (33) [106]					
LF	76 (22) [69]					
MF	73 (31) [85]	63 (45) [78]				
SF	78 (13) [45]	84 (13) [66]	81 (20) [86]			C = 76 \pm 7
LDS						
Richness (S)	42 {8}	64 {16}	52 {2}	42 {3}	80 {21}	S = 50 \pm 10
CF	61 (34) [54]					
LF	66 (27) [52]					
MF	52 (31) [33]	45 (41) [34]				
SF	65 (22) [40]	57 (32) [42]	53 (30) [34]			C = 57 \pm 8

3.4 Discussion

Understanding what determines species richness remains a fundamental concern for ecologists. At very large spatial scales and for long time scales, species richness is determined by rates of speciation, extinction (Rosenzweig 1995) and dispersal. For shorter time periods and smaller spatial scales; richness is determined by the rates of birth, death and colonisation of populations interacting with one another within a community (Crawley & Harral 2001). In both cases, habitat fragmentation plays a vital role, since it places species that survive in remnant patches under a modified environment of reduced area, increased isolation and new ecological boundaries (Hobbs & Yates 2003). Due to fragmentation, species numbers, composition and interactions are altered and several ecological processes are disrupted (Lindenmayer & Fischer 2006, 2007).

In this study, the effect of fragmentation (reduced patch size or habitat loss) on species richness and complementarity in three Cape lowland vegetation types was investigated at four different sampling scales. Species richness in individual fragments and all fragments combined was compared with richness on equivalent-sized sub-plots in the mainlands of these vegetation types. The aim was to determine if and how much the fragments contribute to plant species richness in the region.

Extinction due to habitat loss would be implied if fewer species were recorded in the smaller individual fragments with increasing sampling effort than in the larger fragments and the mainlands, and/or, if fewer species were found in all the fragments combined than in the mainland.

The effect of reduced patch size on species richness was generally weak and inconsistent for all three vegetation types studied, although it was more evident in ASF than in SSR and LDS where the effect seemed to have been masked by site factors, notably the grazing history of the sites. The absence of very strong effects of reduced patch size in this vegetation types could be attributed to the fact the Cape lowland is endowed with lots of rare and endemic species. These occur in small and isolated populations and may have become resistant to inbreeding depression and loss of heterozygosity (Rebelo 1992), predisposing them to withstand extinction due to small population size. Moreover, plants with their characteristically small neighbourhood size (Levin & Kerster 1974) may be more tolerant of the genetic and demographic consequences of small populations (Bond et al. 1988). Furthermore, the long history of grazing in renosterveld (Deacon 1992) and strandveld (Liengme 1987) may have rendered the species in these habitats more tolerant of the deterministic impacts of fragmentation (Kemper et al. 1999; see also Sankaran & McNaughton 1999), although grazing is considered as one of the inhibitors of the establishment of some native species (Krug et al. 2004). On the contrary, fynbos is relatively unpalatable (Johnson 1992; Rebelo et al. 2006) and has not been subjected to heavy grazing compared to renosterveld and strandveld. This may explain why the effect of reduced patch size on species richness was more evident in Atlantis Sand Fynbos than in Swartland Shale Renosterveld and Langebaan Dune Strandveld.

The ASF fragments generally harboured fewer species than equal-sized areas of mainland. However, the loss of species was more severe in the medium-sized fragment (37 ha) at all scales and the smallest fragment (16 ha) at all but the 0.1 m² scale. The largest fragment (600 ha) was not very much lower in species richness than the mainland at all sampling scales. This result compares

well with that of Bond et al. (1988) who, in their study of the effect of insularisation on fynbos “islands” surrounded by afro-montane forest, showed that species richness was significantly lower for fragments less than 600 ha than similar-sized areas in larger habitats. Despite the confounding effect of grazing there was evidence of the fragment size effect in SSR and LDS. The decline in species richness was noticeable in the smallest SSR fragment (15 ha) than in all the other sites. All LDS fragments had a grazing history but species richness was considerably lower in the smallest fragment (8 ha) than in the largest (70 ha) and medium-sized (18 ha) fragments.

There are many possible reasons for the absence of some species from smaller fragments. For instance, small fragments can only support small populations, which easily succumb to environmental, demographic and genetic changes and thus, can easily go extinct locally (Shaffer 1981; Soulé 1987; Pimm et al. 1988; Hobbs & Yates 2003). Also, the mainland and larger fragments are more likely to have a greater variety of microhabitats due to the existence of a wide range of microclimatic conditions. This in effect, increases the extent of the resource spectrum in mainlands and larger fragments compared to smaller ones (Begon et al. 1996).

Changes in disturbance regime might also contribute to the loss of species in the smaller fragments (Pickett & Thompson 1979), although this can be manipulated through prescribed burning, alien clearing, and grazing by wild and domestic animals. The disturbance regimes prevalent in the different sites of this study seemed to confound the effect of fragment size on species richness. Fire, for example, constitutes the major disturbance in fynbos (Le Maitre & Midgley 1992) with natural fires occurring at intervals of 5–50 years (Rebelo et al. 2006), although the recent fire history on the Atlantis Sand Fynbos study sites is poorly documented. Burn pattern analyses from 1960 to 1981 showed these sites burnt on average once every seven years, with minimum and maximum burn periods of four and 25 years respectively (Brownlie & Mustart 1988). The fire regime for the ASF study sites varied considerably. Fire has been excluded from the the smallest fragment for more

than 40 years (see Table 1.1), while there was an intense fire some 15 years ago in the medium-sized fragment which is now heavily infested by *Acacia saligna* as a result (see Table 1.1). Such heavily infested areas were as much as possible, avoided during sampling. In contrast, the mainland (1 100 ha) and the largest fragment have experienced regular fires at intervals of 4 – 25 years (Brownlie & Mustart 1988). The most recent accidental fires occurred in the mainland in 2005 and 2006, with that of 2005 burning one of the sample plots.

Unlike in ASF where variable fire regimes confounded the effect of reduced patch size on species richness, grazing was likely the confounding factor on the effect of reduced patch size on species richness in SSR and LDS. This was evident as species richness was much higher in the SSR medium-sized fragment (70 ha) compared to the other sites at all scales. This former site is currently grazed by large indigenous herbivores while the two smaller sites of this vegetation type are not being grazed. The mainland is grazed but at a much lower intensity than the medium-sized fragment (author's personal observation in the field). Kemper et al. (1999) also found no significant linear relationship between species diversity and fragment area in renosterveld. Generally, grazing in renosterveld has transformed much of the vegetation from shrubby grassland to grassy shrubland (Cowling et al. 1986) and seems to affect species composition, particularly the interplay between grasses, geophytes and shrub components (Rebelo et al. 2006). Renosterveld has been noted to alternate between a grass- and a shrub-dominated state depending on the use of fire and brush cutting techniques (Heydenrych 1995) and is said to be created and sustained by an intermediate level of disturbance (Boucher 1983).

The confounding effect of grazing on the effect of fragment size on species richness was also evident in LDS. Here the largest fragment (70 ha) with sheep and cattle grazing was much more richer in species per unit area sampled than the mainland, which has not been grazed for over 40 years, except by a few cattle that sometimes stray in from neighbouring farms. Grazing animals

may also serve as dispersal agents (for both alien and indigenous species), reducing isolation between patches and therefore restoring and preserving metapopulations (Pueyo et al. 2008). However, they can equally cause long-term changes in ecosystems through their feeding habits and mere physical damage by modifying the structure and species composition of the vegetation (Hobbs 1996; Owen-Smith & Danckwerts 1997; Archibald et al. 2005).

The fact that species richness was generally lower at the smaller scales than at the larger scales for all sites in the three vegetation types indicates a sampling scale effect. Scale dependence is defined as the degree to which ecological phenomena vary as a function of the sampling protocol i.e. sample grain, number, extent, and intensity (Palmer & White 1994). The sampling scale effect was very evident in diversity partitioning as the contribution of α -diversity to total γ -diversity at the smaller scales was very low, but almost tripled at the larger scales, with β -diversity contributing the bulk to γ -diversity for all three vegetation types. Species turnover is therefore the major component of overall diversity in the Cape lowland vegetation types investigated. This is not surprising given that at small scales, species richness depends on the size of individuals and their degree of vertical and horizontal mixing (Crawley & Harral 2001). This clearly highlights the packing problem and the more direct interactions among species at the smaller scales (Gering & Crist 2002; Crist et al. 2003). At the larger scales, species richness depends on the size of the species-pool from which the sample might be drawn (Crawley & Harral 2001). Under-sampling would therefore underestimate β -diversity and γ -diversity since α -diversity remains constant, while β -diversity and γ -diversity would increase as the number of samples increase. In other words, the size of the sample unit affects α -diversity while the extent (i.e. the number and spatial arrangement of samples) affects β -diversity and both sample grain and extent affect γ -diversity (Crist et al. 2006). Limited sampling may therefore reduce the statistical power to detect departures from null patterns (Crist et al. 2003). Generally, the curves did not approach asymptote at all sampling scales, indicating that sampling may not have been adequate to reflect a true representation of species richness. However, average

species richness per 1000 m² for all three vegetation types compares well with figures cited in the literature. The average of 52 ± 16 species per 1 000 m² recorded in ASF is close to the 68 species per 1000 m² cited in the literature for fynbos, with the highest so far recorded being 121 species in 1000 m² (Cowling & Holmes 1992; Goldblatt & Manning 2000). In SSR, an average of 60 ± 33 species per 1000 m² was recorded, which compares well with the average of 66 (Tilman et al. 1983) and 84 species per 1000 m² (Cowling & Holmes 1992). Similarly, the average of 50 ± 10 species per 1000 m² recorded for LDS compares well with the average of 59 that has been cited for thicket vegetation (Tilman et al. 1983). With an average of 60 ± 33 species per 1000 m², SSR stood out as the most diverse of the three vegetation types in terms of species richness.

The generally high percentage complementarity among sites for all three vegetation types clearly indicates the high degree of habitat heterogeneity in the Cape lowlands. Apart from contributing to overall species richness in the region, these fragments may well be the last suitable habitats for some species and therefore warrant conservation attention. Although average percentage complementarity was generally high for all three vegetation types, it was slightly lower for LDS (57 ± 8) compared to ASF (76 ± 4) and SSR (76 ± 7). The low complementarity of LDS sites is evident from the higher proportion of common to unique species recorded between any two sites and indicates a high floristic affinity among these sites. This justifies why all the sites were grouped into one vegetation type (i.e. LDS) even though according to Mucina and Rutherford (2006), the fragments are classified under the Leipoldtville Sand Fynbos.

Whatever the determinant, species richness depends on the area sampled, species' relative abundances (Preston 1960, 1962a, 1962b), and their spatial patterns and degree of mixing (Palmer & White 1994). For any given sampling scheme, the occurrence patterns of species in samples from natural communities are affected by at least three main sources of heterogeneity (Colwell et al. 2004). The first source of heterogeneity is the variation in overall commonness or rarity among

species (i.e. relative abundance), which translates into the variation in the frequency of occurrence among species. The second is the variation among samples in the total abundance of individuals, which translates into variation among samples in the total number of species occurrences. The third source of heterogeneity is the dissociation or association between species among samples, which translates into non-random patterns of co-occurrence of species. The generally weak and inconsistent effects of reduced patch size on species richness found in this study can be attributed to several possible confounding factors.

(1) The temporal scale of the study is a likely confounding factor since human-induced habitat fragmentation in the Cape lowlands is recent in relation to evolutionary time. Long-term effects may be delayed by short-term crowding effects, which may eventually give way to long-term extinction debts (Debinski & Holt 2000; Ewers & Didham 2006; Helm et al. 2006). This process of “species relaxation” is considered an inevitable consequence of area reduction and isolation on the basis of the predictions of island biogeography (MacArthur & Wilson 1967). The rate of species relaxation varies among different taxa, with the most rapid extinctions likely to occur in species that exist at low densities (Saunders et al. 1991). Moreover, the study involved plant species that are mostly long-lived, with life spans ranging from one year (for annuals) to over 100 years for some obligate resprouters (Cowling et al. 1997). Such species may persist for extended periods in environments where their reproductive success is lowered. This is because it takes time for individual-scale changes in reproductive success to be reflected in the population dynamics of long-lived species (Haila et al. 1993). On the other hand, some annuals may persist through their long-lived seed banks (Hester & Hobbs 1992).

(2) The spatial scale of sampling might have also masked the effect of reduced patch size as evident from the inconsistent results obtained at different sampling scales. This is because most ecological events vary as a function of the sampling protocol i.e. sample grain, number, extent, and intensity (Palmer & White 1994; Crawley & Harral 2001).

(3) Patch connectivity is strongly influenced by the surrounding matrix, which affects the movement of propagules of both native and alien species and therefore the demography, genetics, and survival of local populations (Fahrig 2001; Jules & Shahani 2003; Jonas et al. 2006; Wiser & Buxton 2008). The isolation of patches from one another may result in the disruption of plant-animal mutualisms (Brown & Kodric-Brown 1977; Cole 1981; Burkey 1989) causing imbalances of pollinators, dispersers, herbivores and predators (Rebelo et al. 2006) and the loss of viable populations (Pimm et al. 1988). Plant species do not all respond uniformly to the different matrices surrounding remnant patches because there are bound to be differences in susceptibility depending on life history traits related to dispersal, establishment and persistence (Ewers & Didham 2006; Laurance 2008). This may be responsible for the absence or presence of some species at particular sites. However, a better way of determining the species most affected would be to look at plant functional traits, which is the focus of chapters four and five of this study. Within a radius of 1 km, the ASF mainland and the largest fragment are surrounded by alien *Acacia saligna*, *Eucalyptus* species and wheat fields, while the medium-sized and smallest fragments are surrounded by a small settlement, minor roads/railways, alien *Acacia saligna* and *Eucalyptus* species. The SSR mainland and the smallest fragment are surrounded by urban settlement and vineyards, while the largest and medium-sized fragments are in matrices of vineyards and wheat fields. The LDS mainland and the medium-sized and smallest fragments are embedded in a matrix of wheat fields and minor roads while wheat and potato fields surround the largest fragment. These matrices have resistant values ranging from 50–100 (Nikolakaki 2004; Jonas et al. 2006), obstructing dispersers and pollinators, which in turn may affect re-colonisation from other patches. Obligate reseeders, short-distance dispersed and specialist-pollinated species would be more likely affected than resprouters, long-distance dispersed and generalist-pollinated species (Rebelo et al. 2006).

(4) The dynamics of within-remnant patches is also influenced by activities in the surrounding matrix. Most of the remnants are regularly, although accidentally sprayed with herbicides, insecticides and fertilizer from activities in the matrices, which can alter their species composition

(Kemper 1997; Rebelo et al. 2006). Some of the patches are surrounded and others (e.g. the ASF medium-sized fragment) are heavily infested by invasive alien woody plant species. The invasibility of such patches is likely to increase (see Hobbs & Yates 2003; Lindenmayer & Fischer 2006; Wiser & Buxton 2008). Alien species seriously impact on native species by altering the fire regime through increased biomass and fuel loads, which increase fire hazard and soil erosion, and by changing the nutrient status of the soil and also the faunal community (Rebelo et al. 2006). The changed feeding behaviour of some indigenous birds, which may disperse seeds of invasive species with likely detrimental effects on native plant species, has been reported in strandveld (see Richardson & Van Wilgen 2004). Alien grasses are also highly invasive in the Cape lowlands but the extent and impact of their invasions are for the most part unknown, although they seem to badly affect geophytes (Vlok 1988; Musil et al. 2005; Rebelo et al. 2006).

(5) The high number of microhabitats (spatial heterogeneity), which is one of the factors advanced in support of the high level of speciation in the CFR (Cowling et al. 1992; Johnson 1996; Linder 2003) could also be a confounding factor to the fragment size effects. The general high percentage complementarity for all three vegetation types as evident from the high number of unique species and few common species among the sites indicates an abundance of habitat specialists and reflects the degree of habitat heterogeneity in the region. The presence or absence of species in particular sites may not necessarily be due to area, but due to the presence or absence of suitable habitats.

3.5 Conclusion

This study has shown that the effect of reduced patch size on species richness was generally not very severe and unequivocal for all three vegetation types studied. However, the fragment-size effect was more evident in Atlantis Sand Fynbos, and it was masked by disturbance-related site factors in Swartland Shale Renosterveld and Langebaan Dune Strandveld. The generally high levels of complementarities across sites for all three vegetation types also suggest that the fragments contributed significantly to overall regional diversity and deserve conservation attention. The high

competition among different land uses in the Cape lowlands indicates that the region remains vulnerable to habitat fragmentation. Therefore, to adequately conserve and ensure species survival and maintain regional species diversity in these Cape lowland vegetation types, these fragments should be maintained and well managed. To ascertain whether these Cape lowland fragments are still functional, there is need to investigate the effect of habitat loss on plant functional types. This will be addressed in the subsequent chapters.

3.6 References

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Chapter 4

Predicting the response of three Cape lowland vegetation types to habitat fragmentation using plant functional traits

Abstract

Conserving plant diversity in highly fragmented landscapes is particularly challenging because it is difficult to predict plant species response to fragmentation. However, results of studies from different parts of the world indicate that classifying plant species into functional types using sets of co-occurring plant traits can serve as better predictors of global change effects on terrestrial ecosystems. The Cape lowlands of South Africa are dominated by fire-prone and high diversity shrublands that thrive mostly on relatively nutrient-poor soils, and have been severely fragmented by human activities. This study sought to define plant functional types (PFTs) that characterise these lowland habitats and to predict how they will respond to habitat fragmentation. Traits were selected based on their relevance to species' response to habitat fragmentation. Sampling was done within three Cape lowland Atlantis Sand Fynbos (ASF), Swartland Shale Renosterveld (SSR) and Langebaan Dune Strandveld (LDS). Species sampled were classified into eight objectively and 19 subjectively defined PFTs. The results indicated that ASF with most short-distance dispersed, dioecious species was the most susceptible. Next was SSR with many geophytes that exhibit highly-specialised pollination systems. LDS, with many fleshy-fruited, generalist-pollinated, ornithochorous species was the least threatened. However, the magnitude of susceptibility to habitat fragmentation may well depend on the connectivity between remnant patches and how permeable the surrounding matrix is to the movement of plant propagules and pollinators. Therefore, to better understand the impact of habitat fragmentation in the Cape lowlands, it is important to investigate these aspects as well as the effects of fragment size on PFT richness and diversity.

Keywords: fynbos, fragmentation; plant functional types; plant trait 'syndromes'; renosterveld, strandveld

4.1 Introduction

Human-induced habitat fragmentation reduces vast expanses of natural habitats into numerous smaller patches isolated from one another by different land-use types (Wilcove et al. 1986). This fragmentation alters species' richness, composition and interactions and also disrupts vital ecological processes in remnant patches (Saunders et al. 1991; Haila et al. 1993; Fahrig 2003; Hobbs & Yates 2003; Lindenmayer & Fischer 2006). The degree of the fragmentation effect may reach an extent that it affects the functioning of the ecosystem (McCann 2000). Although habitat fragmentation is today regarded as one of the main threats to biodiversity worldwide (Foley et al. 2005; Groom et al. 2005), the precise implications for biodiversity conservation in fragmented landscapes are largely unknown. This is especially so for plants because it is difficult to predict how plant species may respond to global changes such as fragmentation as discussed in Chapter 1.

Researchers worldwide have in recent years increased efforts to search for easily-measured, universally-applicable predictors of global change effects on terrestrial ecosystems (e.g. Woodward & Cramer 1996; Díaz & Cabido 1997; Lavorel et al. 1997; McIntyre et al. 1999a; Weiher et al. 1999; Pausas & Lavorel 2003). Currently there is a general awareness that such predictors do exist in the form of plant functional types (PFTs), or traits 'syndrome' (Smith et al. 1997; Steffen & Cramer 1997; Cornelissen et al. 2003; Rusch et al. 2003).

A PFT is defined as a group of plant species with similarities in a particular set of traits, responding to environmental factors in like manner and/or performing similar roles in ecosystems, no matter their phylogeny (Gitay & Noble 1997). PFTs comprise functional response groups or taxa that respond similarly to environmental factors and functional effect groups or taxa with the same role in the ecosystem (Lavorel & Garnier 2002). PFTs are defined by species demographic and life history features, physiology and resource dynamics, which determine their responses to biotic and abiotic factors and their role in ecosystem functioning (Gitay & Noble 1997; Grime 2001).

Plant communities result from a hierarchy of biotic and abiotic filters (mainly disturbances and available resources) acting at different spatial and temporal scales and successively selecting from the regional species pool those species and traits that can persist at a particular site (Woodward & Diament 1991; Keddy 1992; Weiher & Keddy 1999; Lavorel & Garnier 2002). Disturbance contributes to the long-term maintenance of biodiversity but can also upset dynamic cycles and cause dramatic and irreversible changes in ecosystems (Pickett & White 1985). Although a few traits are generally associated with response to disturbance, plant attributes are specific to particular disturbances and their responses vary with disturbance regimes (Rusch et al. 2003). Plants usually have many survival strategies under a given environmental condition (Westoby et al. 2002) and also display various trade-offs and correlations between traits due to biophysical constraints on their structure and function (Hodgson et al. 1999; Grime 2001). However, there exists a relatively short list of morphological and functional traits that are strongly linked to the establishment and regenerative phases of plants (Weiher et al. 1999; Lavorel & Garnier 2002; Westoby et al. 2002).

It is therefore vital to know and predict how plant communities will respond to recurrent and new disturbances, particularly in the context of global changes that affect land-use patterns and climate. This will improve the understanding of the function of ecosystems. To achieve this, plant species have been classified using various schemes depending on the objective at hand. These include life forms or taxa with similar structure (Raunkiaer 1937); strategies (Grime 1977, 2001); vital attributes (Noble & Slatyer 1980); guilds or taxa making use of the same resources (Noble & Gitay 1996); and the widely used and recently coined PFT (Steffen et al. 1992; Smith et al. 1997). Most plant functional classification schemes emphasise traits that are important for both understanding and prediction (Grime 1977; Box 1996; Lavorel et al. 1997; Weiher et al. 1999). However they do have their shortcomings. Pausas and Lavorel (2003) highlighted these limitations and proposed a hierarchical, scale-dependent approach for identifying plant traits in severely disturbed ecosystems.

Their scheme lays emphasis on mechanisms that ensure persistence at the individual, population, community and landscape levels and therefore focus on traits that would allow:

- (1) Individuals to persist after disturbance;
- (2) Populations to persist at a given site;
- (3) Species that persist to cope with interspecific competition in the community and;
- (4) Allow a species to colonize a site where it is absent from nearby populations in the landscape.

Although there is now consensus on a set of plant traits with standardized and easy measurement protocols that could be applied worldwide for trait-based community descriptions (Cornelissen et al. 2003), there is no universally accepted method for classifying plant species into types. Predicting how plant species will respond to disturbances in general and fragmentation in particular poses two main challenges. First, the relevant traits must be identified and selected. Then, and more importantly, an appropriate method must be used to group the plants into functional types.

In South Africa, habitat fragmentation is particularly evident in the Cape lowlands, which encompass most of the coastal forelands and interior valleys of the Fynbos Biome. These have been severely impacted by agriculture, urbanization, mining and invasion by alien species (Rebelo et al. 2006). These lowlands are dominated by high diversity shrublands (i.e. fynbos and renosterveld which are fire-prone and strandveld which is less fire-prone). They thrive mostly on relatively poor nutrient soils, especially fynbos, although renosterveld occur on relatively nutrient rich shale-derived soils while strandveld occurs on calcareous soils. They also exhibit very low floristic affinities particularly at the species level. This study sought to define the plant functional types or trait ‘syndromes’ that characterise the three vegetation types studied, namely, Atlantis Sand Fynbos, Swartland Shale Renosterveld and Langebaan Dune Strandveld and to make predictions on how they will respond to habitat fragmentation based on the dominant PFTs. These three vegetation types represent the three main Cape lowland habitats (i.e. fynbos, renosterveld and strandveld).

4.2 Methods

4.2.1 Trait selection

Eight simple categorical traits (Table 4.1.) of known relevance to the regenerative and establishment phases of the plant life cycle and which reflect species' abilities to persist within a highly fragmented and heavily disturbed environment were selected. These are easily measurable "soft" traits that are considered reasonable surrogates for more functional, but difficult to measure "hard" traits (McIntyre et al. 1999b).

Table 4.1. Traits assigned to plant species sampled in the three Cape lowland vegetation types. For the ecological significance and measurements of traits, see Cornelissen et al. (2003) and references cited therein as well as Römermann et al. (unpublished) for definition of dispersal modes.

Trait	Description	Categories
Dispersal distance	Based on dispersal mode i) <i>Ombrochory</i> (short) ii) <i>Myrmecochory</i> (short) iii) <i>Unassisted</i> (short) including 'autochory', 'ballochory', 'blastochory', 'boleochory', iv) <i>Anemochory</i> (long), v) <i>Chamaechory</i> (long), vi) <i>Hemerochory</i> (long) including 'agochory', speirochory, 'ethelochory', vi) <i>Nautochory</i> or hydrochory (long) and vii) <i>Zoochory</i> (long) including 'dysochory', 'endozoochory', and 'epizoochory'	Short- or Long-distance dispersal
Dispersal versatility	Based on whether a species possesses several (Poly) or just one dispersal mode (Mono)	Poly or Mono
Pollination specificity	Based on whether a species is pollinated by wind or several agents (generalist) or by a specific pollinator (specialist). All wind-pollinated species and species with a wide range of pollinators from the same taxa e.g. different insects and species pollinated by different agents of different taxa were classified as generalists. Species that are dependent on particular pollinator agents such as long-proboscid flies, the rare oil collecting bees, long-tongued birds, were classified as specialists. This was mostly based on expert knowledge, as there is a paucity of studies on the pollination biology of the species.	Specialist- or Generalist-pollinated
Pollination versatility	Based on whether a species is pollinated in different ways e.g. wind and bird (Poly) or just one way e.g. only insect pollinated (mono)	Poly or Mono
Breeding mode	Based on whether individuals of a species are single-sexed i.e. having male and female flowers on separate plants (dioecious) or not ("non-dioecious")	Dioecious or Non-dioecious
Life span	Based on whether a species produces flowers and dies after one growing season (annual and herbaceous) or not (perennial, mostly woody species and geophytes), which were the dominant categories. No biennials and only one paucennial (<i>Conicosia</i> sp.) were among the species sampled.	Annual or Perennial
Regeneration mode	Based on whether a species possesses clonal growth organ (e.g. bulb, tuber, stolon, rhizome, etc (resprouter) or not (seeder)	Resprouter or Seeder
Spinescence	Based on the presence or absence of spines, thorns etc	Yes or No

4.2.2 Sampling

The study sites and vegetation types selected are as described in Chapter 1 (section 1.4.1) and sampling was as described in Chapter 3 (section 3.2.2). Species were assigned traits based on direct

field observations, gathered expert knowledge and from the literature sources (see Appendix 16). To provide a test for the patterns of co-occurring traits (PFTs) detected and a wide scope for the predictions on the response of the Cape lowland vegetation types to habitat fragmentation entailed the sampling of species of various growth forms. Sampling was based on local assemblages and appropriately puts the trait selection strategy within the category of non-random taxon sampling (Ackerly 2000; Westoby et al. 2002), since the questions addressed were ecological and the aim was to look for consistent patterns across vegetation types.

4.2.3 Defining plant functional types (PFTs)

Only indigenous species were included in the analyses. Data analysis involved the following:

- (1) An objective determination of PFTs using univariate tree model (i.e. classification tree),
- (2) A subjective determination of PFTs by successively splitting the data manually using individual traits and
- (3) The use of univariate statistics (Chi-square tests) to determine trait differences among the three vegetation types. Based on their predicted response to habitat fragmentation, PFTs identified were classified as endangered, vulnerable or least-threatened by habitat fragmentation.

To objectively determine PFTs, the 348 species-by-8 traits matrix was subjected to recursive partitioning using the RPART routines in the statistical package R (Therneau & Atkinson 1997). This analogous classification tree analysis explores relationships between a single response variable and multiple explanatory variables (in this case the vegetation types and plant traits respectively). This technique has several advantages over other traditional statistical data explorative techniques such as linear regression, generalised linear models (GLM) and generalised additive models (GAM). The technique is robust, flexible, and relatively easy to construct and interpret. It is a better way to deal with non-linearity and to better handle and find meaningful ecological patterns from complex ecological data (De'ath & Fabricius 2000; Zuur et al. 2007). The tree is built following the

two-stage procedure of splitting and pruning by cross-validation. Splitting aims to maximise between-group variation and minimise within-group variation. During each successive splitting process, the variable (trait) that best separates the data into two mutually exclusive groups that are as homogeneously far apart as possible is used. Splitting stops when the sub-groups reach a minimum size or until no further improvement is possible. Pruning involves the computation of a cross-validated estimate of risk or complexity parameter (cp) for a nested set of sub-trees. The sub-tree with the lowest estimate of risk is then chosen. This is equivalent to a model selection procedure in linear regression (Zuur et al. 2007). The result is a binary tree with terminal nodes (leaves) to which are assigned a predicted class and the number of observations in each class. In addition, the analysis also identifies the overall importance of predictor explanatory variables, ordered by the degree of improvement and the variable that gives the highest classification score presented (see Therneau & Atkinson 1997; De'ath & Fabricius 2000; Zuur et al. 2007).

To subjectively determine PFTs, the data were manually split successively into two groups that are mutually exclusive and homogeneously as far apart as possible, using five of the eight traits in the following order: dispersal distance (long vs. short), life span (perennials vs. annuals), regeneration (resprouters vs. seeders), breeding mode (dioecious vs. non-dioecious) and pollination specificity (specialists vs. generalists). Finally, using the same 348-species-by-8 trait matrix as for the objective determination of PFTs, Chi-square tests were also performed to determine the occurrence of the eight different traits in the 348 species of the three vegetation types.

4.2.4 Comparing the approaches used to determine PFTs

Trait data for each site in each vegetation type were pooled irrespective of their scale and used to compare the performance of the two approaches used to define PFTs. This was done through a principal component analysis (PCA) using BIOPro (McAleece 1997).

4.3 Results

4.3.1 PFTs defined objectively

In total, 348 indigenous plant species belonging to 57 families were sampled from all three vegetation types (see Appendix 16). The classification tree analysis produced a binary tree with 8 terminal nodes (groups), which represent the PFTs, each grouped under the vegetation type with the highest number of species therein (Figure 4.1.). Species that met the particular splitting criterion were grouped to the left and those that did not were grouped to the right. The first split was based on breeding mode (Breed), separating the 348 species into 46 dioecious and 302 non-dioecious species. Next, the 46 dioecious species were split based on regeneration mode (Regen), with most resprouters (20) assigned to fynbos (i.e. ASF). The 25 seeders were then further split based on dispersal distance (DispDist) with most dioecious short-distance dispersed species (six) found in ASF and most dioecious long-distance dispersed species (six) found in strandveld (i.e. LDS). The 302 non-dioecious species were also further split based on regeneration, giving 104 resprouters and 198 seeders. The 104 non-dioecious resprouters were then split based on pollination versatility (PollVers) with seven species having more than one mode of pollination (Poly) assigned to fynbos and 55 species with one pollination mode (Mono) found in renosterveld (i.e. SSR). The 198 non-dioecious seeders were also split based on pollination versatility with 47 species with more than one pollination mode assigned to SSR. The remaining 98 species with one pollination mode (Mono) were further split based on dispersal distance with most short-distance dispersed species (30) assigned to ASF and most long-distance dispersed species (16) assigned to LDS. Four out of the eight objectively defined PFTs (Table 4.2) were dominated by ASF species (two of which were classified as endangered), and two each by SSR and LDS species. Of the four vulnerable PFTs, two were predominantly LDS species and one each dominated by ASF and SSR species. One each of the two least threatened PFTs was dominated by ASF and SSR species.

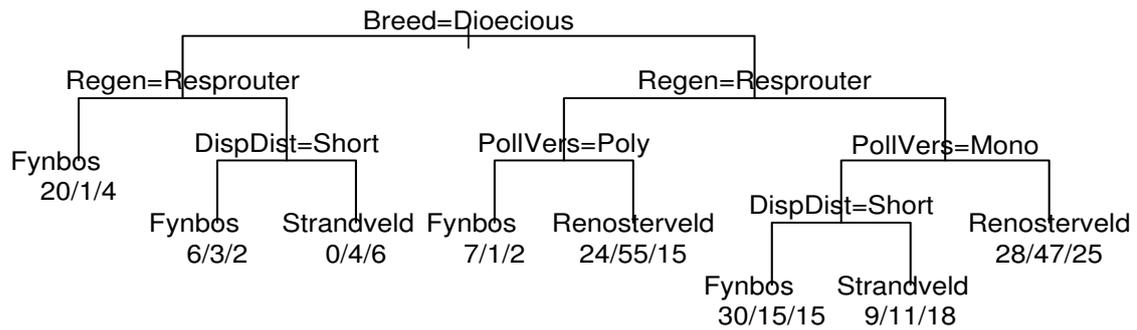


Figure 4.1 Classification tree for traits of 348 plant species sampled in the Cape lowland ASF (Fynbos), SSR (Renosterveld) and LDS (Strandveld). The eight terminal groups (PFTs) are identified by the vegetation with the highest number of species in the group. Numbers represent species in each group for the respective vegetation type.

4.3.2 PFTs defined subjectively

Manually splitting the data (i.e. the subjective approach) resulted in 19 groups representing the PFTs (Figure 4.2). Seven of these were dominated by ASF species, five by SSR species, and three by LDS species, and one each was dominated by SSR/LDS, ASF/LDS and ASF/SSR species and one with equal numbers of species from the three vegetation types. Four of the 19 subjectively defined PFTs were classified as endangered (three of which were composed predominantly of ASF species and one by SSR species). Twelve PFTs were classified as vulnerable (four dominated by ASF, two by SSR species, two by LDS species, one each by SSR/LDS, ASF/LDS and ASF/SSR species, and 1 with equal species representation from all three vegetation types) (Table 4.3). Two of the three least-threatened PFTs were dominated by SSR species and 1 by LDS species.

Table 4.2 Eight PFTs defined objectively using classification tree analysis from eight traits of 348 plant species sampled in the Cape lowland ASF, SSR and LDS, and their predicted response to fragmentation (**Endangered**, **Vulnerable**, and **Least threatened**). PFTs are grouped under the vegetation type with the highest number of species therein. Numbers in the column vegetation represent species represented in each PFT in the respective vegetation types i.e. ASF/SSR/LDS.

PFT (No. of species)	Vegetation	Key Taxa	Predicted responses to fragmentation (threat)
1) Dioecious resprouters (25)	ASF 20/1/4	Mostly Restionaceae, <i>Anthospermum spathulatum</i> , <i>Leucadendron lanigerum</i> , <i>L. brunoides</i>	Although they can persist by clonal growth, the lack of viable populations renders them more susceptible to stochasticity (Vulnerable)
2) Short-distance dispersed, dioecious species (11)	ASF 6/3/2	<i>Elegia</i> and <i>Restio</i> species., <i>Leucadendron cinereum</i> , <i>Anthospermum aethiopicum</i> , <i>A. galiodes</i> , <i>Euphorbia arceuthobioides</i> , <i>E. burmanii</i>	These are poor dispersers and the lack of viable populations renders them very susceptible to stochastic events (Endangered)
3) Long-distance dispersed, dioecious species (10)	LDS 0/4/6	<i>Rhus</i> species., <i>Diospyros glabra</i> , <i>Euclea racemosa</i> , <i>Cissampelos capensis</i> , <i>Arctopus echinatus</i>	Good dispersers but the lack of viable populations may render them more prone to stochastic events (Vulnerable)
4) Non-dioecious, resprouters, with more than one pollination mode (10)	ASF 7/1/2	<i>Agathosma imbricate</i> , <i>Argyrolobium velutinum</i> , <i>Lachnaea grandiflora</i> , <i>L. uniflora</i> , <i>Stilbe ericoides</i> , <i>Salvia lanceolata</i> , <i>Senecio hastatus</i> , <i>Leucospermum hypophyllocarpodendron</i>	Can persist by clonal growth, do not need separate plants of different sexes and have many pollination modes (Least threatened).
5) Non-dioecious, resprouters, with one pollination mode (94)	SSR 24/55/15	Mainly geophytes: e.g. <i>Babiana</i> , <i>Caesia</i> , <i>Cyanella</i> , <i>Cyphia</i> , <i>Geisoorhiza</i> , <i>Moraea</i> , <i>Oxalis</i> , <i>Spiloxene</i> and <i>Trachyandra</i> sp.	Can persist for a while through clonal growth but the disruption of plant-pollinator interactions may affect gene flow and lead to small populations which are prone to stochasticity (Vulnerable)
6) Short-distance dispersed, non-dioecious, seeders with one pollination mode (60)	ASF 30/15/15	<i>Diastella proteoides</i> , <i>Aspalathus</i> , <i>Diosma</i> , <i>Lampranthus</i> , <i>Macrostylis</i> , <i>Muraltia</i> , <i>Phylica</i> , <i>Ruschia</i> , <i>Serruria</i> and <i>Wahlenbergia</i> species.	Poor dispersers with a chance of losing pollinators which may disrupt gene flow and lead to small populations that are more sensitive to stochastic events (Endangered)
7) Long-distance dispersed, non-dioecious, seeders, with one pollination mode (38)	LDS 9/11/16	<i>Olea europaea</i> , <i>Nylandtia spinosa</i> , <i>Asparagus</i> , <i>Ehrharta</i> , <i>Exomis</i> , <i>Lycium</i> , <i>Microloma</i> , <i>Solanum</i> , <i>Tetragonia</i> , <i>Tribolium</i> and <i>Zygophyllum</i> sp.	Good dispersers but the possibility that plant-pollinator interactions may be disrupted may lead to small populations which are prone to stochasticity (Vulnerable)
8) Non-dioecious, seeders, with more than one pollination mode (100)	SSR 28/47/25	Mainly Asteraceae species and some Fabaceae, e.g. <i>Lessertia excissa</i> , <i>Otholobium hirtum</i> , <i>Rafnia</i> and <i>Indigofera</i> sp.	Good dispersers and gap exploiters that are not threatened by the disruption of plant-pollinator relationships or lack of viable population (Least threatened)

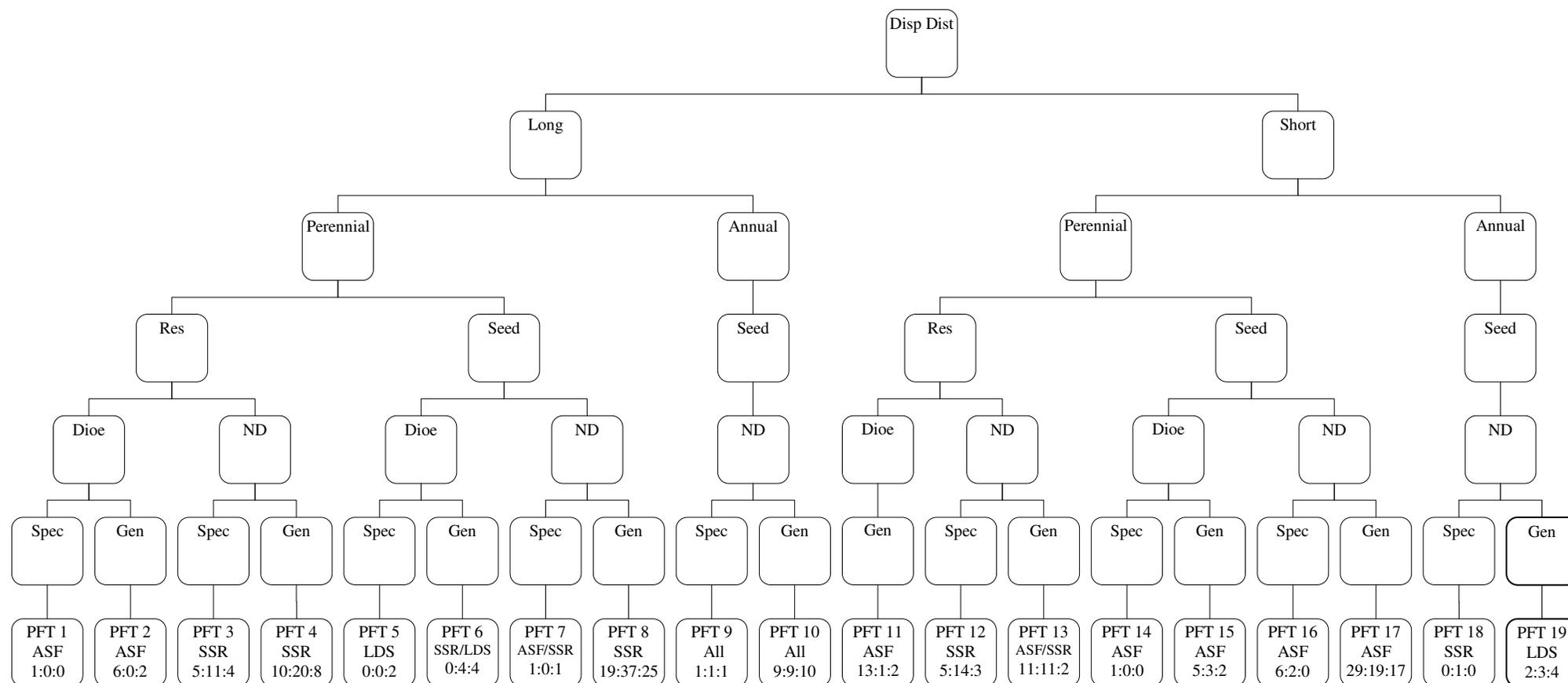


Figure 4.2 Flow chart showing the subjective determination of 19 PFTs. Each PFT is grouped under the vegetation type with the highest number of species therein i.e. ASF, SSR, LDS, and All = All three vegetation types. Numbers represent species per PFT in the respective vegetation types. Disp Dist = Dispersal distance, Res = Resprouter, Seed = Seeder, Dioe = Dioecious, ND = Non-dioecious, Spec = Specialist pollinated, Gen = Generalist pollinated.

Table 4.3 Nineteen PFTs subjectively defined by splitting data using five traits of 348 plant species sampled in the Cape lowland ASF, SSR and LDS, deemed relevant to species response to fragmentation and their predicted response to fragmentation (**Endangered**, **Vulnerable**, and **Least threatened**). The vegetation with the highest number of species defines each PFT therein. Numbers in the column vegetation are species in each PFT in the respective vegetation types i.e. ASF/SSR/LDS and All = All three vegetation types.

PFT (No. of species)	Vegetation	Key Taxa	Predicted responses to fragmentation (<i>threat</i>)
1) Long-distance dispersed, dioecious, specialist-pollinated, resprouters (1)	ASF 1/0/0	<i>Leucadendron lanigerum subsp. lanigerum</i>	Good dispersers that can persist through clonal growth but the fact that they need separate plants of both sexes to maintain viable populations and the possibility that plant-pollinator interactions may be disrupted may lead to small populations which are prone to stochasticity (Vulnerable)
2) Long-distance dispersed, dioecious, generalist-pollinated, resprouters (8)	ASF 6/0/2	All restios: <i>Calopsis vininea</i> , <i>Staberoha distachyos</i> , <i>Thamnochortus erectus</i> , <i>T. fruticosus</i> , <i>T. obtusus</i> , <i>T. punctutus</i> and <i>Willdenowia arescens</i>	Good dispersers that can persist for a while by clonal growth but the fact that they need separate plants of both sexes to maintain viable populations may lead to small populations which are prone to stochasticity (Vulnerable)
3) Long-distance dispersed, non-dioecious, specialist-pollinated, resprouters (20)	SSR 5/11/4	Mostly Geophytes: <i>Albuca cooperi</i> , <i>Aristea africana</i> , <i>Bulbinella</i> sp., <i>Brunsvigia marginata</i> , <i>Chasmanthe floribunda</i> , <i>Corycium orobanchoides</i> , <i>Ornithogalum suaveolens</i> , <i>Pterygodium catholicum</i> , <i>Watsonia coccinea</i> , some <i>Chlorophytum</i> , <i>Drimia</i> , <i>Pelargonium</i> and <i>Trachyandra</i> species.	Good dispersers that can persist for a while through clonal growth but in the long run, the disruption of plant-pollinator mutualisms may affect gene flow, leading to small populations which are more vulnerable to stochastic events (Vulnerable)
4) Long-distance dispersed, non-dioecious, generalist-pollinated, resprouters (38)	SSR 10/20/8	Some geophytes, grasses and sedges: <i>Aristida diffusa</i> , <i>Brunsvigia bosmaniae</i> , <i>Cynanchum africanum</i> , <i>Hesperantha falcata</i> , <i>Rumex lativalvis</i> , <i>Zantedeschia aethiopica</i> , <i>Ornithogalum</i> sp., <i>Chaetobromus dregeanus</i> , <i>Ehrharta calycina</i> , <i>E. villosa</i> , <i>Festuca scabra</i> , <i>Helictotrichon capense</i> , <i>Hyparrhenia hirta</i> , <i>Melica racemosa</i> , <i>Pentaschistis barbata</i> , <i>P. curvifolia</i> , <i>Pseudopentameris caespitosa</i> , <i>Stipagrostis zeyheri</i> , <i>Themeda triandra</i> , <i>Tribolium</i> and <i>Ficinia</i> sp.	Not likely to be affected by fragmentation due to their long life span, long-distance dispersal and resprouting ability and the availability of pollinators. Should be widely distributed (Least threatened)
5) Long distance dispersed, dioecious, perennial, specialist-pollinated, seeders. (2)	LDS 0/0/2	<i>Diospyros glabra</i> and <i>Euclea racemosa</i>	Although good dispersers, they may be threatened in the long run by the lack of viable population and disruption of plant-pollinator relationships leading to small populations that are more prone to stochasticity (Vulnerable)
6) Long-distance dispersed, generalist-pollinated, dioecious, perennial seeders (8)	SSR/LDS 0/4/4	<i>Arctopus echinatus</i> , <i>Cissampelos capensis</i> and <i>Rhus</i> sp.	Although they are good dispersers, they need plants of different sexes (male and female) to maintain viable populations (Vulnerable)
7) Long-distance dispersed, non-dioecious, specialist-pollinated, perennial seeders (2)	ASF/LDS 1/0/1	<i>Microloma sagittatum</i> , <i>Pelargonium oenothera</i>	Although good dispersers, it is possible that plant-pollinator mutualisms may be disrupted leading poor gene flow and small populations which are susceptible to stochastic events (Vulnerable)

PFT (No. of species)	Vegetation	Key Taxa	Predicted responses to fragmentation (<i>threat</i>)
8) Long-distance dispersed, generalist-pollinated, non-dioecious, perennial seeders. (81)	SSR 19/37/25	Mostly wind dispersed Asteraceae shrub species: <i>Athanasia</i> , <i>Berkheya</i> , <i>Eriocephalus</i> , <i>Helichrysum</i> , <i>Metalasia</i> , <i>Othonna</i> , <i>Pterona</i> , <i>Senecio</i> , <i>Stoebe</i> sp., <i>Chrysanthemoides monilifera</i> , <i>Chrysocoma ciliata</i> , <i>Conyza scabrida</i> , <i>Cotyledon orbiculata</i> , <i>Euryops thunbergii</i> , <i>Elytropappus rhinocerotis</i> , <i>Felicia fruticosa</i> , <i>Nidorella foetida</i> , <i>Leysera gnaphalodes</i> , <i>Osteospermum spinosum</i> , <i>Petalacte coronata</i> , <i>Printzia polifolia</i> ; Some bird dispersed: <i>Asparagus</i> , <i>Lycium</i> sp., <i>Gymnosporia buxifolia</i> , <i>Nylandtia spinosa</i> , <i>Olea europaea</i> , <i>Putterlickia pyracantha</i> , <i>Solanum guineense</i> ; Wind dispersed: <i>Tetragonia</i> sp., <i>Exomis microphylla</i> , <i>Zygophyllum morgsana</i> ; Others; <i>Anisodontia scabrosa</i> , <i>Hermannia</i> sp., <i>Lebeckia multiflora</i> , <i>Lobostemon glaber</i> , <i>Pelargonium hirtum</i> , <i>Protea burchellii</i> , <i>P. scolymocephala</i> , <i>Pseudoselago spuria</i>	Long-lived generalist-pollinated, good dispersers that should be widely distributed regionally and unaffected by habitat fragmentation (Least threatened)
9) Long-distance dispersed, specialist-pollinated, annual, seeders (2)	All 1/1/1	<i>Pelargonium senecioides</i> , <i>Crassula strigosa</i>	Good dispersers but the disruption of plant-pollinator interactions may lead to small populations which are susceptible to stochastic events (Vulnerable)
10) Long-distance dispersed, generalist-pollinated, annual, seeders (28)	LDS 9/9/10	Mainly Asteraceous herbs: <i>Arctotheca calendula</i> , <i>Cotula turbinata</i> , <i>Dimorphotheca pluvialis</i> , <i>Felicia tenella</i> , <i>Gorteria personata</i> , <i>Gymnodiscus capillaries</i> , <i>Helichrysum indicum</i> , <i>H. moeserianum</i> , <i>Monoculus monstruosus</i> , <i>Nestlera biennis</i> , <i>Oncosiphon grandiflorum</i> , <i>Pseudognaphalium undulatum</i> , <i>Ursina anthemoides</i> and some <i>Senecio</i> species. Some Poaceae <i>Bromus pectinatus</i> , <i>Ehrharta</i> sp. <i>Pentaschistis patula</i> , <i>Tribolium echinatum</i> ,	Short-lived, generalist-pollinated, good dispersers and gap exploiters that should be widely distributed regionally and unaffected by habitat fragmentation (Least threatened)
11) Short distance dispersed, generalist-pollinated, dioecious, resprouters (16)	ASF 13/1/2	Mostly restios: <i>Cannomois parviflora</i> , <i>Elegia neesii</i> , <i>Chondropetalum nudum</i> , <i>Restio triticeus</i> , <i>Hypodiscus</i> , <i>Willdenowia</i> and <i>Ischyrolepis</i> species, Other taxa: <i>Leucadendron brunoides</i> subsp. <i>flumenlupinum</i> , <i>Anthospermum spathulatum</i>	May persist locally through clonal growth but at risk in the long run due to poor dispersal ability which may affect gene flow and the fact that they also need plants of different sexes (male and female) to maintain viable population. These may lead to small populations which are more prone to stochasticity (Vulnerable)
12) Short-distance dispersed, specialist-pollinated, non-dioecious, resprouters (22)	SSR 5/14/3	Mostly geophytes: <i>Babiana</i> , <i>Cyphia</i> , <i>Moraea</i> , <i>Spiloxene</i> species, <i>Bulbine praemorsa</i> , <i>Caesia</i> sp., <i>Cyanella hyacinthioides</i> , <i>Ixia dubia</i> , <i>Geissorhiza aspera</i> , <i>Trachyandra chlamydophylla</i> , <i>Wachendorfia multiflora</i> ; Other: <i>Erica mammosa</i> , <i>Muraltia filiformis</i> , <i>Salvia africana-lutea</i>	Can persist locally through clonal growth but at risk in the long run due to poor dispersal ability and the disruption of plant-pollinator relationships leading to small populations which are susceptible to stochastic events (Vulnerable)

PFT (No. of species)	Vegetation	Key Taxa	Predicted responses to fragmentation (<i>threat</i>)
13) Short-distance dispersed, generalist-pollinated, non-dioecious, resprouters (24)	ASF/SSR 11/11/2	<i>Oxalis</i> species, <i>Cyanella lutea</i> , <i>Agathosma imbricate</i> , <i>Argyrolobium velutinum</i> , <i>Berzelia abrotanoides</i> , <i>Lachnaea</i> species, <i>Xiphotheca reflexa</i> , <i>Leucospermum hypophyllocarpodendron</i> , <i>Salvia lanceolata</i> , <i>Staavia radiata</i> , <i>Stilbe ericoides</i> , and <i>Trichocephalus stipularis</i> .	Can persist locally through clonal growth but at risk in the long run due to poor dispersal ability which may affect gene flow and lead to small populations which are more prone to stochasticity (Vulnerable)
14) Short-distance dispersed, specialist-pollinated, dioecious, perennial seeders (1)	ASF 1/0/0	<i>Leucadendron cinereum</i>	At high risk due to poor dispersal ability, the possible disruption of plant-pollinator interactions and the lack of viable population, leading to small populations which are susceptible to stochastic events. (Endangered)
15) Short-distance dispersed, generalist-pollinated, dioecious, perennial seeders (10)	ASF 5/3/2	<i>Anthospermum galiodes</i> , <i>A. hirtum</i> , <i>A. aethiopicum</i> , <i>Elegia filacea</i> , <i>Ischyrolepis monanthos</i> , <i>Restio bifurcus</i> , <i>R. quinquefarius</i> , <i>R. praeacutus</i> , <i>Euphorbia arceuthobioides</i> , <i>E. burmanii</i>	At high risk due to poor dispersal ability and the fact that they need plants of different sexes (male and female) to maintain viable population (Endangered)
16) Short-distance dispersed, specialist-pollinated, non-dioecious, perennial, seeders (8)	ASF 6/2/0	<i>Diastella proteoides</i> , <i>Polygala garcinii</i> , <i>Salvia africana-caerulea</i> , <i>Muraltia</i> sp.	At high risk due to poor dispersal ability and the possible disruption of plant-pollinator interactions leading to small populations which are susceptible to stochastic events (Endangered)
17) Short-distance dispersed, generalist-pollinated, non-dioecious, perennial seeders (65)	ASF 29/19/17	<i>Aspalathus</i> , <i>Indigofera</i> , <i>Rafnia</i> sp., <i>Lessertia excissa</i> , <i>Otholobium hirtum</i> , <i>Wiborgia fusca</i> , <i>Aizoon sarmentosa</i> , <i>Lampranthus</i> , <i>Ruschia</i> sp., <i>Macrostylis villosa</i> , <i>Phylica cephalantha</i> , <i>P. imberbis</i> , <i>Roella ciliata</i> , <i>Selago fruticosa</i> , <i>Serruria</i> , <i>Diosma</i> , <i>Wahlenbergia</i> sp., <i>Zygophyllum sessilifolium</i> , <i>Scabiosa columbaria</i> , <i>Silene</i> sp., <i>Sutera</i> sp., <i>Stachys aethiopica</i> , <i>Agathosma bisulca</i> , <i>Chironia linoides</i> , <i>Erica plumosa</i> , <i>Euphorbia genistoides</i> , <i>Hermannia multiflora</i> , <i>Lachnaea capitata</i> , <i>Leucospermum parile</i> , <i>Macrostylis cassioides</i> , <i>Melianthus elongatus</i> , <i>Montinia caryophyllacea</i> , <i>Muraltia</i> sp., <i>Selago corymbosa</i> , <i>Struthiola ciliata</i> , <i>Thesium strictum</i> , <i>Euphorbia caput-medusae</i> , <i>Tylecodon wallichii</i>	Although poor dispersers which may affect gene flow, they are also generalist-pollinated and do not need plants of different sexes to maintain viable populations since they are non-dioecious (Vulnerable)
18) Short-distance dispersed, specialist-pollinated, annual seeders (1).	SSR 0/1/0	<i>Hemimeris racemosa</i>	At high risk due to poor dispersal ability and the possible disruption of plant-pollinator interactions leading to small populations which are susceptible to stochastic events (Endangered)
19) Short-distance dispersed, generalist-pollinated, annual seeders. (9)	LDS 2/3/4	<i>Apatesia pillansii</i> , <i>Cysticapnos cracca</i> , <i>Heliophila digitata</i> , <i>Nemesia</i> sp., <i>Phyllopodium cephalophorum</i> , <i>Sebaea exacoides</i> , <i>Sisymbrium capense</i> , <i>Wahlenbergia androsacea</i>	Their poor dispersal ability is compensated for by the fact that they are generalist-pollinated and good gap exploiters (Vulnerable)

4.3.3 Trait differences among the three vegetation types

The Chi-square tests results presented here are only those for the five (i.e. dispersal distance, dispersal versatility, breeding mode, regeneration mode and spinescence) out of the eight traits that showed significant differences in the occurrence of the 348 species among the three vegetation types (Table 4.4). More short-distance dispersed species occurred in Atlantis Sand Fynbos (ASF) than in Swartland Shale Renosterveld (SSR) and Langebaan Dune Strandveld (LDS), while more long-distance dispersed species occurred in SSR than in ASF and LDS. More specialist-pollinated species and species with one pollination mode were found in SSR than in ASF and LDS whereas more species with more than one pollination mode occurred in LDS than in SSR and ASF. ASF had more dioecious species and SSR, more non-dioecious species. SSR also had more resprouters (mostly geophytes), seeders and species with spines compared to ASF and LDS.

Table 4.4 Results of the Chi-square test showing significant differences in the occurrences of five of the eight traits for species in the three Cape lowland vegetation types. Numbers and percentages denote species with particular traits for each vegetation type.

Trait	Trait category	ASF	SSR	LDS	Total	p-value
Dispersal distance	Short	72 (46%)	54 (35%)	30 (19%)	156	0.00082
	Long	52 (27%)	83 (43%)	57 (30%)	192	
Dispersal versatility	Poly	27 (31%)	28 (32%)	33 (38%)	88	0.00928
	Mono	97 (37%)	109 (42%)	54 (21%)	260	
Breeding mode	Non-dioecious	98 (32%)	129 (43%)	75 (25%)	302	0.00108
	Dioecious	26 (57%)	8 (17%)	12 (26%)	46	
Regeneration	Resprouter	51 (40%)	57 (44%)	21 (16%)	129	0.01288
	Seeder	73 (33%)	80 (37%)	66 (30%)	219	
Spinescence	Yes	2 (9%)	13 (59%)	7 (32%)	22	0.01147
	No	122 (37%)	124 (38%)	80 (25%)	326	
Total number of species		124	137	87	348	

4.3.4 PCA comparing the two approaches used to define PFTs

The objective and subjective approaches gave very similar results (Figure 4.3). Both produced three distinct groups, the SSR medium-sized fragment, all LDS and some SSR sites, and a group of one SSR and all ASF sites.

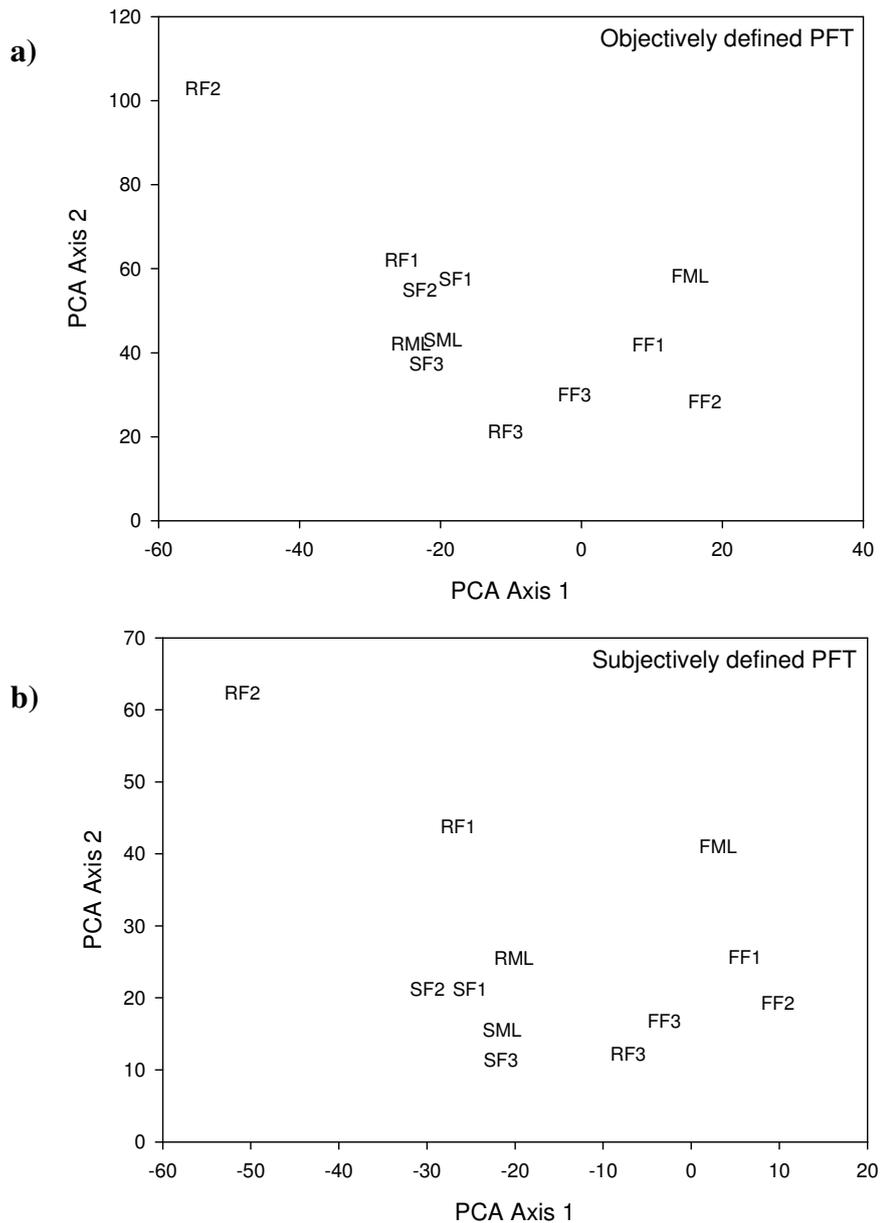


Figure 4.3 PCA ordination diagram showing PFT occurrence in three studied Cape lowland vegetation types **a)** Eight objectively defined PFTs and **b)** Nineteen subjectively defined PFTs. F = Atlantis Sand Fynbos, R = Swartland Shale Renosterveld and S = Langebaan Dune Strandveld, ML = mainland, F1 = largest fragment, F2 = medium-sized fragment and F3 = smallest fragment.

4.4 Discussion

In order to predict how the three Cape lowland vegetation types, studied hereunder, would respond to habitat fragmentation, the species were grouped into a total of 27 plant functional types (PFTs) (eight objectively and 19 subjectively) based on the selected traits. The objective and subjective approaches gave remarkably similar results as both showed that species within particular PFTs

occurred in particular sites within three distinct groups. The fact that SSR medium-sized fragment which is being grazed by indigenous herbivores stood out alone indicates that grazing is very vital for the functioning this vegetation type. After all, renosterveld is created and maintained by an intermediate level of disturbance (Boucher 1983) and often fluctuates between a predominantly shrub- or grass-dominated state, depending on fire or the use of brush-cutting techniques (Heydenrych 1995). As expected, SSR that has been subjected to grazing for a long period of time, had more resprouters (mostly geophytes) and more species with spines than ASF and LDS. Therefore, grazing in renosterveld plays a crucial role in the interchange between grasses, geophytes and shrub components (Rebelo et al. 2006). Similarly, ASF, which is a characteristically fire-prone ecosystem, had more short-distance dispersed perennial resprouters. These were mostly species of the Restionaceae family, known to fuel fires in fynbos (Rebelo et al. 2006). Interestingly, the ASF and LDS sites were separated while some SSR sites were grouped closer to ASF sites and others closer to LDS sites as depicted in the PCA ordination diagrams. This clearly highlights the low level of floristic composition, structural and functional affinities among fynbos, renosterveld and strandveld (see also Rebelo et al. 2006). This was also evident from the Chi-square tests, which showed significant differences in the occurrence of traits among the three vegetation types. ASF was dominated by many short-distance dispersed species whereas LDS was dominated by many long-distance (ornithochorous) species. SSR is somehow in between ASF and LDS as it was dominated by mostly long-distance dispersed asteraceous species and many short-distance dispersed geophytes (see also Cowling et al. 1997; Rebelo et al. 2006).

Despite the remarkable similarity in the groupings produced by these two approaches each approach has its merits and demerits. The objective approach required the identification of actual plant functional groups from expert knowledge of relevant traits and scaling from individual plant traits to ecosystem functioning (Cornelissen et al. 2003). This poses two major problems as pointed out by Woodward and Cramer (1996). The first problem is picking out the plant functional attribute or

mechanistic basis that puts a species in a particular PFT. This problem arises from the likelihood that as environmental conditions change, the plant attribute used for the classification may change for some species and not for others, even if they are grouped under the same PFT. The second problem stems from the fact that species are treated as individual data points. Complications may arise where closely related species are grouped into a PFT because of a common trait inherited from one genus. However, this trait may not have the same functional impact in all the species due to species-specific trait modifications.

The subjective approach on the other hand may be biased because the PFTs were derived based on the researcher's general understanding of the key processes relevant to species' responses to habitat fragmentation. This might not have covered all vital and limiting processes (see e.g. Woodward & Cramer 1996) and may lead to little functional explanatory power (Cornelissen et al. 2003). However, only eight PFTs were identified with the objective approach compared to the 19 PFTs using the subjective approach. This means that details might be lost by using an objective approach.

Since plant species often have many strategies to cope with any given environmental condition (Westoby et al. 2002), predicting vegetation response to fragmentation can be very challenging. This situation is further complicated by the fact that plant species usually exhibit a number of trade-offs and correlations between traits due to the biophysical constraints on their structure and function (Grime 1977; Grime et al. 1997; Hodgson et al. 1999; Grime 2001). However, based on the PFTs defined the species in the three vegetation types studied were classified as endangered, vulnerable or least threatened by habitat fragmentation. The result showed that all the three vegetation types are susceptible to habitat fragmentation although at varying degrees. This is obvious since these vegetation types have many rare and endemic species with low re-colonisation potential and low probability of maintaining viable population sizes (Hanski 1994).

Six of the total 27 PFTs defined were classified as endangered, five composed predominantly of fynbos species and one by renosterveld species. The ASF PFTs were mostly short-distance dispersed, dioecious and non-dioecious seeders of the Ericaceae, Proteaceae, Restionaceae, Rhamnaceae, Rutaceae and Thymelaeaceae families. These species tend to allocate more resources to seed production (Rebelo et al. 2006) and many of them are myrmecochorous (Bond & Slingsby 1984; Johnson 1992). Myrmecochorous species usually have small, transient seed banks and are therefore more vulnerable to fragmentation (Cowling et al. 1994). Some of these species (mainly Proteaceae) are serotinous i.e. they retain their seeds in fireproof seed heads on the plants, releasing them only after a fire when conditions for germination are favourable (Le Maitre & Midgley 1992; Rebelo et al. 2006). Serotinous species with winged seeds are wind-dispersed, although rarely beyond 100 m (Cowling et al. 1997). The poor dispersal ability of these species therefore reduces their rate of re-colonisation from nearby patches (see also Bond et al. 1988; Bond 1994).

The dioecious species within the endangered PFTs are at risk of not having viable population sizes due to fragmentation. Re-colonisation may also be more difficult since both sexes are needed to establish a population. This is because the loss of habitat as a result of fragmentation leads to smaller (sub) populations, which are more prone to higher extinction risks due to environmental, demographic or genetic stochasticity (Franklin 1980; Shaffer 1981; Lindenmayer & Fischer 2006). Moreover, small plant populations are often less attractive to pollinators (Morgan 1999; Pauw 2004). Such small plant populations are often made up of closely related individuals whose offspring may suffer from inbreeding depression and reduced genetic diversity (Ellstrand & Elam 1993; Young et al. 1996; Matthies et al. 2004; Bruna & Oli 2005).

Many of the species in the endangered PFTs also exhibit a high degree of pollinator specificity (Johnson & Steiner 2000, 2003) such as long-proboscid fly and long-beaked bird pollination. Ornithophily occurs in about 5% of fynbos plant taxa, for example the Ericaceae, Proteaceae,

Amaryllidaceae, Iridaceae, and Orchidaceae (Johnson 1992, 1996; Goldblatt et al. 1999). Pollination by long-proboscid nectar feeding Bombyliidae, Nemestrinidae, and Tabanidae fly species is also common in Ericaceae, Geraniaceae and Orchidaceae species with long tubular corolla (Manning & Goldblatt 1996; Goldblatt & Manning 2000). Some rare fynbos species of the Iridaceae and Orchidaceae families are pollinated by the satyrine butterfly (*Aeropetes tulbaghia*) on which they depend for their survival (Bond 1994). The only renosterveld species, *Hemimeris racemosa* (Scrophulariaceae) within the endangered PFT also exhibits a very highly specialised pollination system. This species provides an unusual floral reward and is pollinated by oil-collecting bees in the genus *Rediviva* (Melittidae) that are low in diversity (Steiner 1989, 1993; Manning & Goldblatt 2002; Steiner & Whitehead 2002; Johnson & Steiner 2003; Pauw 2004). Species with such highly specialised pollination systems are at high risk of extinction. The disruption of such plant-pollinator relationships by fragmentation has severe ramifications for genetic diversity as pollinators may visit flowers less frequently, leading to reduced fecundity and low seed set (Bond 1994; Donaldson et al. 2002; Bruna & Oli 2005; Ward & Johnson 2005; Aguilar et al. 2006; Lawson et al. 2008). Other consequences of habitat fragmentation with negative impact on plant-pollinator interactions include the increased isolation of plant populations and less habitat area available for animal pollinators (Lamont et al. 1993; Steffan-Dewenter & Tscharntke 1999; Wolf & Harrison 2001).

Most species in the three Cape lowland vegetation types were under the PFTs classified as vulnerable. The ASF species within this group are specialist- or generalist-pollinated dioecious resprouters (mostly Restionaceae) with either long- or short-distance dispersal abilities. Most of these species require fire to regenerate (Rebelo et al. 2006). Although these species can persist through clonal growth, they risk losing genetic diversity in the long run due to lack of viable populations. These species do exhibit trade-offs whereby some compensate for being dioecious and having specialised pollination systems with their long-distance dispersal and resprouting abilities.

Others compensate for being dioecious and having poor dispersal abilities with their resprouting abilities and by being generalist-pollinated. The SSR species within the vulnerable PFTs are all non-dioecious, specialist-pollinated resprouters (mostly geophytes), with either short or long-distance dispersal abilities. These species are considered vulnerable to habitat fragmentation because of the risk of the disruption of their highly specialised plant-pollinator interactions that has serious ramifications for genetic diversity as earlier explained. Specialised pollination by long-proboscid flies is particularly common in species of the Geraniaceae and Orchidaceae families (Manning & Goldblatt 1996; Goldblatt & Manning 2000). However some of the species compensate for this by their dispersal in space (long-distance) and time (clonal growth). The LDS species that were within the vulnerable group are all long-distance dispersed, mostly fleshy-fruited ornithochorous species (Knight 1988; Cowling et al. 1997), specialist-pollinated dioecious and non-dioecious seeders and resprouters. Some of these species compensate for their specialised pollination systems by being long distance-dispersed e.g. *Microlooma sagittatum*, *Diospyros glabra*, and *Euclea racemosa*. Others such as *Arctopus echinatus*, *Cissampelos capensis*, or *Rhus* species compensate for being dioecious by being long distance dispersed.

Of the five PFTs classified as least threatened, three were dominated by SSR species and one each by ASF and LDS species. This group consisted of long-distance dispersed generalist-pollinated non-dioecious resprouters as well as perennial and annual seeders. As expected, these traits confer high persistence ability at the individual, population, community and landscape levels. The species in this group are the most widely distributed across the three vegetation types. The resprouters can persist for long periods because of their clonal growth abilities. Clonal growth can be considered as the rescue effect in time (Piessens et al. 2005) and is complementary to the rescue effect in space (Brown & Kodric-Brown 1977). Since the seeders within this group were mostly wind dispersed asteraceous species, re-colonization from other patches is possible (see also Kemper et al. 1999). Long distance dispersal also allows re-colonization in fragmented environments that harbour

metapopulations (Trakhtenbrot et al. 2005; Aparicio et al. 2008) and is generally assumed to be important for the regional survival of plant species (Soons & Ozinga 2005). Pollen and seed inflow from one population can preserve and enhance genetic diversity and reduce inbreeding within another population, thereby rescuing it from extinction (Richards 2000; Ingvarsson 2001). This may only occur if the patches are somehow connected and/or are not too isolated from one another. Habitat fragmentation can disrupt dispersal across patches, one of the reasons being that the matrix between patches often impedes movement of dispersers and pollinators (Ricketts 2001; Higgins et al. 2003; Jonas et al. 2006). This group of species were also considered least threatened because they are generalist pollinated and are therefore not threatened by the disruption of plant-pollinator interactions. The perennial seeders can persist for extended periods even with reduced reproductive success because it takes time for changes in the reproductive success of individual scale to manifest at the population level of long-lived species (Haila et al. 1993). The annuals, on the other hand, have a high probability of re-colonising and establishing in disturbed areas owing to their larger and persistent seedbanks (Hester & Hobbs 1992).

4.5 Conclusion

This study brought to light the two main challenges involved in predicting how plant species may respond to habitat fragmentation. First, relevant traits had to be selected and appropriate methods used to classify species into PFTs or sets of co-occurring traits (i.e. trait 'syndromes'). Traits selected for this study reflected species' responses to habitat fragmentation. Using these traits, the plant species of the three Cape lowland vegetation types studied were classified into eight objectively and 19 subjectively defined PFTs. Both approaches produced remarkably similar results in terms of PFTs associated to particular vegetation types and sites. Based on their predicted response to habitat fragmentation, Atlantis Sand Fynbos with more short-distance dispersed dioecious species than the other two vegetation types, stood out as the most susceptible, which ties with results from the species diversity study (Chapter 3). Next was Swartland Shale Renosterveld

with many geophytes that exhibit highly specialised pollination systems. Langebaan Dune Strandveld, which had many fleshy-fruited generalist-pollinated ornithochorous species than the other two vegetation types, was the least threatened. However, based on the assessment of the surrounding matrix types and vulnerability to further transformation, SSR is considered the most critically endangered of the three vegetation types (Jonas et al. 2006). This indicates that the magnitude of susceptibility to habitat fragmentation may well depend on the connectivity between patches and the resistance of the surrounding matrix to the movement of plant propagules and plant pollinators (see also Jules & Shahani 2003). To fully understand the impact of habitat fragmentation in the Cape lowlands, it is necessary to investigate these aspects as well as the effects of fragmentation (reduced patch size) on PFT richness and diversity.

4.6 References

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Chapter 5

Effects of habitat fragmentation on plant functional type richness and diversity in three Cape lowland vegetation types of South Africa

Abstract

Biodiversity loss due to habitat fragmentation involves losses in functional diversity, which is most relevant to ecosystem functioning. It is therefore, vital to assess how ecosystems will respond to such changes. I investigated the impact of patch size and sampling scale on plant functional type (PFT) richness and diversity at four sites in three Cape lowland vegetation types. PFT accumulation curves of the different sites and scales for the eight objectively and 19 subjectively defined PFTs were constructed and compared. The Gini-Simpson and Shannon-Wiener indices of PFT diversity were calculated and converted to effective number of species per PFT to facilitate comparison between sites. Patch size had a greater effect on PFT diversity than on richness. Langebaan Dune Strandveld where habitat fragmentation is more recent was the least affected of the three vegetation types. This indicates a degree of functional redundancy in the Cape lowlands, which is important for ecosystem resistance and resilience. PFT richness relative to fragment size was not consistent at all scales in all three vegetation types, indicating a scale effect. The Atlantis Sand Fynbos mainland and the largest fragment were higher in PFT diversity than the medium-sized and the smallest fragments, and the mainland higher in PFT diversity than the fragments combined. PFT richness and diversity was lowest in the smallest Swartland Shale Renosterveld fragment than in the other sites. Meanwhile, the grazed fragment was higher in PFT richness and diversity than the ungrazed sites, indicating that grazing is vital for the functioning of renosterveld. PFTs absent from sites consisted mostly of short-distance dispersed dioecious and non-dioecious species, some with highly specialised pollination systems. This indicates that dispersal and pollination are vital functional attributes for the persistence of such fragmented ecosystems.

Keywords: biodiversity; ecosystem functioning; functional diversity; functional redundancy; habitat fragmentation.

5.1 Introduction

The function of an ecosystem embodies its processes, properties and the invaluable goods and services it provides for the survival of mankind (Gamfeldt et al. 2008). Biodiversity, be it genes, species or plant functional type diversity, plays a role in the magnitude and efficiency of ecosystem processes and properties (Chapin et al. 1997, 2000). There is now growing awareness that functional diversity is probably the biodiversity component most relevant to ecosystem functioning (Díaz & Cabido 2001; Hooper et al. 2002; Naeem & Wright 2003; Balvanera et al. 2006; Petchey & Gaston 2006). Functional diversity comprises the diversity and range of functional traits possessed by the biota of an ecosystem (Díaz & Cabido 2001; Wright et al. 2006). However, human activities now dominate most ecosystems (Vitousek et al. 1997; Sanderson et al. 2002) and several species have been introduced from one part of the globe to another (Jenkins 1996; French 2000; McNeely 2000; Hobbs et al. 2006). This has resulted in vast areas of natural habitats being transformed and fragmented into several smaller patches that are “isolated” from each other by matrices of different land use types (Wilcove et al. 1986). Due to its negative effects, habitat fragmentation currently constitutes the greatest threat to biodiversity worldwide (Saunders et al. 1991; Debinski & Holt 2000; Fahrig 2003; Henle et al. 2004; Groom et al. 2005).

Despite the growing awareness that plant functional traits are better predictors of ecosystem response to global changes (Steffen et al. 1992; Smith et al. 1997; Lavorel & Garnier 2002; Cornelissen et al. 2003) such as habitat fragmentation, there has been no study on the effect of fragmentation on plant functional types in the Cape region. Most fragmentation studies worldwide have focused on the consequence of species loss on single process rates or properties, with little attention given to aspects of biodiversity such as functional diversity. This can be misleading, especially if the study ultimately aims to provide knowledge and advice for successful biodiversity conservation and management. In fact, most species-based studies have either shown weak or inconsistent fragmentation effects, particularly with regards to species richness and abundance in

relation to fragment size (e.g. Chapter 3). These, coupled with the challenges involved in predicting how plants may respond to habitat fragmentation, can undermine efforts to better understand and mitigate its negative effects. Functional diversity is a likely solution to these problems, but quantifying it is a challenge (Petchey & Gaston 2006; Wright et al. 2006).

One commonly used approach to quantify functional diversity is to cluster species with shared taxonomic, physiological and/or morphological traits into functional groups, assuming that plant species with similar traits will respond in the same way to global changes and have similar effects on ecosystem processes (Lavorel & Garnier 2002; Petchey & Gaston 2002). The number (richness) of functional types or groups is often used as an approximation of functional diversity (Wright et al. 2006). However, there is continuing debate as to whether all plant species or just a few representatives of each general functional type are required at any time to maintain major ecosystem processes. Some studies have shown that one or few key species can dictate certain ecosystem processes (Paine 2002; Bellwood et al. 2003; Solan et al. 2004). A small range of species may also carry out the same ecological function, resulting in a high degree of redundancy, thus promoting ecosystem stability (Walker 1992; Cowling et al. 1994; Walker 1995; Naeem 1998; but see Loreau 2004). Ecosystem stability is best described as the long-term consequence of its resistance and resilience to extreme events (Grime 2001). Therefore, understanding ecosystem function requires the development and testing of theories that can assess the impact of declining plant species diversity at the landscape scale on the reassembly of communities. This can be done by quantifying the ecosystem's immediate response (resistance) to, and speed of recovery (resilience) from such events (Grime 2001).

Several theories have been advanced to explain how plant communities may respond to extreme events. One is that species-rich communities with a greater diversity in traits conferring either tolerance or resistance and resilience, are likely to be more resistant and resilient to extreme events

(MacArthur 1955; Tilman & Downing 1994). The response of a plant community to an event may also be highly influenced by previous exposure to similar events, as species with traits that represent resistance and/or resilience are selected for (Sankaran & McNaughton 1999). Functional redundancy within a community may result in some species being dispensable with respect to ecosystem functioning if their loss does not drastically impact on ecosystem processes, since the remaining species can compensate for the loss (Walker 1992, 1995; Cowling et al. 1994). This implies that an ecosystem with high numbers of similar functional species has a better chance of persisting as some species will survive environmental changes and continue to maintain the functions of the system. Analogous to functional redundancy is the “insurance” hypothesis (Loreau 2000), whereby a greater variation in responses among species in a community will mean that fewer species will be required to buffer the system. Greater functional richness will likely contribute to an ‘ecological insurance’ effect because of the increased chances of some species responding differently to environmental conditions and global change events. A very popular theory is the triangular C-S-R hypothesis (Grime 1977, 2001). This stipulates that differences in the adaptive responses of plants can be predicted and explained by considering the role of the disturbance regime and habitat productivity in plant evolution and ecology. Based on this theory, competitors (C) with spatially dynamic root and shoot systems are better adapted to quickly monopolise and capture resources; stress-tolerators (S) with long-lived tissues are more adapted to resist extreme conditions like herbivory and stress in nutrient poor environments; while ruderals (R) tend to allocate more resources to reproduction. These theories, and results from many studies (e.g. Johnson et al. 1996; Díaz & Cabido 2001), suggest that different responses by different species to environmental factors can contribute to the long-term maintenance of ecosystem processes, particularly in the context of global changes such as habitat fragmentation.

This study aimed to better understand how severely fragmented ecosystems in the Cape lowlands function by investigating the impact of habitat fragmentation (reduced patch size) and sampling

scale on plant functional type (PFT) richness and diversity. It is assumed that habitat loss due to fragmentation will lead to the loss of PFTs, the magnitude of which will be proportional to the fragment size, sampling scale, connectivity and the resistance value of the surrounding matrix (i.e. the difficulty of species to cross the matrix) of the remnant patch. If habitat fragmentation leads to the disruption of dispersal, pollination and insularisation, which are linked to small population size, then in the smaller and/or less connected patches there will be more PFTs with traits conferring persistence at the individual, local and landscape scales (such as perennials, long distance dispersal ability, generalist-pollinated and resprouting ability) and fewer short-distance dispersed, specialist-pollinated and dioecious species. On the other hand, if there are selective processes in play, then the effect of reduced patch size would be confounded by site factors such as disturbance regime (grazing and fire), and alien plant invasion. Thus one would expect more PFTs of species with traits that can enable them to cope with the prevalent disturbance regime in a particular site. For instance, more resprouters and spiny species should be found in sites that are prone to grazing and in fire-prone areas, a high representation of short- and long-distance dispersed, perennial, resprouters and annual seeders that require fire to regenerate.

5.2 Methods

The study sites and vegetation types are as described in Chapter 1 (section 1.4.1), the sampling procedure was as described in Chapter 3 (section 3.2.2). Plant traits were selected and assigned to species sampled as described in Chapter 4 (section 4.2.1) and the PFTs defined in Chapter 4 (eight objectively and 19 subjectively) were used.

5.2.1 Comparing PFT richness among sites

Sample-based accumulation curves for the eight objectively and 19 subjectively defined PFTs were constructed and compared following the same procedure as for species accumulation curves (Chapter 3 section 3.2.3). An analysis of the presence-absence of PFTs in the different sites of the

three vegetation types was also done to determine the PFTs missing from particular sites. Habitat fragmentation leads to reduced patch size, which may result in the following:

(1) Significant higher PFT accumulation (richness) with increasing sampling effort as patch size increases i.e. PFT richness in the mainland > PFT in the largest fragment (LF) > PFT in the medium-sized fragment (MF) > PFT in the smallest fragment (SF) and;

(2) Significant higher PFT accumulation (richness) with increasing sampling effort in the mainland than in all the combined fragments (CF). These null hypotheses were rejected in favour of the alternative hypotheses if there were no overlaps in the 95% CIs of the PFT accumulation curves and/or the p -value of the maximum likelihood Chi-square test < α (0.05).

5.2.2 Comparing PFT diversity among sites

Given that replicate samples were taken, the Gini-Simpson and Shannon-Wiener indices were calculated using the number of species represented in each PFT as the abundance value. Standard statistical techniques (ANOVA and t-tests) were then used to compare PFT diversity between the sites (see Sokal & Rohlf 1995; Lande et al. 2000; Magurran 2004). The Simpson's Index gives the probability of any two individuals (in this case species) drawn at random from an infinitely large community belonging to different species (in this case PFTs). The Simpson's Index is considered a dominance index because it weighs towards the most common species (in this case PFT). The

Simpson's Index (D) was calculated as $D = \sum_{i=1}^k p_i * p_i$. Since the Simpson's Index and diversity are

negatively related, the complementary form (Gini-Simpson Index: $D = 1 - \sum_{i=1}^k p_i * p_i$) was used so

that the index and diversity are positively related. The Shannon-Wiener Index of PFT diversity was

calculated in natural logarithm using the formula $H' = -\sum_{i=1}^k p_i \ln p_i$. In these formulas, k is the

number of PFTs and p_i is the proportion of species found in the i^{th} PFT (see e.g. Zar 1999; Magurran 2004). The Shannon-Wiener Index assumes that all species are represented in a sample

and that the sample was obtained randomly, it does not favour rare or common species and weighs each exactly by its frequency. These indices are not themselves real diversities and therefore need to be converted to true diversity, which is the effective number of species, to obtain a unified and intuitive interpretation of diversity (Jost 2006, online article). The Gini-Simpson Index was converted to true diversity by subtracting it from unity and inverting it (i.e. $1 / 1 - D$), and the Shannon-Wiener Index by taking the exponential of the index (Jost 2006, unpublished). The effective numbers of species is the number of equally-common species required to give a particular value of an index. Converting the indices to effective number of species, gives them common properties and behaviour, eliminates non-linearity associated with the indices and allows for easy comparison and interpretation (Jost 2006, online article). Thus, it is possible to go beyond the statistical significance of an effect and appreciate the real magnitude of the effect, which is biologically more important. For example, if one site has a true diversity of four effective species based on a particular index of diversity, and another has a true diversity of 12 effective species based on the same index, the second site is three times as diverse as the first according to that index.

The normality of the data was tested using the Shapiro Wilk's, W test. If normality was not met, the Kruskal-Wallis ANOVA and Mann-Whitney U test were used to compare sites, otherwise, one-way ANOVA with a post hoc (Bonferroni) and t-test were used in Statistica 8 (StatSoft Inc 1984-2008). Seven pairwise comparisons were done: the mainland vs. each fragment; the mainland vs. the fragments combined; the largest vs. the medium-sized fragment, the largest vs. the smallest fragment and the medium-sized vs. the smallest fragment.

5.3 Results

For PFT richness, only the general trends of PFT accumulation curves for the three vegetation types at the four sampling scales are presented (Figure 5.1 and 5.2). Comparisons of confidence intervals (CIs) of the PFT accumulation curves and maximum likelihood Chi-square tests presented are only those for vegetation types and scales that showed significant results (Tables 5.1 and 5.2).

For PFT diversity, the Gini-Simpson and the Shannon-Wiener indices and their corresponding effective number of species per PFT (i.e. true diversity) gave very similar results (Tables 5.5 – 5.9). Only details of significant results based on the Gini-Simpson Index are presented here. Significant results based on the effective number of species per PFT for the Gini-Simpson Index, and those based on the Shannon-Wiener Index and the effective numbers of species per PFT are presented in appendices 14 and 15.

5.3.1 Richness in the eight objectively defined PFTs

PFT richness in Atlanits Sand Fynbos - ASF (Figure 5.1 A-D) generally increased with increasing patch size, although not consistently for all scales. PFT richness for fragments combined was higher than for the mainland. In Langebaan Dune Strandveld (LDS), PFT richness was not positively related to patch size at all scales, although it was highest in the fragments combined at all scales (Figure 5.1 I-M). Differences in PFT richness between ASF sites and LDS sites were not significant (not shown). In Swartland Shale Renosterveld (Figure 5.1 E-H), the largest fragment (300 ha) and the medium-sized fragment (70 ha) were generally higher and almost equal in PFT richness, while the smallest fragment (15 ha) consistently had the lowest richness at all scales. The combined fragments were also higher in PFT richness than the mainland at all scales. As shown in Table 5.1, PFT richness was slightly, albeit significantly, higher in the medium-sized than in the smallest fragment ($p < 0.05$) at the 0.1 and 1 m² scales, and higher in the largest than in the smallest fragment at the 1, 50 and 100 m² scales. PFT richness was also slightly higher in all the fragments combined than in the mainland at 1 m² ($p < 0.05$). All eight PFTs were represented in SSR and LDS while one PFT was absent in ASR (Table 5.2). All seven PFTs recorded in ASF were represented by at least one species in all the sites of this vegetation type. Three of the eight PFTs were absent from the smallest SSR fragment (15 ha), one (i.e. dioecious resprouters) was absent from the mainland (600 ha) and from the medium-sized fragment (70 ha), while all eight PFTs were represented in the largest fragment (300 ha) as well as in LDS sites (Table 5.2). The PFTs found in

each vegetation type were represented in the fragments combined for the respective vegetation types (Table 5.2).

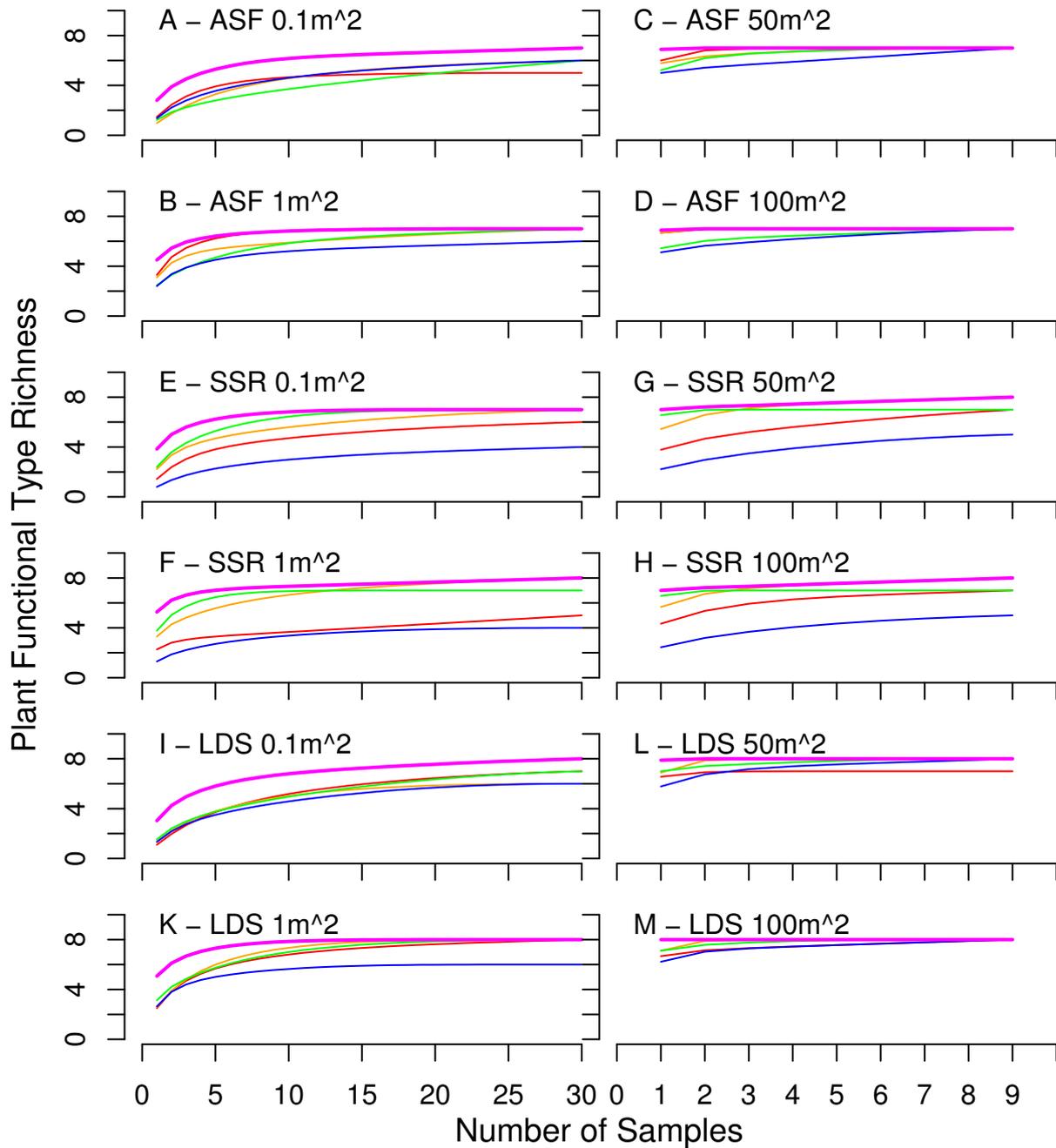


Figure 5.1 Sampled-based accumulation curves for the eight objectively defined PFTs for the mainland and fragments at 0.1, 1, 50, and 100 m² in ASF (A-D), SSR (E-H) and LDS (I-M). PFT richness is based on the Mao Tau moment-based estimator computed using EstimateS. **Mainland**, **Largest fragment**, **Medium-sized fragment**, **Smallest fragment** and **Combined fragments**.

Table 5.1 Significance of 95% confidence intervals (CI) of PFT accumulation curves and maximum likelihood (Max L) tests between SSR sites at the four sampling scales for the eight objectively derived PFTs (p-value for maximum likelihood test = Median for all samples). ns = no significant difference; * = very small difference; marginal = slight overlap of CI).

Scale	Site	ML		LF		MF	
		CI	Max L	CI	Max L	CI	Max L
0.1 m ²	CF	ns	ns				
	LF	ns	ns				
	MF	ns	ns	ns	ns		
	SF	ns	ns	ns	ns	marginal	*
1 m ²	CF	marginal	*				
	LF	ns	ns				
	MF	ns	ns	ns	ns		
	SF	ns	ns	marginal	*	marginal	*
50 m ²	CF	ns	ns				
	LF	ns	ns				
	MF	ns	ns	ns	ns		
	SF	ns	ns	marginal	*	ns	ns
100 m ²	CF	ns	ns				
	LF	ns	ns				
	MF	ns	ns	ns	ns		
	SF	ns	ns	marginal	*	ns	n

Table 5.2 Presence-Absence of the eight PFTs in the vegetation types and sites

	Atlantis Sand Fynbos	Swartland Shale Renosterveld	Langebaan Dune Strandveld
	Seven PFTs present One PFT absent (long-distance dispersed, dioecious species)	All eight PFTs were represented	All eight PFTs were represented
ML	All seven PFTs represented	One PFT absent (dioecious resprouters)	All eight PFTs were represented
LF	All seven PFTs represented	All eight PFTs represented	All eight PFTs were represented
MF	All seven PFTs represented	One PFT absent (dioecious resprouters)	All eight PFTs were represented
SF	All seven PFTs represented	Three PFTs absent (1) dioecious resprouters (<i>Ischyrolepis capense</i>) (2) long-distance dispersed, dioecious species (<i>Arctopus echinatus</i> , <i>Cissampelos capensis</i> and <i>Rhus</i> sp.) (3) generalist-pollinated, non-dioecious resprouters (<i>Senecio hastatus</i>)	All eight PFTs were represented
CF	All seven PFTs were represented	All eight PFTs were represented	All eight PFTs were represented

5.3.2 Richness in the 19 subjectively defined PFTs

Apart from the fact that in ASF, PFT richness was generally higher in the mainland and in all fragments combined at all scales, the other sites showed no consistent positive relationship with fragment size and PFT richness (Figure 5.2 A-D). PFT richness was significantly higher in the mainland than in the medium-sized fragment (37 ha) and in the largest fragment (600 ha) than in the smallest fragment (16 ha) at the 50 m² scale (Table 5.3). In LDS, there was generally no consistent trend except that the combined fragments was richer in PFTs than the mainland at all scales (Figure 5.2 I-M), although this was only significant at 50 m² (Table 5.3). In SSR, the medium-sized fragment (70 ha) was generally richer and the smallest fragment (15 ha) lower in PFTs than all the other sites at all the scales, and significantly higher in the fragments combined than in the mainland at all scales (Figure 5.2 E-H and Table 5.3) The medium-sized fragment was richer in PFTs than the smallest fragment at all scales as well as the mainland at the 0.1 and 50 m² scales. PFT richness was significantly higher in the SSR mainland than in the smallest fragment at the 50 and 100 m² scales and also higher in the largest than in the smallest fragment at the 1, 50 and 100 m² scales. Sixteen of the 19 PFTs were represented in ASF, and three were absent (Table 5.4), two of which were absent from the mainland, three from the largest fragment, four from the medium-sized fragment and five from the smallest fragment. Five of the 19 PFTs were absent from SSR, and of the 14 PFTs present, seven were absent from the smallest fragment (15 ha), two from the mainland and one from the medium-sized fragment. Four of the 19 PFTs were absent from LDS (Table 5.4) and of the 15 PFTs present, three were absent from the mainland and two from each of the fragments (Table 5.4). All the PFTs found in each vegetation type were represented in the fragments combined.

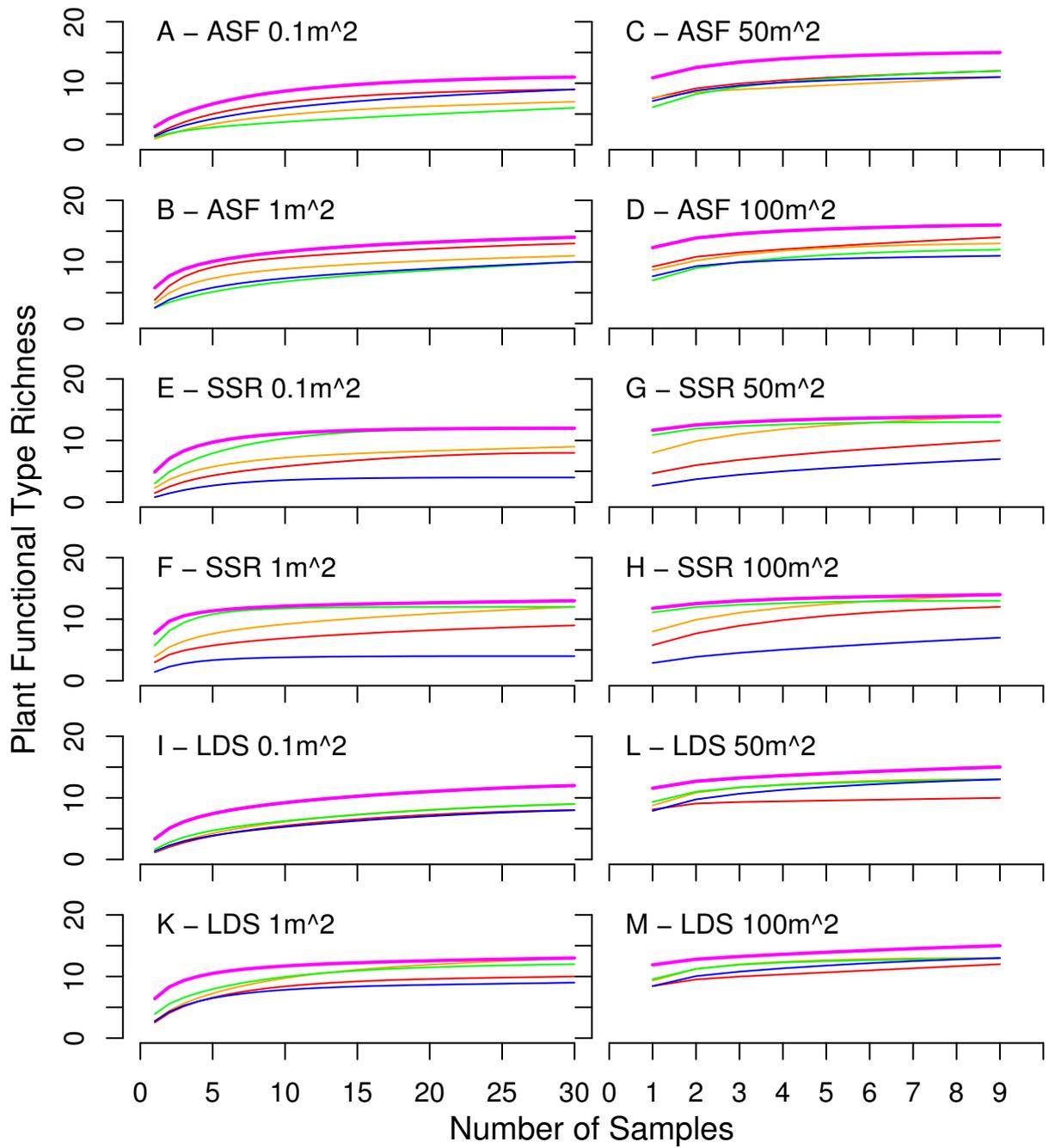


Figure 5.2 Sampled-based accumulation curves for the 19 objectively defined PFTs for the mainland and fragments at 0.1, 1, 50, and 100 m² in **ASF** (A-D), **SSR** (E-H) and **LDS** (I-M). PFT richness is based on the Mao Tau moment-based estimator computed using EstimateS. **Mainland**, **Largest fragment**, **Medium-sized fragment**, **Smallest fragment** and **Combined fragments**.

Table 5.3 Significance of 95% CI of PFT accumulation curves and maximum likelihood (Max L) tests between sites of the Cape lowland ASF, SSR and LDS for the 19 intuitively defined PFTs at scales with significant differences between some sites. ns = no significant difference; * = very small difference; ** = small difference; *** = large difference; marginal = slight overlap of CI).

	Scale	Site	ML		LF		MF	
			CI	Max L	CI	Max L	CI	Max L
Atlantis Sand Fynbos	50 m ²	CF	ns	ns				
		LF	ns	ns				
		MF	marginal	*	ns	ns		
		SF	ns	ns	marginal	*	ns	ns
Swartland Shale Renosterveld	0.1 m ²	CF	marginal	*				
		LF	ns	ns				
		MF	marginal	*	ns	ns		
		SF	ns	ns	ns	ns	*	***
	1 m ²	CF	marginal	*				
		LF	ns	ns				
		MF	ns	ns	ns	ns		
		SF	ns	ns	marginal	*	*	***
	50 m ²	CF	ns	**				
		LF	ns	ns				
		MF	marginal	*	ns	ns		
		SF	marginal	*	marginal	**	*	***
100 m ²	CF	marginal	*					
	LF	ns	ns					
	MF	ns	ns	ns	ns			
	SF	marginal	*	marginal	*	*	***	
Langebaan Dune Strandveld	50 m ²	CF	marginal	*				
		LF	ns	ns				
		MF	ns	ns		ns		
		SF	ns	ns		ns	ns	ns

Table 5.4 Presence-Absence of the 19 PFTs in the different vegetation types and sites

Atlantis Sand Fynbos	Swartland Shale Renosterveld	Langebaan Dune Strandveld
16 PFTs represented Three PFTs absent (1) long-distance dispersed, specialist-pollinated, dioecious, perennial, seeders (2) long-distance dispersed, dioecious, perennial, generalist-pollinated seeders (3) short-distance dispersed, specialist-pollinated, annual seeders	14 PFTs represented Five PFTs absent (1) long-distance dispersed, specialist-pollinated, dioecious resprouters (2) long-distance dispersed, generalist-pollinated, dioecious resprouters (3) long-distance dispersed, specialist-pollinated, dioecious, perennial seeders (4) long-distance dispersed, specialist-pollinated, non-dioecious, perennial seeder (5) short-distance dispersed, specialist-pollinated, dioecious, perennial seeders	15 PFTs represented Four PFTs absent (1) long-distance dispersed, specialist-pollinated, dioecious resprouters (2) short-distance dispersed, specialist-pollinated, dioecious, perennial seeders (3) short-distance dispersed, specialist-pollinated, non-dioecious, perennial seeders (4) short-distance dispersed, specialist-pollinated, annual seeders
mainland	mainland	mainland
Two of the 16 PFTs absent (1) long-distance dispersed, specialist-pollinated, non-dioecious, perennial seeders (<i>Pelargonium oenothera</i>) (2) long-distance dispersed, specialist-pollinated, annual seeders (<i>Pelargonium senecioides</i>)	One of the 14 PFTs absent The short-distance dispersed, generalist-pollinated, dioecious resprouters (<i>Ischyrolepis capense</i>)	Three of the 15 PFTs absent (1) long-distance dispersed, specialist-pollinated, annual seeders (<i>Pelargonium senecioides</i>) (2) short-distance dispersed, generalist-pollinated, dioecious resprouters (<i>Leucadendron brunoides</i> subsp. <i>flumenlupinum</i> and <i>Anthospermum spathulatum</i>) (3) short-distance dispersed, specialist-pollinated, non-dioecious resprouters (mostly geophytes e.g. <i>Bulbine praemorsa</i> , <i>Caesia</i> sp. and <i>Cyanella hyacinthioides</i>)
largest fragment	largest fragment	largest fragment
Three of the 16 PFTs absent (1) long-distance dispersed, specialist-pollinated, annual seeders (<i>Pelargonium senecioides</i>) (2) short-distance dispersed, specialist-pollinated, non-dioecious resprouters (<i>Babiana</i> species) (3) short-distance dispersed, specialist-pollinated, dioecious perennial seeders (<i>Leucadendron cinereum</i>)	All 14 PFTs represented	Three of the 15 PFTs absent (1) long-distance dispersed, specialist-pollinated, non-dioecious perennial seeders (<i>Microloma sagittatum</i>) (2) long-distance dispersed, specialist-pollinated, dioecious perennial seeders (<i>Diospyros glabra</i> and <i>Euclea racemosa</i>)
medium-sized fragment	medium-sized fragment	smallest fragment
Four of the 16 PFTs absent (1) long-distance dispersed, specialist-pollinated, non-dioecious perennial seeders (<i>Pelargonium oenothera</i>) (2) long-distance dispersed, specialist-pollinated, annual seeders (<i>Pelargonium senecioides</i>) (3) long-distance dispersed, generalist-pollinated, annual seeders mainly asteraceous herbs (e.g. <i>Felicia tenella</i> , <i>Gymnodiscus capillaries</i> , <i>Helichrysum indicum</i> , <i>Pseudognaphalum undulatum</i> , <i>Senecio elegans</i> , <i>Ursinia anthemoides</i>) and Poaceae (e.g. <i>Pentaschistis patula</i>) (4) short-distance dispersed, generalist-pollinated, annual seeders (<i>Nemesia affinis</i> , <i>Wahlenbergia androsacea</i>)	One of the 14 PFTs absent The short-distance dispersed, generalist-pollinated, dioecious resprouters (<i>Ischyrolepis capense</i>)	Two of the 15 PFTs absent (1) long-distance dispersed, specialist-pollinated, dioecious perennial seeders (<i>Diospyros glabra</i> and <i>Euclea racemosa</i>) (2) short-distance dispersed, generalist-pollinated, dioecious resprouters (<i>Leucadendron brunoides</i> subsp. <i>flumenlupinum</i> and <i>Anthospermum spathulatum</i>)

Table 5.4 (continued) Presence-Absence of the 19 PFTs in the different vegetation types and sites.

Atlantis Sand Fynbos	Swartland Shale Renosterveld	Langebaan Dune Strandveld
smallest fragment	smallest fragment	smallest fragment
Five of the 16 PFTs absent (1) long-distance dispersed, specialist-pollinated, dioecious resprouters (<i>Leucadendron lanigerum</i> subsp. <i>lanigerum</i>) (2) long-distance dispersed, specialist-pollinated, non-dioecious, perennial seeders (<i>Pelargonium oenothera</i>) (3) short-distance dispersed, specialist pollinated, non-dioecious perennial seeders (4) short-distance dispersed, specialist-pollinated, dioecious, perennial seeders (<i>Leucadendron cinereum</i>) (5) short-distance dispersed, generalist-pollinated, annual seeders (<i>Nemesia affinis</i> , and <i>Wahlenbergia androsacea</i>)	Seven of the 14 PFTs absent (1) long-distance dispersed, generalist-pollinated, dioecious perennial seeders (<i>Rhus</i> species, <i>Arctopus echinatus</i> , and <i>Cissampelos capensis</i>) (2) long-distance dispersed, specialist-pollinated, annual seeders (<i>Crassula strigosa</i>) (3) short-distance dispersed, generalist-pollinated, dioecious resprouters (<i>Ischyrolepis capense</i>) (4) short-distance dispersed, specialist-pollinated, non-dioecious resprouters mostly geophytes e.g. <i>Babiana stricta</i> , <i>Geissorhiza aspera</i> , <i>Cyphia</i> , <i>Moraea</i> and <i>Spiloxene</i> sp. (5) short-distance dispersed, specialist-pollinated, non-dioecious, perennial seeders e.g. <i>Salvia africana-caerulea</i> (6) short-distance dispersed, specialist-pollinated, annual seeders (<i>Hemimeris racemosa</i>) (7) short-distance dispersed, generalist-pollinated, annual seeders (<i>Sebaea exacoides</i>)	Two of the 15 PFTs absent (1) long-distance dispersed, specialist-pollinated, non-dioecious perennial seeders (<i>Microlooma sagittatum</i>) (2) short-distance dispersed, generalist-pollinated, dioecious resprouters (<i>Leucadendron brunoides</i> subsp. <i>flumenlupinum</i> and <i>Anthospermum spathulatum</i>)
combined fragments	combined fragments	combined fragments
All 16 PFTs represented	All 14 PFTs represented	All 15 PFTs represented

5.3.3 Diversity of the eight objectively defined PFTs

Results in Atlantis Sand Fynbos (Table 5.5), were not significant at the 0.2 m x 0.5 m and 5 m x 10 m scales (statistic not shown). At the 1 m x 1 m scale, PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,120} = 9.003721$, $p = 0.0292$ for the Gini-Simpson Index). The largest fragment was more diverse in PFT than the medium-sized fragment (Mann-Whitney U = 2.592631, $p = 0.0095$) and slightly more diverse in PFT than the smallest fragment (Mann-Whitney U = 2.255049, $p = 0.02413$). All other comparisons were not significant (statistics not shown).

At the 10 m x 10 m scale, PFT diversity did not differ with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 6.514852$, $p = 0.0891$ for the Gini-Simpson Index), although the mainland was slightly more diverse than the smallest fragment (Mann-Whitney U = 2.119252, $p = 0.034070$). However, results based on the effective number of species for the Gini-Simpson Index and results based on the

Shannon-Wiener Index and the effective number of species showed that PFT diversity differed between some sites (details in Appendix 14).

Table 5.5 Results of PFT diversity for the eight objectively defined PFTs based on the Shannon-Wiener and Gini-Simpson indices and their effective number of species per PFT in ASF. Entries are the mean index \pm standard deviation (SD), mean number of species per PFT \pm SD and N = number of samples.

1 m x 1 m scale				
Site (N= samples)	Shannon-Wiener		Gini-Simpson	
	Index \pm SD	Effective number of species \pm SD	Index \pm SD	Effective number of species \pm SD
Mainland (N=30)	1.053 \pm 0.414 ^{abc}	3.06 \pm 1.26 ^{abc}	0.594 \pm 0.187 ^{abc}	2.91 \pm 1.25 ^{abc}
Largest fragment (N=30)	1.056 \pm 0.316 ^a	3.01 \pm 0.94 ^a	0.625 \pm 0.119 ^a	2.94 \pm 0.92 ^a
Medium-sized fragment (N=30)	0.800 \pm 0.392 ^b	2.25 \pm 1.08 ^b	0.500 \pm 0.221 ^b	2.17 \pm 1.04 ^b
Smallest fragment (N=30)	0.778 \pm 0.431 ^b	2.20 \pm 1.21 ^b	0.489 \pm 0.242 ^b	2.17 \pm 1.19 ^b
Combined fragments (N=90)	0.878 \pm 0.399 ^c	2.49 \pm 1.13 ^c	0.538 \pm 0.208 ^c	2.43 \pm 1.12 ^c
10 m x 10m scale				
Mainland (N=9)	1.731 \pm 0.104 ^a	5.67 \pm 0.60 ^a	0.795 \pm 0.031 ^a	4.98 \pm 0.84 ^a
Largest fragment (N=9)	1.643 \pm 0.102 ^{ab}	5.20 \pm 0.49 ^{ab}	0.777 \pm 0.025 ^{ab}	4.54 \pm 0.46 ^{ab}
Medium-sized fragment (N=9)	1.543 \pm 0.159 ^b	4.73 \pm 0.698 ^b	0.759 \pm 0.05 ^{ab}	4.26 \pm 0.66 ^{ab}
Smallest fragment (N=9)	1.492 \pm 0.124 ^b	4.47 \pm 0.55 ^b	0.747 \pm 0.038 ^b	4.03 \pm 0.59 ^b
Combined fragments (N=27)	1.559 \pm 0.141 ^c	4.80 \pm 0.64 ^c	0.761 \pm 0.038 ^c	4.28 \pm 0.59 ^c

In Swartland Shale Renosterveld (Table 5.6), the differences in PFT diversity between sites was very significant at all the four scales. At the 0.2 m x 0.5 m scale, PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,111} = 33.37729$, $p < 0.00001$ for the Gini-Simpson Index), with the mainland being less diverse in PFT than the largest fragment (Mann-Whitney U = -2.95318, $p = 0.003145$) and also less diverse in PFT than the medium-sized fragment (Mann-Whitney U = -3.07274, $p = 0.002121$). PFT diversity was also slightly lower in the mainland than in the combined fragments (Mann-Whitney U = -1.96326, $p = 0.049617$). The largest and medium-sized fragments were both much more diverse in PFT than the smallest fragment (Mann-Whitney U = 4.626252, $p < 0.00001$), and (Mann-Whitney U = 5.052648, $p < 0.00001$) respectively. The difference in PFT diversity between the mainland and the smallest fragment was not significant (statistic not shown).

At the 1 m x 1 m scale, results based on the Gini-Simpson Index and the effective number of species per PFT were exactly the same (Kruskal-Wallis ANOVA: $H_{3,118} = 57.02758$, $p < 0.00001$).

PFT diversity was very significantly lower in the mainland than in the largest fragment (Mann-Whitney $U = -3.42727$, $p = 0.000610$) and also lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -4.23583$, $p = 0.000023$), but significantly higher in the mainland than in the smallest fragment (Mann-Whitney $U = 3.323227$, $p = 0.000890$). The largest and the medium-sized fragments were both much more diverse in PFT than the smallest fragment (Mann-Whitney $U = 5.764940$, $p < 0.00001$) and (Mann-Whitney $U = 6.478110$, $p < 0.00001$) respectively. PFT diversity between the mainland and the combined fragments was not significantly different based on both the Gini-Simpson Index and the effective number of species, but based on both the Shannon-Wiener Index and the effective number of species; the mainland was slightly less diverse in PFT than the combined fragments (statistic shown in Appendix 14).

At the 5 m x 10 m scale, the results were the same for the Gini-Simpson Index and the effective number of species per PFT (Kruskal-Wallis ANOVA: $H_{3,36} = 15.82089$, $p = 0.0012$). The mainland was slightly more diverse in PFT than the smallest fragment (Mann-Whitney $U = 2.386622$, $p = 0.017005$). PFT diversity was significantly higher in the largest and medium-sized fragments than in smallest fragment (Mann-Whitney $U = 3.003824$, $p = 0.002666$) and (Mann-Whitney $U = 3.445562$, $p = 0.000570$) respectively. All other comparisons were not significant (statistic not shown). The mainland and medium-sized fragment were not significantly different in PFT diversity based on both the Gini-Simpson Index and effective number of species per PFT, but based on both the Shannon-Wiener Index and effective number of species, PFT diversity was lower in the mainland than in the medium-sized fragment (statistic in Appendix 14).

Results at the 10 m x 10 m scale were also the same for the Gini-Simpson Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,36} = 16.09116$, $p = 0.0011$). PFT diversity was significantly higher in the mainland than in the smallest fragment (Mann-Whitney $U = 2.297042$, $p = 0.021617$), and also higher in the largest and in the medium-sized fragments than in the smallest one (Mann-Whitney $U = 3.003824$, $p = 0.002666$) and (Mann-Whitney $U = 3.445562$, $p =$

0.000570) respectively. All other comparisons were not significant (statistic not shown). The Shannon-Wiener Index and effective number of species both showed that the mainland was slightly less diverse in PFT than the largest and than the medium-sized fragment (details in Appendix 14), but the Gini-Simpson Index and effective number of species showed no significant differences.

Table 5.6 Results of PFT diversity for the eight objectively defined PFTs based on the Shannon-Wiener and Gini-Simpson indices and their effective number of species per PFT in SSR. Entries are the same as in Table 5.5.

0.2 m x 0.5 m Scale				
Site (N= samples)	Shannon-Wiener		Gini-Simpson	
	Index \pm SD	Effective number of species \pm SD	Index \pm SD	Effective number of species \pm SD
Mainland (N=29)	0.324 \pm 0.395 ^a	0.92 \pm 1.12 ^a	0.216 \pm 0.266 ^a	0.89 \pm 1.11 ^a
Largest fragment (N=30)	0.700 \pm 0.440 ^b	1.96 \pm 1.21 ^b	0.444 \pm 0.264 ^b	1.92 \pm 1.19 ^b
Medium-sized fragment (N=30)	0.741 \pm 0.373 ^b	2.10 \pm 1.02 ^b	0.464 \pm 0.210 ^b	1.97 \pm 0.96 ^b
Smallest fragment (N=22)	0.063 \pm 0.204 ^{ac}	0.18 \pm 0.59 ^{ac}	0.045 \pm 0.147 ^{ac}	0.18 \pm 0.59 ^{ac}
Combined fragments (N=82)	0.544 \pm 0.465 ^d	1.53 \pm 1.29 ^d	0.344 \pm 0.282 ^d	1.47 \pm 1.24 ^d
1 m x 1 m scale				
Mainland (N=30)	0.695 \pm 0.394 ^a	1.98 \pm 1.08 ^a	0.440 \pm 0.228 ^{ad}	1.90 \pm 1.05 ^{ad}
Largest fragment (N=30)	1.068 \pm 0.330 ^b	3.02 \pm 0.96 ^b	0.611 \pm 0.158 ^b	2.83 \pm 0.94 ^b
Medium-sized fragment (N=30)	1.174 \pm 0.258 ^b	3.35 \pm 0.93 ^b	0.654 \pm 0.088 ^b	3.10 \pm 0.92 ^b
Smallest fragment (N=28)	0.264 \pm 0.335 ^c	0.77 \pm 0.97 ^c	0.188 \pm 0.239 ^c	0.76 \pm 0.96 ^c
Combined fragments (N=88)	0.849 \pm 0.506 ^d	2.41 \pm 1.47 ^d	0.491 \pm 0.269 ^d	2.26 \pm 1.40 ^d
5 m x 10 m scale				
Mainland (N=9)	1.099 \pm 0.276 ^{ad}	3.10 \pm 0.84 ^{ad}	0.608 \pm 0.110 ^{ac}	2.74 \pm 0.78 ^{ac}
Largest fragment (N=9)	1.357 \pm 0.262 ^{ab}	3.40 \pm 0.93 ^{ab}	0.678 \pm 0.089 ^a	3.28 \pm 0.74 ^a
Medium-sized fragment (N=9)	1.420 \pm 0.093 ^b	4.15 \pm 0.37 ^b	0.695 \pm 0.021 ^a	3.29 \pm 0.22 ^a
Smallest fragment (N=9)	0.557 \pm 0.420 ^c	1.66 \pm 1.13 ^c	0.330 \pm 0.239 ^b	1.48 \pm 1.01 ^b
Combined fragments (N=27)	1.111 \pm 0.488 ^d	3.27 \pm 1.43 ^d	0.568 \pm 0.222 ^c	2.68 \pm 1.12 ^c
10 m x 10m scale				
Mainland (N=9)	1.149 \pm 0.280 ^{ad}	3.26 \pm 0.84 ^{ad}	0.609 \pm 0.117 ^{ac}	2.75 \pm 0.73 ^{ac}
Largest fragment (N=9)	1.372 \pm 0.241 ^b	4.03 \pm 0.84 ^b	0.679 \pm 0.081 ^a	3.26 \pm 0.65 ^a
Medium-sized fragment (N=9)	1.410 \pm 0.076 ^b	4.11 \pm 0.30 ^b	0.692 \pm 0.018 ^a	3.26 \pm 0.19 ^a
Smallest fragment (N=9)	0.631 \pm 0.397 ^c	1.90 \pm 0.98 ^c	0.368 \pm 0.230 ^b	1.69 \pm 0.91 ^b
Combined fragments (N=27)	1.138 \pm 0.449 ^d	3.35 \pm 1.27 ^d	0.580 \pm 0.204 ^c	2.74 \pm 0.98 ^c

In Langebaan Dune Strandveld, there were no significant results at all four scales for both the Gini-Simpson and the Shannon-Wiener Indices and their corresponding effective number of species per PFT (statistic not shown).

5.3.4 Diversity of the 19 subjectively defined PFTs

In Atlantis Sand Fynbos (Table 5.7), PFT diversity based on both the Gini-Simpson and Shannon-Wiener indices and their corresponding effective number of species per PFT, did not differ significantly with fragment size at the 0.2 m x 0.5m scale (details not shown).

At the 1 m x 1 m scale, PFT diversity differed with fragment size for both the Gini-Simpson Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,120} = 22.31807$ $p = 0.0001$). For the Gini-Simpson Index, PFT diversity was significantly higher in the mainland than in the medium-sized and the smallest fragments (Mann-Whitney $U = 4.134332$, $p = 0.000036$) and (Mann-Whitney $U = 3.143281$, $p = 0.001671$) respectively. The mainland was also more diverse in PFT than the combined fragments (Mann-Whitney $U = 3.690568$, $p = 0.000224$), and the largest fragment more diverse than the medium-sized one (Mann-Whitney $U = 3.129832$, $p = 0.001749$).

At the 5 m x 10 m scale, results based on the Gini-Simpson Index showed that PFT diversity did not differ significantly with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 7.053087$ $p = 0.0702$). However, the mainland was slightly more diverse in PFT than the medium-sized fragment (Mann-Whitney $U = 2.252868$, $p = 0.024268$). Based on the effective number of species, PFT diversity differed slightly between the mainland and the three fragments (details in Appendix 14). PFT diversity based on both the Shannon-Wiener Index and the effective number of species per PFT did not differ with fragment size (data not shown).

Results for the Gini-Simpson Index at the 10 m x 10 m scale, showed that the differences in PFT diversity between sites was only marginal (Kruskal-Wallis ANOVA: $H_{3,36} = 7.702426$, $p = 0.05$), with the mainland being slightly more diverse in PFT than the medium-sized fragment (Mann-Whitney $U = 2.231871$, $p = 0.025624$) and than in the combined fragments (Mann-Whitney $U = 2.058963$, $p = 0.039499$).

Table 5.7 Results of PFT diversity for the 19 subjectively defined PFTs based on the Shannon-Wiener and Gini-Simpson indices and their effective number species per PFT in ASF. Entries are the same as in Table 5.5.

1 m x 1 m scale				
	Shannon-Wiener		Gini-Simpson	
Site (N= samples)	Index \pm SD	Effective number of species \pm SD	Index \pm SD	Effective number of species \pm SD
Mainland (N=30)	1.267 \pm 0.280 ^a	3.68 \pm 1.00 ^a	0.695 \pm 0.091 ^a	3.54 \pm 0.96 ^a
Largest fragment (N=30)	1.100 \pm 0.336 ^{ac}	3.12 \pm 1.01 ^{ac}	0.636 \pm 0.151 ^{ac}	3.01 \pm 0.95 ^{ac}
Medium-sized fragment (N=30)	0.807 \pm 0.440 ^b	2.32 \pm 1.30 ^b	0.497 \pm 0.228 ^b	2.25 \pm 1.27 ^b
Smallest fragment (N=30)	0.830 \pm 0.479 ^{bc}	2.37 \pm 1.36 ^{bc}	0.515 \pm 0.255 ^{bc}	2.38 \pm 1.35 ^{bc}
Combined fragments (N=90)	0.916 \pm 0.435 ^d	2.61 \pm 1.27 ^d	0.549 \pm 0.222 ^d	2.55 \pm 1.24 ^d
5 m x 10 m scale				
Mainland (N=9)	1.895 \pm 0.256 ^{ac}	6.83 \pm 1.56 ^{ac}	0.830 \pm 0.047 ^{ac}	6.24 \pm 1.46 ^{ac}
Largest fragment (N=9)	1.853 \pm 0.097 ^{ab}	6.40 \pm 0.62 ^{ab}	0.815 \pm 0.022 ^{ab}	5.48 \pm 0.65 ^{ab}
Medium-sized fragment (N=9)	1.641 \pm 0.298 ^b	5.35 \pm 1.39 ^b	0.775 \pm 0.067 ^b	4.72 \pm 1.10 ^b
Smallest fragment (N=9)	1.845 \pm 0.182 ^{ab}	6.42 \pm 1.14 ^{ab}	0.822 \pm 0.035 ^{ab}	5.81 \pm 1.14 ^{ab}
Combined fragments (N=27)	1.780 \pm 0.224 ^c	6.06 \pm 1.17 ^c	0.804 \pm 0.049 ^c	5.33 \pm 1.06 ^c
10 m x 10m scale				
Mainland (N=9)	2.208 \pm 0.178 ^{ac}	9.22 \pm 1.56 ^{ac}	0.888 \pm 0.021 ^{ac}	9.22 \pm 1.56 ^{ac}
Largest fragment (N=9)	2.150 \pm 0.145 ^{ab}	8.67 \pm 1.22 ^{ab}	0.882 \pm 0.017 ^{ab}	8.67 \pm 1.22 ^{ab}
Medium-sized fragment (N=9)	1.909 \pm 0.293 ^b	7.00 \pm 1.94 ^b	0.846 \pm 0.048 ^b	7.00 \pm 1.94 ^b
Smallest fragment (N=9)	2.014 \pm 0.231 ^{ab}	7.67 \pm 1.66 ^{ab}	0.863 \pm 0.033 ^{ab}	7.67 \pm 1.66 ^{ab}
Combined fragments (N=27)	2.025 \pm 0.244 ^c	7.78 \pm 1.72 ^c	0.864 \pm 0.037 ^c	7.78 \pm 1.72 ^c

In Swartland Shale Renosterveld (Table 5.8) results based on both the Gini-Simpson and Shannon-Wiener indices and their corresponding effective number of species per PFT, showed that PFT diversity differed very significantly with fragment size at all four scales, for the 19 subjectively defined PFTs. At the 0.2 m x 0.5 m scale, the same result was obtained for both the Gini-Simpson Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,111} = 44.90176$, $p < 0.00001$). The mainland was less diverse in PFT than the largest and medium-sized fragments and the combined fragments, (Mann-Whitney $U = -2.95868$, $p = 0.003090$), (Mann-Whitney $U = -4.63514$, $p < 0.00001$) and (Mann-Whitney $U = -2.58926$, $p = 0.009619$) respectively, but more diverse in PFT than the smallest fragment (Mann-Whitney $U = 2.731809$, $p = 0.006299$). PFT diversity was also much higher in the largest fragment than in the smallest one (Mann-Whitney $U = 4.535826$, $p < 0.00001$) and higher in the medium-sized fragment than in the smallest one (Mann-Whitney $U = 5.669375$, $p < 0.00001$). PFT diversity did not differ significantly between the largest and the medium-sized fragment (statistic not shown).

At the 1 m x 1 m scale, the same results were obtained for the Gini-Simpson Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,118} = 65.21664$, $p < 0.00001$). Results for the Gini-Simpson Index showed that PFT diversity was very significantly lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -5.07293$, $p < 0.00001$), but much higher in the mainland than in the smallest fragment (Mann-Whitney $U = 5.132248$, $p < 0.00001$). The largest fragment was less diverse in PFT than the medium-sized one (Mann-Whitney $U = -3.19868$, $p = 0.001381$), but much more diverse than the smallest fragment (Mann-Whitney $U = 5.488497$, $p < 0.00001$). PFT diversity was very significantly higher in the medium-sized fragment than in the smallest one (Mann-Whitney $U = 6.392610$, $p < 0.00001$). There was no difference in PFT diversity between the mainland and the combined fragments (statistics not shown). Based on both the Shannon-Wiener Index and the effective numbers of species, PFT diversity was slightly higher in the mainland than in the largest fragment (statistic in Appendix 15), but was not significantly different for the Gini-Simpson Index and the effective number of species (statistic not shown).

At the 5 m x 10 m scale, the same results were obtained for both the Gini-Simpson Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,36} = 31.83312$, $p < 0.00001$), which showed that PFT diversity differed very significantly with fragment size. PFT diversity was significantly lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -3.59189$, $p = 0.000328$) and also lower in the largest fragment than in the medium-sized one (Mann-Whitney $U = -3.47392$, $p = 0.000513$). The largest and the medium-sized fragments were both much more diverse in PFT than the smallest fragment (Mann-Whitney $U = -3.597657$, $p = 0.000321$) and (Mann-Whitney $U = 3.611215$, $p = 0.000305$) respectively. PFT diversity was significantly lower in the mainland than in the largest fragment based on the Shannon-Wiener Index and effective number of species (statistics in Appendix 15), but not for the Gini-Simpson Index and effective number of species (statistic not shown).

Results at the 10 m x 10 m scale were equally highly significant and the same for both the Gini-Simpson Index and effective number of species per PFT (Kruskal-Wallis ANOVA: $H_{3,36} = 30.87005$, $p < 0.00001$). The mainland was slightly less diverse in PFT than the largest fragment (Mann-Whitney $U = -2.56196$, $p = 0.010409$), and also less diverse in PFT than the medium-sized fragment (Mann-Whitney $U = -3.58045$, $p = 0.000343$). The largest and medium-sized fragments were both more diverse in PFT than the smallest one (Mann-Whitney $U = -3.617072$, $p = 0.000298$) and (Mann-Whitney $U = 3.628874$, $p = 0.000285$) respectively. PFT diversity was lower in the largest fragment than the medium-sized one (Mann-Whitney $U = -3.57666$, $p = 0.000348$).

Table 5.8 Results of PFT diversity for the 19 subjectively defined PFTs based on the Shannon-Wiener and Gini-Simpson indices and their effective number species per PFT in SSR. Entries are the same as in Table 5.5.

0.2 m x 0.5 m Scale				
Site (N= samples)	Shannon-Wiener		Gini-Simpson	
	Index \pm SD	Effective number of species \pm SD	Index \pm SD	Effective number of species \pm SD
Mainland (N=29)	0.337 \pm 0.393 ^a	0.96 \pm 1.11 ^a	0.234 \pm 0.267 ^a	0.96 \pm 1.11 ^a
Largest fragment (N=30)	0.710 \pm 0.483 ^b	2.00 \pm 1.33 ^b	0.446 \pm 0.286 ^b	1.98 \pm 1.32 ^b
Medium-sized fragment (N=30)	0.994 \pm 0.412 ^b	2.85 \pm 1.24 ^b	0.584 \pm 0.193 ^b	2.74 \pm 1.16 ^b
Smallest fragment (N=22)	0.063 \pm 0.204 ^c	0.18 \pm 0.59 ^c	0.045 \pm 0.147 ^c	0.18 \pm 0.59 ^c
Combined fragments (N=82)	0.644 \pm 0.543 ^d	1.82 \pm 1.55 ^d	0.389 \pm 0.309 ^d	1.77 \pm 1.50 ^d
1 m x 1 m scale				
Mainland (N=30)	1.006 \pm 0.374 ^a	2.83 \pm 1.07 ^a	0.593 \pm 0.188 ^{ad}	2.74 \pm 1.03 ^{ad}
Largest fragment (N=30)	1.210 \pm 0.427 ^b	3.60 \pm 1.42 ^b	0.650 \pm 0.179 ^a	3.37 \pm 1.35 ^a
Medium-sized fragment (N=30)	1.595 \pm 0.338 ^c	5.19 \pm 1.62 ^c	0.764 \pm 0.091 ^b	4.73 \pm 1.47 ^b
Smallest fragment (N=28)	0.349 \pm 0.362 ^d	1.01 \pm 1.04 ^d	0.245 \pm 0.251 ^c	0.99 \pm 1.02 ^c
Combined fragments (N=88)	1.067 \pm 0.640 ^a	3.32 \pm 2.20 ^a	0.560 \pm 0.287 ^d	3.08 \pm 2.01 ^d
5 m x 10 m scale				
Mainland (N=9)	1.511 \pm 0.255 ^{ac}	4.67 \pm 1.22 ^{ac}	0.733 \pm 0.057 ^{acd}	4.67 \pm 1.22 ^{acd}
Largest fragment (N=9)	2.072 \pm 0.133 ^b	8.00 \pm 1.00 ^b	0.873 \pm 0.018 ^a	8.00 \pm 1.00 ^a
Medium-sized fragment (N=9)	2.384 \pm 0.089 ^c	10.89 \pm 0.93 ^c	0.908 \pm 0.009 ^b	10.89 \pm 0.93 ^b
Smallest fragment (N=9)	0.918 \pm 0.407 ^d	2.56 \pm 1.13 ^d	0.565 \pm 0.227 ^c	2.56 \pm 1.13 ^c
Combined fragments (N=27)	1.792 \pm 0.687 ^c	7.15 \pm 3.66 ^c	0.782 \pm 0.202 ^d	7.15 \pm 3.66 ^d
10 m x 10m scale				
Mainland (N=9)	1.668 \pm 0.326 ^{ad}	5.56 \pm 1.81 ^{ad}	0.802 \pm 0.066 ^{ad}	5.56 \pm 1.81 ^{ad}
Largest fragment (N=9)	2.057 \pm 0.139 ^b	7.89 \pm 1.05 ^b	0.871 \pm 0.019 ^b	7.89 \pm 1.05 ^b
Medium-sized fragment (N=9)	2.385 \pm 0.72 ^c	10.89 \pm 0.78 ^c	0.908 \pm 0.007 ^c	10.89 \pm 0.78 ^c
Smallest fragment (N=9)	1.040 \pm 0.218 ^a	2.89 \pm 0.60 ^a	0.639 \pm 0.083 ^a	2.89 \pm 0.60 ^a
Combined fragments (N=27)	1.828 \pm 0.602 ^d	7.22 \pm 3.46 ^d	0.806 \pm 0.130 ^d	7.22 \pm 3.46 ^d

In Langebaan Dune Strandveld, results based on both indices and their corresponding effective number of species for the 19 subjectively defined PFTs also showed that PFT diversity differed with fragment size at all four scales (Table 5.9). At the smallest scale (0.2 m x 0.5 m), the Simpson Index and the effective number of species per PFT gave the same result (Kruskal-Wallis ANOVA: $H_{3,116} = 8.988464$, $p = 0.0294$). The mainland and the largest fragment were both less diverse in PFT than the medium-sized fragment (Mann-Whitney $U = -2.45726$, $p = 0.014001$) and (Mann-Whitney $U = -2.41205$, $p = 0.015864$), respectively.

At the 1 m x 1 m scale, the same result was obtained for both the Simpson Index and the effective number of species per PFT (Kruskal-Wallis ANOVA: $H_{3,120} = 20.69605$, $p = 0.0001$). Based on the Gini-Simpson Index, the mainland and the largest fragment were both significantly less diverse in PFT than the medium-sized fragment (Mann-Whitney $U = -4.00070$, $p = 0.000063$), and (Mann-Whitney $U = -3.09035$, $p = 0.001999$) respectively. PFT diversity was significantly higher in the medium-sized fragment than in the smallest one (Mann-Whitney $U = 3.520317$, $p = 0.000431$). PFT diversity was also slightly lower in the mainland than in the combined fragments (Mann-Whitney $U = -2.49373$, $p = 0.012641$). Other comparisons were not significant (statistics not shown).

At the 5 m x 10 m scale, results based on the Gini-Simpson Index also showed that PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 13.81175$, $p = 0.0032$), with the largest and the medium-sized fragments being much more diverse in PFT than the smallest fragment (Mann-Whitney $U = 2.633607$, $p = 0.008449$) and (Mann-Whitney $U = 3.139558$, $p = 0.001692$) respectively. Based on the effective number of species, PFT diversity also differed with fragment size (statistics in Appendix 14). Whereas results based on the Shannon-Wiener Index showed that the mainland was slightly less diverse in PFT than the medium-sized fragment (statistics in Appendix 15), the Gini-Simpson Index did not.

At the 10 m x 10 m scale, the same results were obtained for the Gini-Simpson Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,36} = 12.67994$, $p = 0.0054$), with the

mainland being slightly less diverse in PFT than the medium-sized fragment (Mann-Whitney U = 2.02152, p = 0.043227), while the the largest and medium-sized fragments were slightly more diverse in PFT than the smallest fragment (Mann-Whitney U = 2.431023, p = 0.015057) and (Mann-Whitney U = 2.984085, p = 0.002844) respectively.

Table 5.9 Results of PFT diversity for the 19 subjectively defined PFTs based on the Shannon-Wiener and Gini-Simpson indices and their effective number species per PFT in LDS. Entries are the same as in Table 5.5.

0.2 m x 0.5 m Scale				
Site (N= samples)	Shannon-Wiener		Gini-Simpson	
	Index \pm SD	Effective number of species \pm SD	Index \pm SD	Effective number of species \pm SD
Mainland (N=27)	0.163 \pm 0.287 ^{ac}	0.49 \pm 0.85 ^{ac}	0.126 \pm 0.217 ^{ac}	0.50 \pm 0.87 ^{ac}
Largest fragment (N=30)	0.175 \pm 0.331 ^a	0.50 \pm 0.94 ^a	0.122 \pm 0.227 ^a	0.50 \pm 0.94 ^a
Medium-sized fragment (N=29)	0.432 \pm 0.420 ^b	1.23 \pm 1.18 ^b	0.293 \pm 0.276 ^b	1.22 \pm 1.17 ^b
Smallest fragment (N=30)	0.221 \pm 0.351 ^{ab}	0.63 \pm 1.00 ^{ab}	0.156 \pm 0.243 ^{ab}	0.63 \pm 1.00 ^{ab}
Combined fragments (N=89)	0.274 \pm 0.381 ^c	0.78 \pm 1.08 ^c	0.189 \pm 0.257 ^c	0.78 \pm 1.07 ^c
1 m x 1 m scale				
Mainland (N=30)	0.795 \pm 0.459 ^a	2.27 \pm 1.30 ^a	0.493 \pm 0.247 ^a	2.21 \pm 1.25 ^a
Largest fragment (N=30)	0.962 \pm 0.276 ^a	2.72 \pm 0.77 ^a	0.597 \pm 0.106 ^a	2.67 \pm 0.77 ^a
Medium-sized fragment (N=30)	1.270 \pm 0.264 ^b	3.68 \pm 1.00 ^b	0.693 \pm 0.080 ^b	3.49 \pm 0.98 ^b
Smallest fragment (N=30)	0.864 \pm 0.461 ^a	2.48 \pm 1.33 ^a	0.525 \pm 0.233 ^a	2.41 \pm 1.29 ^a
Combined fragments (N=90)	1.036 \pm 0.378 ^c	2.97 \pm 1.16 ^c	0.605 \pm 0.168 ^c	2.86 \pm 1.12 ^c
5 m x 10 m scale				
Mainland (N=9)	1.927 \pm 0.283 ^{acd}	7.11 \pm 1.96 ^{acd}	0.849 \pm 0.045 ^{acd}	7.11 \pm 1.96 ^{acd}
Largest fragment (N=9)	2.140 \pm 0.217 ^{ab}	8.67 \pm 1.73 ^{ab}	0.880 \pm 0.028 ^{ab}	8.67 \pm 1.73 ^{ab}
Medium-sized fragment (N=9)	2.199 \pm 0.158 ^b	9.11 \pm 1.36 ^{ab}	0.888 \pm 0.019 ^{ab}	9.11 \pm 1.36 ^{ab}
Smallest fragment (N=9)	1.790 \pm 0.219 ^c	6.11 \pm 1.27 ^c	0.829 \pm 0.039 ^c	6.11 \pm 1.27 ^c
Combined fragments (N=27)	2.043 \pm 0.266 ^d	7.96 \pm 1.95 ^d	0.866 \pm 0.039 ^d	7.96 \pm 1.95 ^d
10 m x 10m scale				
Mainland (N=9)	2.072 \pm 0.223 ^{acd}	8.11 \pm 1.69 ^{acd}	0.871 \pm 0.031 ^{acd}	8.11 \pm 1.69 ^{acd}
Largest fragment (N=9)	2.210 \pm 0.241 ^{ab}	9.33 \pm 1.94 ^{ab}	0.887 \pm 0.031 ^{ab}	9.33 \pm 1.94 ^{ab}
Medium-sized fragment (N=9)	2.269 \pm 0.162 ^b	9.78 \pm 1.48 ^{ab}	0.895 \pm 0.018 ^{ab}	9.78 \pm 1.48 ^{ab}
Smallest fragment (N=9)	1.913 \pm 0.197 ^c	6.89 \pm 1.27 ^c	0.850 \pm 0.031 ^c	6.89 \pm 1.27 ^c
Combined fragments (N=27)	2.131 \pm 0.251 ^d	8.67 \pm 2.00 ^d	0.877 \pm 0.033 ^d	8.67 \pm 2.00 ^d

5.4 Discussion

Functional diversity is now seen as the component of biodiversity that is most relevant to ecosystem functioning (Díaz & Cabido 2001; Hooper et al. 2002; Naeem & Wright 2003), although there is still no consensus among ecologists on how to define and quantify it (Petchey & Gaston 2006; Wright et al. 2006). However, clustering species with shared traits into functional types is one approach that is gaining ground (Lavorel & Garnier 2002; Petchey & Gaston 2002). Functional

diversity has different components (Mason et al. 2005), depending on how it is defined and on the ecosystem process it is meant to reflect (Lavorel & Garnier 2002). According to Petchey and Gaston (2006), “functional diversity” is used when species distance in trait space is weighted by species’ abundance (e.g. Botta-Dukat 2005; De Bello et al. 2006) and “functional richness” when species abundance is not considered. For this study, a similar approach was adopted. The premise of this study was that habitat fragmentation (i.e. reduced patch size) would negatively affect plant functional type (PFT) richness and diversity in the three Cape lowland vegetation types studied. The absence of any such effects would imply that these fragments exhibit a high degree of redundancy of plant species with sets of co-occurring traits and are therefore stable and functional ecosystems.

The effect of reduced patch size on PFT richness was more evident in Swartland Shale Renosterveld (SSR) and in Atlantis Sand Fynbos (ASF) than in Langebaan Dune Strandveld (LDS) for both the eight objectively and the 19 subjectively defined PFTs. Evidence of the fragment size effect on PFT richness was documented in both ASF and SSR for the 19 subjectively defined PFTs, albeit at different scales, which highlights the sampling scale effect. The largest (300 ha) and the medium-sized (70 ha) SSR fragments were richer in the eight objectively defined PFTs than the smallest fragment (15 ha), while all the other sites had significantly more of the 19 subjectively defined PFTs than the smallest fragment. However, this was not consistent for all scales, which indicates a sampling scale effect. The SSR fragments combined also had more PFTs than the mainland at all the scales for the 19 subjectively defined PFTs and at the 1-m² scale for the eight objectively defined PFTs. Similarly, in ASF, richness in the 19 subjectively defined PFTs was significantly higher only in the mainland than in the medium-sized fragment, and also higher in the largest, than in the smallest fragment at the 50-m² scale. This again reiterates the sampling scale effect. Apart from the fact that the fragments combined had significantly more PFTs than the mainland at the 50-m² scale, which also highlights a sampling scale effect, there was no evidence of fragment size on PFT richness in LDS. A possible explanation for the evident effect of reduced

patch size on PFT richness in both SSR and ASF for the 19 subjectively defined PFTs could be the fact that more PFTs were defined using the subjective approach than with the objective approach.

In ASF, more PFTs were lost as patch size decreased, although this was not significant among all the sites and scales. PFTs lost from ASF sites ranged from two in the mainland to five in the smallest fragment. In LDS, three PFTs were absent from the mainland and two from each of the three fragments. In contrast, only one PFT was missing from the SSR mainland and the medium-sized fragment and up to seven PFTs were missing from the smallest fragment. The fact that some PFTs were not found in some sites, especially where these PFTs were represented by single or very few species in other sites, could also be due to undersampling. Sampling in these vegetation types was not quite sufficient for a full representation of all the species in the different sites as highlighted in Chapter three. Therefore, the absence of species of some PFTs from some of the sites could be due to mere chance. For example, the absence of annuals from some ASF sites could simply be due to the fact that annuals are generally few in fynbos (Rebelo et al. 2006).

This notwithstanding, the absence of species of some PFTs from some sites could equally be attributed to one or a combination of the following reasons: the lack of a viable population, the disruption of plant-pollinator mutualisms and the poor dispersal ability of the species. Habitat fragmentation may affect these processes in various ways. The establishment of a population requires an effective population size, and dioecious species need plants of both sexes to achieve this. Habitat fragmentation may disrupt the establishment of this effective population size, rendering the small sub-populations more prone to stochastic perturbations, ultimately leading to higher local extinction risks (Franklin 1980; Shaffer 1981; Lindenmayer & Fischer 2006). Some of the species belonging to the PFTs missing from the different sites (e.g. many geophytes) exhibit highly-specialised pollination systems, which may be disrupted by habitat fragmentation with severe ramifications for genetic diversity. For instance, the rate at which pollinators visit flowers may be

seriously reduced, leading to reduced fecundity and low seed set (Bond 1994; Donaldson et al. 2002; Ward & Johnson 2005; Aguilar et al. 2006; Lawson et al. 2008). The influence of habitat fragmentation on plant-pollinator interactions is mainly through the type of matrix surrounding the patch that may obstruct the movement of dispersers and pollinators (Ricketts 2001; Higgins et al. 2003; Jonas et al. 2006). The sites used for this study were surrounded by various matrices such as agricultural fields (e.g. cereal, potato and vineyards), alien *Acacia* and *Eucalyptus* species, minor/major roads, and semi-urban and urban settlement. These matrices have resistant values of 50-100 (Jonas et al. 2006). In particular, the smallest SSR fragment was surrounded by urban settlement and vineyards, the smallest ASF fragment surrounded by *Acacia saligna*, a *Eucalyptus* sp. plantation and a small settlement. These matrices increase the isolation of the fragments therein, and the small sizes of these fragments also mean that there is less habitat area available for animal pollinators, with negative consequences for plant-pollinator interactions (Lamont et al. 1993; Steffan-Dewenter & Tschamtkke 1999; Wolf & Harrison 2001). The situation is even worse for the short-distance dispersed species, which may not easily re-colonise these fragments from neighbouring patches because of their poor dispersal ability (see also Bond et al. 1988; Bond 1994).

The absence of species of particular PFTs in some of the sites could also be attributed to factors such as a lack of suitable habitat, the land-use history or the disturbance regime of the site (e.g. alien infestation, fire, and grazing). The three Cape lowland vegetation types studied are endowed with so many endemic species and habitat specialists that require particular microhabitats. Given that some of the species missing from the different sites have long-distance dispersal abilities, their absence from these sites could probably be due to the lack of their particular microclimatic conditions in these sites. For example, some of the geophytes found missing from the LDS mainland and the other fragments could simply be due to habitat type. In general, more geophytes are found in strandveld at the transition towards Sand Fynbos (Rebelo et al. 2006). Evidence of the effect of land-use history was clearly documented in the smallest SSR fragment, which had been

previously used for farm workers' houses and is only now being rehabilitated. This site is in an early successional stage and dominated by *Otholobium hirtum*, which is characteristic of disturbed SSR sites (Rebelo et al. 2006), which could explain the absence of the many PFTs from this fragment. The influence of disturbance regime was particularly evident in SSR (and in LDS to a lesser degree). Three PFTs were absent from the LDS mainland that has not been grazed for over 40 years, while two were missing from each of the fragments, which all have a grazing history. In SSR, the medium-sized fragment that is being grazed by indigenous herbivores had significantly more PFTs than the mainland and higher PFT diversity than the smallest fragment, which are both ungrazed. Grazing, particularly in renosterveld, has been noted to influence species composition, notably the interchange between grasses, geophytes and shrub components (Rebelo et al. 2006). This implies that grazing may be very vital for PFT richness in SSR and to a lesser extent in LDS. The influence of disturbance regime was also documented in ASF, particularly in the medium-sized fragment that has been heavily invaded by *Acacia saligna*. This fragment had a fire about 10 years ago resulting in a dense regeneration of the *Acacia saligna*. *Acacia saligna* generates a large seed bank, which might have enabled it to out-compete some of the native species which were absent from this fragment.

The results also revealed differences in the distribution of PFTs in the three Cape lowland vegetation types studied. This shows that, although these vegetation types can be found within fairly small distances, they differ significantly in species composition, structure and function (Rebelo et al. 2006). They are very different floristically, especially at the species level, despite some common families and genera. Therefore, the remnant patches of these lowland vegetation types may be the only remaining suitable habitat or refuge for some species and therefore deserve conservation attention. After all, most of them are considered to be 100% irreplaceable (Cowling & Pressey 2003). They are all required to meet the target of about 30% of the original extent required under conservation to represent 75% of the species in these vegetation types (Rouget et al. 2006). Some

PFTs, such as the long-distance dispersed, dioecious, perennial seeders and the short-distance dispersed, specialist-pollinated, annual seeders were completely absent from ASF. The former consists of ornithochorous species that are found mostly in strandveld with many fleshy-fruited plant species and frugivorous birds (Knight 1988), as well as in fire-safe areas such as termitaria that harbour thicket renosterveld species (Le Maitre & Midgley 1992). These species are virtually absent in fynbos due to the lack of a regeneration niche where the fruits and seedlings are killed by fire (Rebelo et al. 2006). The absence of some annuals from ASF is not surprising given that native annual species are very few in fynbos (Rebelo et al. 2006). The low soil nutrient status does not permit them to complete their life cycles and produce seeds in one growing season (Wisheu et al. 2000). The PFTs absent from SSR consisted mostly of characteristic fynbos species of the Restionaceae and Proteaceae families and some long-distance dispersed species found only in strandveld such as *Microlooma sagittatum*, *Euclea racemosa* and *Diospyros glabra*. PFTs absent from LDS comprised mainly typical fynbos species such as *Diastella proteoides*, *Polygala garcinii*, *Muraltia* species, *Leucadendron cinereum* and *L. lanigerum* subsp. *lanigerum*, and *Hemimeris racemosa*, found mainly in renosterveld.

As for PFT richness, the effect of reduced patch size on PFT diversity was more evident for the 19 subjectively defined than for the eight objectively PFTs in all three vegetation types. This could be attributed to the relatively few numbers of PFTs defined objectively. This suggests that details may be lost when PFTs are determined objectively with serious ramifications for management recommendations. Although there was evidence of reduced patch size on PFT diversity in all three vegetation types, the effect was stronger in SSR and ASF than in LDS.

There was clear evidence of the effect of reduced patch size in ASF, particularly at the 1 m² and 100 m² scales, which indicates a sampling scale effect. The mainland and the largest fragment were clearly higher in PFT diversity than the medium-sized and the smallest fragments at these scales for

both the eight objectively defined and more so for the 19 subjectively defined PFTs. The mainland was also higher in PFT diversity than the fragments combined, particularly at the larger scales. These results tie with the effect of reduced patch size on species richness (Chapter three) as well as the predictions made in Chapter four, where ASF with most of the endangered PFTs was highlighted as being very susceptible to habitat fragmentation.

In SSR, there was also evidence of reduced patch size on PFT diversity as the mainland, the largest and the medium-sized fragments were significantly higher in PFT diversity than the smallest fragment. This could be attributed to the type of matrices surrounding this fragment (i.e. urban settlement and vineyards), which negatively impact on fragment connectivity. This affects the movement of dispersers and pollinators and ultimately the demography, genetics, and survival of local populations in this patch (see also Jules & Shahani 2003; Laurance 2008; Wisser & Buxton 2008). Moreover, this fragment is in an early successional stage and dominated few species, notably *Otholobium hirtum* and *Helichrysum* species, which could also explain its low PFT diversity. There was also a conspicuous absence of geophytes, which generally characterise the understorey renosterveld vegetation from this smallest fragment. This may explain why PFT diversity was significantly lower for this site. Grazing also seems to influence PFT diversity and thus the functioning of SSR. This was evident from the fact that the medium-sized fragment that is grazed was significantly higher in PFT richness and diversity than the other sites that are not grazed.

As predicted in chapter four, LDS was the least affected of the three vegetation types, probably because of the fact that habitat fragmentation in this vegetation type is more recent compared to that in ASF and SSR. There were virtually no significant differences in PFT diversity between sites for the eight objectively defined PFTs. Generally, habitat fragmentation is still recent in all three vegetation types in evolutionary terms. We might not yet see the full effects habitat fragmentation has on diversity and processes Although there was some evidence of fragment size effects on PFT

diversity for the 19 subjectively defined PFTs, with the largest and medium-sized fragments being more diverse than the smallest fragment, this effect was however, not very strong and was seemingly being confounded by land-use history. This shows that grazing may also be influencing PFT diversity in this LDS. Although the fragments have a grazing history, PFT diversity was higher in the medium-sized fragment than the other sites. The fact that the medium-sized fragment was higher in PFT diversity than the largest fragment, which also has a grazing history, could be attributed to the fact that the largest fragment has only been under rehabilitation since 1990 (A. Coetzee Senior, pers. comm.). This fragment used to be strip-ploughed (50 m) and planted with pasture to increase stocking density for livestock since 1985. The site was now dominated by pioneer Fabaceae (*Aspalathus* spp.), which could explain its low PFT diversity.

The fact that the effect of reduced patch size on PFT diversity was relatively weak, particularly in LDS, is an indication of some degree of functional redundancy in these Cape lowland vegetation types, which suggests that these Cape lowland fragments are functionally stable (see also Cowling et al. 1994). It has been noted that the stability of an ecosystem is improved if each important functional type consists of many ecologically equivalent species, each responding differently to environmental factors (Walker 1995). Having several species within a functional type is crucial for conserving biodiversity because, if one goes extinct, ecological equivalence allows functional compensation by those that are left. If a functional type consists of only a single species, no such compensation will be possible. Plant functional types with a single or very few species should be given priority in conservation because their functions in the ecosystem could be lost should these go extinct (Walker 1995). Ecological redundancy is therefore positive in that it enhances the resilience of an ecosystem, although this may be influenced by the traits of the less abundant species (Walker et al. 1999).

The degree of functional redundancy revealed by an ecological community depends on the number of traits used, correlations between traits and their relative weighting (Rosenfeld 2002). It has been shown that the fewer the number of traits, the less the effect of changes in species richness on functional diversity leading to a higher level of redundancy. Also, the more the traits the less the degree of redundancy exhibited, making the concept of redundancy rather subjective (Petchey & Gaston 2006). However, redundancy becomes subjective only if the traits used are irrelevant to the ecological question addressed (Walker et al. 1999). Bearing this in mind, it could be said that the degree of redundancy exhibited in the Cape lowland vegetation types investigated could be due to the fact that only eight traits were used. According to Petchey & Gaston (2006) a suitable counter argument could be that there is usually no specific number of traits needed in functional classifications; rather, the emphasis is on traits that are functionally relevant to the process. In this study, the traits chosen were based on their relevance to species' response to habitat fragmentation and the knowledge of specialists in the field. These included traits related to species dispersal, pollination and longevity. Thus, the redundancy found in this study is not subjective.

5.5 Conclusion

The study has highlighted some challenges involved in research in plant functional types such as choosing traits relevant to the question being addressed and defining the functional types. The results have also shown that Swartland Shale Renosterveld and Atlantis Sand Fynbos are the most vulnerable and threatened of the three vegetation types. The study also showed how the three vegetation types differ in species composition, structure and function and that they exhibit some degree of functional redundancy, which is vital for the stability of the fragments. However, the Cape lowlands remain susceptible to further human-induced loss of biodiversity and understanding the full impact of such loss remained a challenge to ecologists. With the growing awareness that functional diversity is the component of biodiversity that is most relevant to the functioning of ecosystems, conservation efforts should be geared towards species of important functional types.

These should be determined by identifying the vital attributes that are pertinent to the persistence of the system. Pollination and dispersal are typical examples of important functional attributes for the persistence of fragmented ecosystems such as the Cape lowlands. In order to promote these attributes, measures geared towards linking fragments should be implemented and conservation priority should be given to plant functional types that have one or very few species.

5.6 References

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Chapter 6

Trait-convergence and trait-divergence assembly patterns in the fragmented lowland vegetation of the Western Cape (South Africa)

Abstract

This study investigated whether habitat fragmentation in selected Cape lowland vegetation types plays a role in trait-convergence assembly patterns (TCAP) in plant communities, and distinguishes this TCAP from the component reflecting trait-divergence assembly patterns (TDAP). Three representative vegetation types of the West Coast of South Africa, namely Atlantis Sand Fynbos, Swartland Shale Renosterveld and Langebaan Dune Strandveld, were studied. Four sites of decreasing size (one mainland and three fragments) were selected in each vegetation type, where species were sampled in nine 10 m x 10 m plots. A three-matrix approach was adopted in the data analysis. One matrix contained the species described by selected functional traits depicting species' response to habitat fragmentation. A second matrix described cover-abundance patterns by species, while a third matrix described the sites by variables such as soil fertility, patch size, distance of patch from nearest neighbour, matrix type, fire and grazing history, and alien infestation. An iterative algorithm was used to search for the optimal trait subset that maximized the expression of TCAP and TDAP. These traits were used to define two- and three-plant functional types (PFTs) by cluster analysis using sum of squares based on Gower's Index of Similarity as the data contained nominal and quantitative traits. These were PFTs that were significant following bootstrap analysis for cluster level of partition of species ($p < 0.05$ for the two PFTs and $p < 0.01$ for the three PFTs). Principal coordinate analysis (PCoA) based on chord distances computed on the composition of species after fuzzy-weighting by traits illustrated TCAP and TDAP. Both TCAP and TDAP were significant ($p = 0.001$). Therefore, habitat fragmentation influences plant community patterns in the Cape lowlands.

Keywords: Filters; fragmentation; plant functional types; species coexistence, over-dispersion, under-dispersion

6.1 Introduction

Human-induced habitat fragmentation is regarded as one of the main threats to biodiversity globally today (Saunders et al. 1991; Fahrig 2003; Foley et al. 2005; Groom et al. 2005; Rouget et al. 2006). Large-scale disturbances and habitat transformation upset dynamic cycles and cause dramatic and sometimes irreversible changes in ecosystems (Pickett & White 1985; Lindenmayer & Fischer 2006). Predicting how plant communities may respond to these changes and continue to persist remains a fundamental challenge to ecologists. However, plants' ability to endure displacement from control levels (resistance) and the resilience (pace and fullness of the subsequent return of the system to control levels) determine how individual plants or a plant community may respond to a severe event (Grime 2001). Therefore, suitable protocols are needed to quantify the immediate response (resistance) and the speed of recovery (resilience) of individual plants or plant communities, to test theories on community and ecosystem responses to extreme events (Grime 2001). This is particularly important in the context of global changes that affect land-use patterns and climate (Box 1996; Díaz & Cabido 1997; Lavorel et al. 1999). Plant functional types (PFTs) are now considered as an important concept in this regard. Many studies have recently been undertaken in different parts of the world to better understand how ecosystems function and respond to global changes using plant functional traits (e.g. papers in Woodward & Cramer 1996; McIntyre et al. 1999a; Rusch et al. 2003). However, little is known still about the links between PFTs associated with responses to environmental factors such as disturbance (response traits), and those that determine plants' effects (effect traits) on ecosystem processes. Grouping plants *a priori*, based on knowledge of their function or observed correlations among traits, would make it possible to directly predict changes in ecosystem processes from projected changes in plant composition in response to global change (Woodward & Cramer 1996). This predictability is based on the idea that *functional effect* groups and *functional response* groups should overlap (Gitay & Noble 1997; Lavorel et al. 1997; Blanco et al. 2007). However, studies of functional redundancy and ecosystem resilience clearly distinguish between effect and response groups (Walker et al. 1999).

In addition, plant communities result from various abiotic and biotic filters that, on short and long temporal scales, select from the regional species pool the species with attributes that enable them to cope with the prevalent site factors (Keddy 1992; Weiher & Keddy 1995, 1999; Wilson 1999). This means that the composition and functioning of a plant community is the final product of these filters operating at different spatio-temporal scales and selecting species with appropriate responses, resulting in assemblages with varying trait compositions (Lavorel & Garnier 2002). Therefore, a plant community is basically composed of species with traits that enable them withstand the prevalent abiotic and biotic conditions and to equally coexist (Pillar et al. 2009). Species with very traits within the community will likely reveal trait-convergence assembly patterns (TCAP) or under-dispersion. In contrast, trait-divergence assembly patterns (TDAP) or over-dispersion will occur when the coexistence of species is constrained by their trait similarity (Pillar et al. 2009), that is, when the communities contain species with less-similar traits. It is possible to find both TCAP and TDAP in species composition of plant communities along ecological gradients (site factors). It is vital to separate these two components when studying plant community assembly patterns, therefore, because these patterns' relation to ecological gradients may reveal certain limitations or species assembly rules that may predict plant community structure (Weiher & Keddy 1995). This study aimed to find out whether the extensive human-induced habitat fragmentation in the Cape lowlands of South Africa has resulted in any trait-convergence assembly patterns of the plant communities and if so, to separate the components reflecting TCAP and TDAP. To achieve these goals, analytical tools proposed by Pillar et al. (2009) were used for data analyses. It is expected that if the composition and functioning of plant communities in the region are influenced by factors related to fragmentation such as patch size, patch distance from nearest neighbour, matrix type and other site factors such as disturbance regime and soil fertility, then species with similar traits and similar responses to these site factors should coexist, thus expressing TCAP. TDAP should be found if the plant communities contain species with less similar traits due to differences in the prevalent sites factors.

6.2 Methods

6.2.1 Trait selection

Six easy to measure ("soft") traits considered as reasonable surrogates for more functional, but difficult to measure ("hard") traits (McIntyre et al. 1999b) were selected based on their relevance to species' responses to habitat fragmentation. These included five nominal (categorical) traits and one ratio trait (height), as featured in Table 6.1.

Table 6.1 Traits and trait symbols selected and assigned to plant species sampled in three Cape lowland vegetation types.

Dispersal mode (used as a surrogate for dispersal distance)	Long distance dispersal (LD); Short distance dispersal (SD)
Breeding mode	Dioecious (Di); Non-dioecious (ND)
Plant pollinator specificity	Generalist pollinated (GP); Specialist pollinated (SP)
Regeneration mode	Seeder (Se); Resprouter (Rs)
Life span	Perennial (Pe); Annual (An)
Plant height (average of 5-25 individuals of each species)	Height in metres (Ht)

Table 6.2 Environmental variables (ecological gradients) used to describe the sites sampled.

Soil fertility (increasing from fynbos to renosterveld)	One = fynbos, Two = strandveld, Three = renosterveld
Patch size (decreasing from 1100 ha to 8 ha)	Four = mainland, Three = largest fragment, Two = medium-sized fragment, One = smallest fragment
Patch distance to nearest neighbour (as proxy for connectivity)	One = 0-1 km, Two = >1-2 km, Three = >2-3 km, Four = >3-4 km, Five = > 4 km
Landscape matrix (as proxy for resistance to movement of propagules (see also Jonas et al 2006))	One = agriculture and alien trees; Two = agriculture, roads and settlement; Three = agriculture, alien trees, roads and settlement
Alien plant infestation:	One = less than 1%, Two = 1-10%, Three = more than 10%
Fire history	One = less than 10 years, Two = 11-20 years, Three = >20-40 years, Four = more than 40 years ago, Five = no information
Grazing intensity (increasing)	One = no grazing, Two = light grazing by indigenous herbivores, Three = sheep grazing for more than 20 years, Four = grazing by large indigenous herbivores

6.2.2 Sampling

The same study sites, vegetation types and sampling procedure as described in Chapter 3 were employed, but only the data for the 10 m x 10 m plots were used. Nine 10 m x 10 m plots were sampled in each of the four sites in each of the three vegetation types, giving a total of 108 plots.

The modified Braun-Blanquet cover-abundance values (Barkman et al. 1964) of species were recorded. Species were assigned the selected traits based on direct field observations, gathered expert knowledge, and from the literature sources.

6.2.3 *Scaling-up of traits to community level*

The data for the indigenous species were organized into three matrices and analysed following the procedure described in Pillar et al. (2009), which represents an interesting new analytical tool for PFT classification studies. The matrix **B** contained the species described by traits. Nominal traits are not suitable for the expression of TCAP and TDAP. Therefore the nominal traits were expanded into as many binary traits as the number of states, which are more suitable for TCAP and TDAP. The matrix **W** featured the importance value of species in each plot (with the original Braun-Blanquet cover-abundance values converted into numerical importance values using van der Maarel's (1979) transformation as follows: *absent*: 0, *r*: 1, *+*: 2, *1*: 3, *2m*: 4, *2a*: 5, *2b*: 6, *3*: 7, *4*: 8, and *5*: 9). The matrix **E** described the sites by various ecological or environmental variables prevalent in the study sites (Table 6.2). These three matrices served as input for data analysis in the software SYNCSEA (available online at <http://ecoqua.ecologia.ufrgs.br>) with details of the computation and explanation of the procedure involved found in Pillar (1999a), Pillar & Sosinski (2003) and Pillar et al. (2009).

The scaling up of species traits to community level involved, for TCAP, matrix multiplication $\mathbf{T} = \mathbf{B}'\mathbf{W}$ (see also Díaz & Cabido 1997) with the trait quantities in the communities. Relating **T** to **E** required the computation of a distance matrix of communities (\mathbf{D}_T) using **T**, and another distance matrix of the community sites (\mathbf{D}_E) using the matrix **E**. The matrix correlation $\rho(\mathbf{TE}) = \rho(\mathbf{D}_T; \mathbf{D}_E)$ then measures the level of congruence between site distances based on **T** (\mathbf{D}_T) and site distances based on **E** (\mathbf{D}_E). This is equivalent to the correlation used in a Mantel test. The scaling of species traits to community level for TDAP, involved matrix multiplication $\mathbf{X} = \mathbf{U}'\mathbf{W}$, which contained the

composition of the communities in terms of PFTs (each row in \mathbf{X} referring to a PFT), since the matrix \mathbf{U} was derived following the classification of species into PFTs. The matrix \mathbf{U} was defined based on an incidence matrix \mathbf{C} of each species i belonging to each type g , with the species having crisp or fuzzy degrees of belonging to the types. Relating matrix \mathbf{X} to matrix \mathbf{E} was done by the partial Mantel correlation $\rho(\mathbf{X}\mathbf{E}, \mathbf{T}) = \rho(\mathbf{D}_X; \mathbf{D}_E)$ between site distances based on \mathbf{X} (\mathbf{D}_X) and \mathbf{E} (\mathbf{D}_E), while controlling for \mathbf{D}_T . These calculations were done in the software SYNCOSA (Pillar et al. 2009).

6.2.4 Search for traits that maximised the expression of TCAP and TDAP

The species trait data scaled up to community level was imported into the software SYNCOSA, which applied an iterative method to search for the subset of traits in matrix \mathbf{B} that maximised the expression of TCAP and of TDAP, related to the environmental (site) variables in Table 2. This was based on Euclidean Distance between the plots using matrix \mathbf{T} for TCAP and matrices \mathbf{X} and \mathbf{T} for TDAP, both generated using a subset of traits from matrix \mathbf{B} (see also Pillar 1999a).

6.2.5 Test of significance TCAP and TDAP

The statistical significance of the matrix correlation $\rho(\mathbf{TE})$ for TCAP and the observed partial Mantel correlation $\rho(\mathbf{X}\mathbf{E}, \mathbf{T})$ for TDAP were tested against a null model, which retained the real data structure except the one that was being tested. Details of testing the significance of the expression of TCAP and TDAP are found in Pillar et al. (2009). A large $\rho(\mathbf{TE})$ indicates that communities that are more similar in traits, are also more similar for the ecological gradient or site factors, thus $\rho(\mathbf{TE})$ measures trait-convergence (TCAP). A large $\rho(\mathbf{XE})$ indicates that either or both TCAP and TDAP are related to \mathbf{E} . Once the trait-convergence component from $\rho(\mathbf{XE})$ was removed, the partial Mantel correlation matrix was then computed, where $\rho(\mathbf{XT}) = \rho(\mathbf{D}_X; \mathbf{D}_T)$ is the matrix correlation between the distance matrices \mathbf{D}_X and \mathbf{D}_T . Thus, the partial matrix correlation $\rho(\mathbf{X}\mathbf{E}, \mathbf{T})$ measures the magnitude of the effect of TDAP in $\rho(\mathbf{XE})$.

6.2.6. Defining PFTs

Once TCAP and TDAP were identified, PFTs were defined in order to simplify the complexity of interpreting patterns in terms of species (see Pillar et al. 2009). PFTs were defined based on the matrix of species by optimal traits in the software programme MULTIV version 2.63b (available online at: <http://ecoqua.ecologia.ufrgs.br/>). The classification of species into PFTs was done by applying cluster analysis using the sum of squares method based on the Gower Index of Similarity, which has an advantage of being able to handle mixed-trait measurement scales (Gower & Legendre 1986; Podani 1999). To determine the appropriate number of PFTs (groups), group sharpness was tested by bootstrap resampling and only groups (PFTs) that were significant for alpha were chosen (see Pillar 1996; Pillar & Orlóci 1996; Pillar 1999b). For a sufficient sample size, a p larger than alpha indicates sharp groups (see Pillar 1999b). Following bootstrap resampling, two different sets of PFTs were identified. The first set comprised two PFTs that were significant following bootstrap analysis for cluster level of partition of species ($p > 0.05$), with an alpha threshold of 0.05. The second set comprised three PFTs that were significant following bootstrap analysis for cluster level of partition of species ($p > 0.01$), with an alpha threshold of 0.01 (see Pillar et al. 2009). In total, five PFTs were identified, which definition was based on species' responses to the different site factors in Table 6.2. These are functional response groups, not functional effect groups (Gitay & Noble 1997; Lavorel et al. 1997; Lavorel & Garnier 2002), consisting of various growth forms.

6.2.7 Principal coordinate analysis

Once TCAP and TDAP were identified, an exploratory analysis was done to interpret the results. Any of the well-known ordination techniques can be used to display matrices **B**, **T** and **X** separately, and canonical ordination on **T** or **X** restricted by **E**. For this study, the PCoA were done based on matrix **X** after optimization for the most convergent traits for TCAP, and optimization for the trait (annual) expressing TDAP. This is similar to the method applied by Pillar et al. (2009).

PCoA, just like principal component analysis (PCA), is based on an eigen-value equation, but uses any measure of association and the axes plotted against each other in a Euclidean space. PCoA was used because it calculates the distance matrix and produces a graphical configuration in a low-dimensional (two or three) Euclidean space, such that the distances between points (as measured by the Pythagoras theorem) in the configuration reflect the original distances as much as possible (Zuur et al. 2007).

6.3 Results

6.3.1 Trait-convergence and trait-divergence assembly patterns

The results (Table 6.3) show that the level of TCAP expressed by these traits was significant for the environmental variables used, with a matrix correlation $\rho(\text{TE}) = 0.45694$, $p = 0.001$. The optimal traits that revealed TCAP of species were: *long distance dispersal*, *short distance dispersal*, *perennial*, *seeders*, *dioecious*, and *generalist pollinated species*. Only one trait (*annual*) revealed TDAP of species related to the site variables with a significant partial correlation $\rho(\text{XE.T}) = 0.581785$, $p = 0.001$.

Table 6.3 Optimal traits and significance of the matrix correlation $\rho(\text{TE})$ for trait-convergence (TCAP) and partial Mantel correlation $\rho(\text{XE.T})$ for trait-divergence (TDAP) assembly patterns in plant communities of the fragmented Cape lowlands. The partial matrix correlation $\rho(\text{XE.T})$ measures the magnitude of the effect of TDAP in $\rho(\text{XE})$

Environmental variables used	Fertility, patch size, patch distance to nearest neighbour, matrix type, alien infestation, fire and grazing history	
	TCAP	TDAP
Optimal subset of traits	Long distance dispersal (LD), Short distance dispersal (SD) Perennial (Pe), Seeder (Se), Dioecious (Di), Generalist pollinated (GP)	Annual (An)
$\rho(\text{TE})$	0.45694 (p = 0.001)	0.102459 (p = 0.003)
$\rho(\text{XE})$	0.377424 (p = 0.001)	0.583084 (p = 0.001)
$\rho(\text{XE.T})$	0.0451854 (p = 0.008)	0.581785 (p = 0.001)

6.3.2 Community composition by species and PFTs

The variation of communities by species and PFT composition after fuzzy-weighting is depicted in the PCoA ordination diagrams (Figures 6.1, 6.2 and 6.3). Only the optimal subsets of traits are projected on the PCoA diagrams, based on their correlations with the axes. In the figures, species are plotted according to their rescaled correlations with the ordination axes and are identified by the PFTs defined (two PFTs for Figure 6.1, three PFTs for Figure 6.2 and five PFTs for Figure 6.3).

The first two ordination axes accounted for a high proportion of total variation in trait data (92% in Figures 6.1a and 6.2a) and (57% in Figures 6.1b and 6.2b). In Figure 6.3, the first two ordination axes accounted for only 35% of the variation in trait data. In figures 6.1b and 6.2b, the more correlated traits, i.e. *dioecious* (Di) and *perennial* (Pe) were closer together. By integrating the information at community and species levels based on the site factors or environmental variables used and the PFTs identified, the results showed the occurrence of particular PFTs in particular communities (sites). The sites of each vegetation type were generally grouped together, albeit at varying degrees (Figures 6.1a and 6.2a). Most Atlantis Sand Fynbos (ASF) sites were grouped together and most Langebaan Dune Strandveld (LDS) sites together along Axis 1, while most Swartland Shale Renosterveld (SSR) sites were grouped together along Axis 2. Communities in the ASF mainland and the largest and medium-sized fragments were closer together, while communities in the smallest fragment were closer to those in the SSR largest and medium-sized fragments. A number of communities in the smallest SSR fragment were found along Axis 1 together with most of the LDS and ASF sites. Communities in SSR (particularly those in the mainland and the smallest fragment), were generally more scattered across the ordination diagram and showed more variability in trait composition compared to the ASF and LDS communities (Figures 6.1a and 6.2a). This trait variability was also slightly depicted in the communities of the medium-sized LDS fragment, which were generally not very close together.

6.3.3 Distribution of the two PFTs defined by traits expressing TCAP

The occurrence of the set of two PFTs in the different communities based on the site factors is depicted in figure 6.1. PFT-1 was composed of 237 species (three climbers; 34 dwarf shrubs; 48 geophytic herbs; 42 graminoids i.e. grasses, sedges and restios; 19 herbs or forbs; 79 shrubs and 12 succulents). The traits of species in this PFT were as follows: - dispersal distance (121 short-: 116 long-distance dispersed), life span (229 perennials: eight annuals), regeneration mode (134 seeders: 103 resprouters), breeding mode (205 non-dioecious: 32 dioecious), pollinator specificity (194 generalist-: 43 specialist-pollinated). As can be seen from figure 6.1b, most of the species in this PFT were found in the ASF, LDS and in some of the smallest SSR fragment sites along Axis 1. PFT-2 was composed of only 68 species (five climbers; three dwarf shrubs; three geophytic herbs; eight graminoids i.e. grasses, sedges and restios); 25 herbs or forbs; 17 shrubs and seven succulents). The traits of species in this PFT were: dispersal distance (18 short-: 50 long-distance dispersed), life span (40 perennials: 28 annuals), regeneration mode (59 seeders: nine resprouters), breeding mode (62 non-dioecious: six dioecious), pollinator specificity (57 generalist-: 11 specialist-pollinated). Almost all the species in this PFT were along Axis 2 in most of the SSR mainland, the largest and medium-sized fragments, as well as in some of the ASF mainland and smallest fragment sites (Figure 6.1b).

6.3.4 Distribution of the three PFTs defined by traits expressing TCAP

The occurrence of the three PFTs in the different communities based on the environmental variables used is depicted in figure 6.2. PFT-1 was composed of 114 species (four climbers; six dwarf shrubs; 20 geophytic herbs; 15 graminoids i.e. grasses, sedges and restios; 24 herbs; 36 shrubs and nine succulents). The traits of species in this PFT were: dispersal distance (36 short-: 78 long-distance dispersed), life span (95 perennials: 19 annuals), regeneration mode (77 seeders: 37 resprouters), breeding mode (106 non-dioecious: eight dioecious), pollinator specificity (94 generalist-: 20 specialist-pollinated). Species in this PFT were widely distributed along both axes and therefore

found in most of the sites in the three vegetation types (Figure 6.2b). PFT-2 was composed of only 95 species (one climber; 19 dwarf shrubs; 18 geophytic herbs; 16 graminoids, four herbs; 32 shrubs and five succulents). The trait composition of the species in this PFT was as follows: - dispersal distance (88 short-: seven long-distance dispersed), life span (90 perennials: five annuals), regeneration mode (53 seeders: 42 resprouters), breeding mode (75 non-dioecious: 20 dioecious), pollinator specificity (77 generalist-: 18 specialist-pollinated). Species in this PFT were also widely distributed, although slightly more were found along Axis 1 and within most of the ASF and LDS, as well as some of the smallest SSR fragment communities (Figure 6.2b). PFT-3 was composed of 96 species (three climbers; 12 dwarf shrubs; 13 geophytic herbs; 19 graminoids; 16 herbs; 28 shrubs and five succulents). The traits of species in this PFT were: - dispersal distance (15 short-: 81 long-distance dispersed), life span (84 perennials: 12 annuals), regeneration mode (63 seeders: 33 resprouters), breeding mode (86 non-dioecious: ten dioecious), pollinator specificity (80 generalist-: 16 specialist-pollinated). Most of the species in this PFT occurred along Axis 2 within most of the SSR mainland, largest and medium-sized fragments as well as in some of the ASF mainland and smallest fragment communities (Figure 6.2b).

6.3.5 Distribution of PFTs defined by the trait expressing TDAP

The occurrence of the five PFTs defined by the trait expressing TDAP in the different communities based on the environmental variables used is depicted in figure 6.3. PFT-1 was composed of 32 species (two climbers; one dwarf shrub; six geophytic herbs; two graminoids i.e. grasses, sedges and restios; nine herbs; ten shrubs and two succulents). The traits of species in this PFT were: dispersal distance (18 short-: 14 long-distance dispersed), life span (23 perennials: 9 annuals), regeneration mode (24 seeders: eight resprouters), breeding mode (31 non-dioecious: one dioecious), pollinator specificity (25 generalist-: seven specialist-pollinated). Species in this PFT were mostly found in the LDS communities and a few in the SSR communities (Figure 6.3). PFT-2 was composed of 237 species (two climbers; 34 dwarf shrub; 44 geophytic herbs; 42 graminoids; 22

herbs; 80 shrubs and 13 succulents). The trait composition of the species in this PFT was as follows: - dispersal distance (111 short-: 126 long-distance dispersed), life span (226 perennials: 11 annuals), regeneration mode (139 seeders: 98 resprouters), breeding mode (203 non-dioecious: 34 dioecious), pollinator specificity (195 generalist-: 42 specialist-pollinated). Species in this PFT were widely distributed, although more were found within the ASF and SSR compared to the LDS communities (Figure 6.3). PFT-3 was composed of 19 species (two climbers; one geophytic herb; three graminoids; four herbs; six shrubs and three succulents). The traits of species in this PFT were: - dispersal distance (four short-: 15 long-distance dispersed), life span (15 perennials: four annuals), regeneration mode (15 seeders: four resprouters), breeding mode (17 non-dioecious: two dioecious), pollinator specificity (15 generalist-: four specialist-pollinated). The species in this PFT occurred within the LDS communities (Figure 6.3). PFT-4 was composed of three species (one climber; one herb; and one succulent). The traits of species in this PFT were: - dispersal distance (two short-: one long-distance dispersed), life span (one perennial: two annuals), regeneration mode (three seeders: zero resprouters), breeding mode (two non-dioecious: one dioecious), pollinator specificity (two generalist-: one specialist-pollinated). The species in this PFT occurred within the LDS communities (Figure 6.3). PFT-5 was composed of 14 species (one climber; two dwarf shrubs; three graminoids; and eight herbs). The traits of species in this PFT were: - dispersal distance (three short-: 11 long-distance dispersed), life span (four perennials: ten annuals), regeneration mode (12 seeders: two resprouters), breeding mode (14 non-dioecious: zero dioecious), pollinator specificity (14 generalist-: zero specialist-pollinated). Most of the species in this PFT occurred within the LDS communities (Figure 6.3).

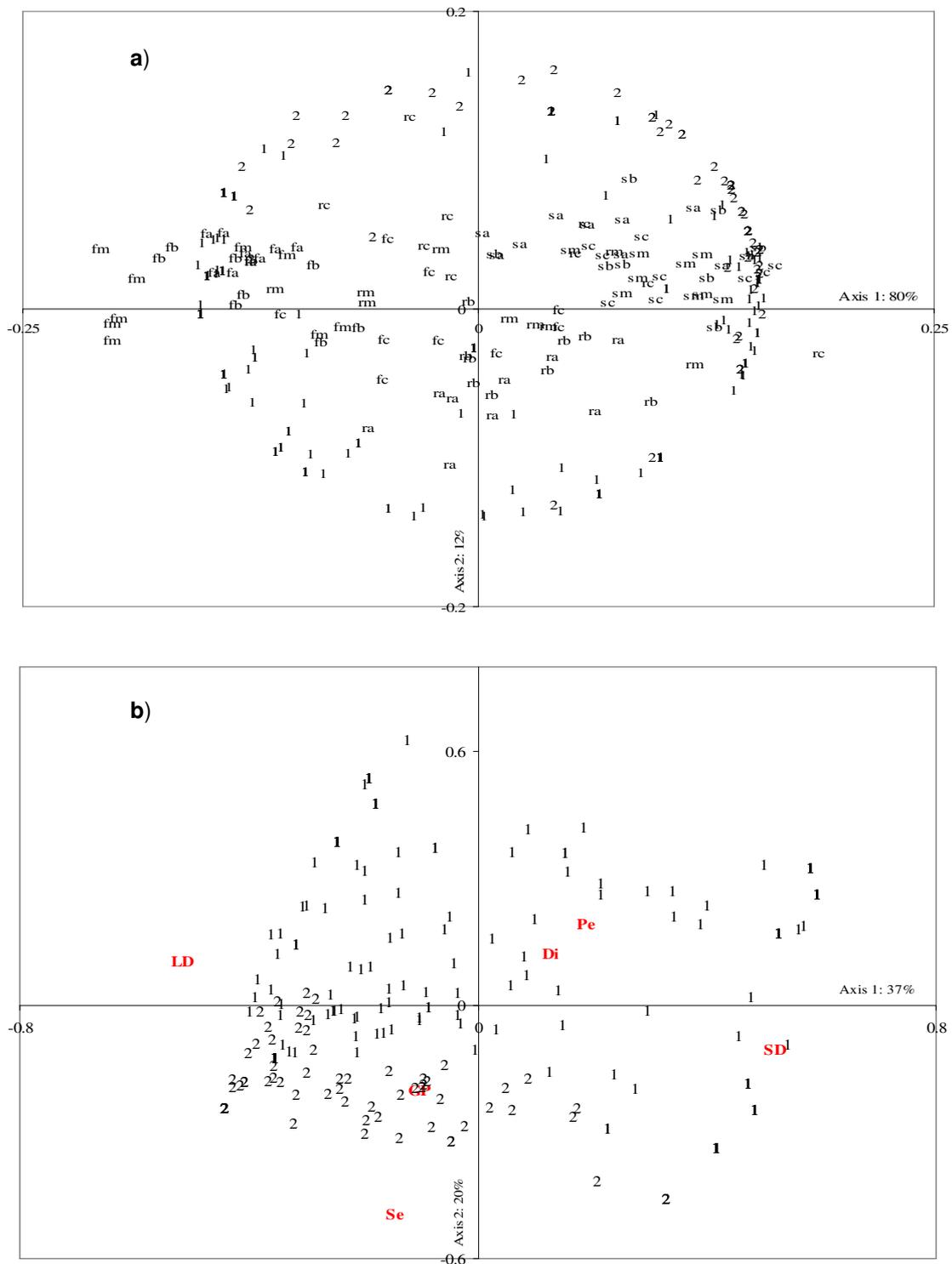


Figure 6.1 PCoA ordination diagrams with **two** PFTs showing TCAP of species sampled in 108, 10 m x 10 m plots at four different sized patches (one mainland, three fragments) in three Cape lowland vegetation types. **(a)** PCoA of sites based on chord distances computed on species composition after fuzzy-weighting by traits that produced two PFTs (1 & 2). Fuzzy-weighting was defined by the optimal traits that expressed TCAP related to environmental variables i.e. **LD** (long distance dispersal), **SD** (short distance dispersal), **Pe** (perennial), **Se** (seeder), **Di** (dioecious) and **GP** (generalist pollinated); the labels identify sites: f = Atlantis Sand Fynbos, r = Swartland Shale Renosterveld and s = Langebaan Dune Strandveld while m = mainland, a = largest fragment, b = medium-sized fragment and c = smallest fragment. Species were plotted according to their rescaled correlations with the ordination axes and identified by the two PFTs. **(b)** PCoA of species as described by the optimal traits and by the two PFTs. The PFTs were found by cluster analysis based on the optimal traits, using the sum of square method based on Gower's Index of Similarity.

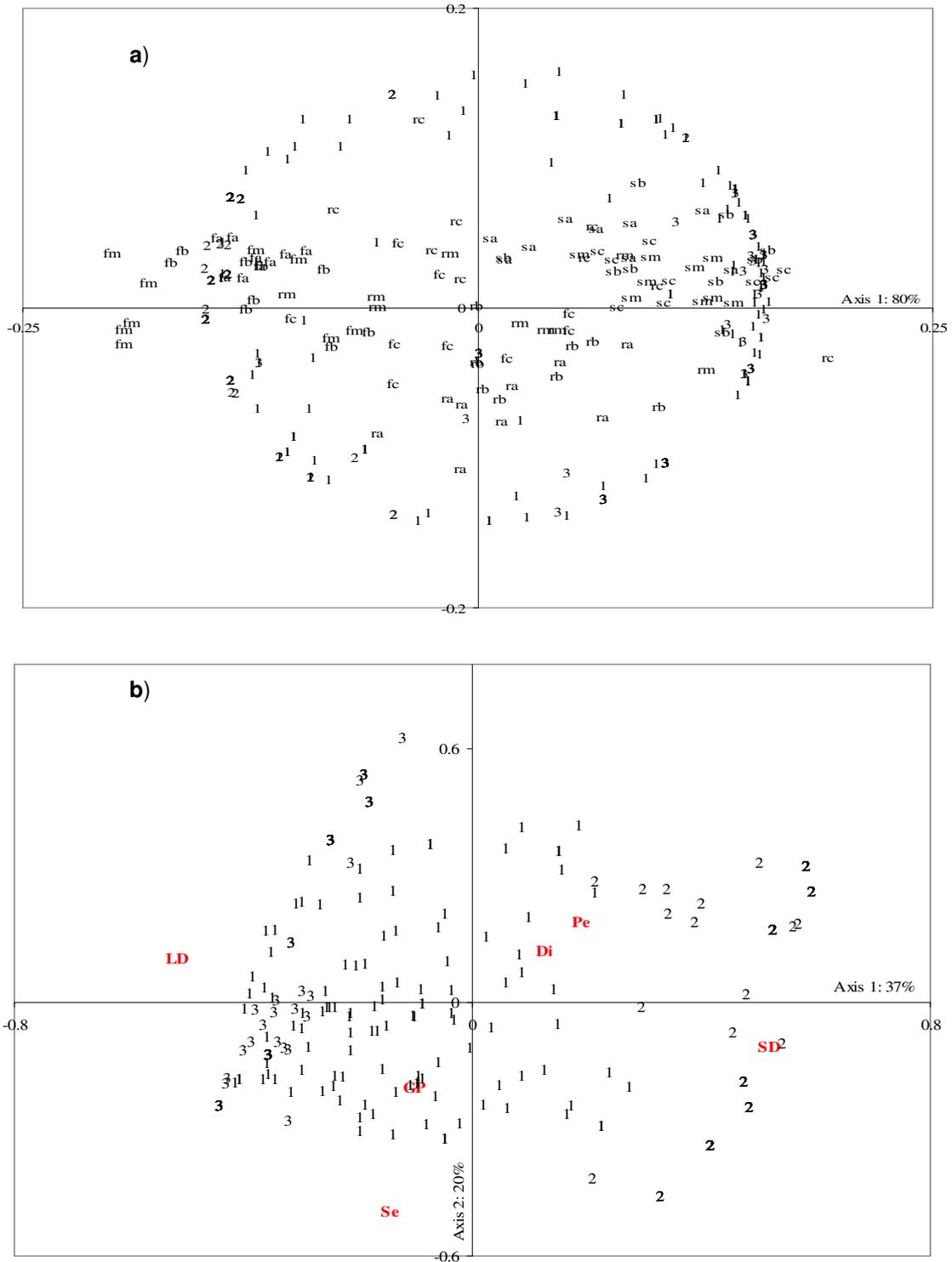


Figure 6.2 PCoA ordination diagrams with **three** PFTs showing TCAP of species sampled in 108, 10 m x 10 m plots at four different sized patches (one mainland, three fragments) in three Cape lowland vegetation types. **(a)** PCoA of sites based on chord distances computed on species composition after fuzzy-weighting by traits that produced three PFTs (1, 2 & 3). Fuzzy-weighting was defined by the optimal traits that expressed TCAP related to environmental variables (symbols and labels same as in figure 6.1a). Species were plotted according to their rescaled correlations with the ordination axes and identified by the three PFTs. **(b)** PCoA of species as described by the optimal traits and by the three PFTs defined by following the same procedure as in figure 6.1b.

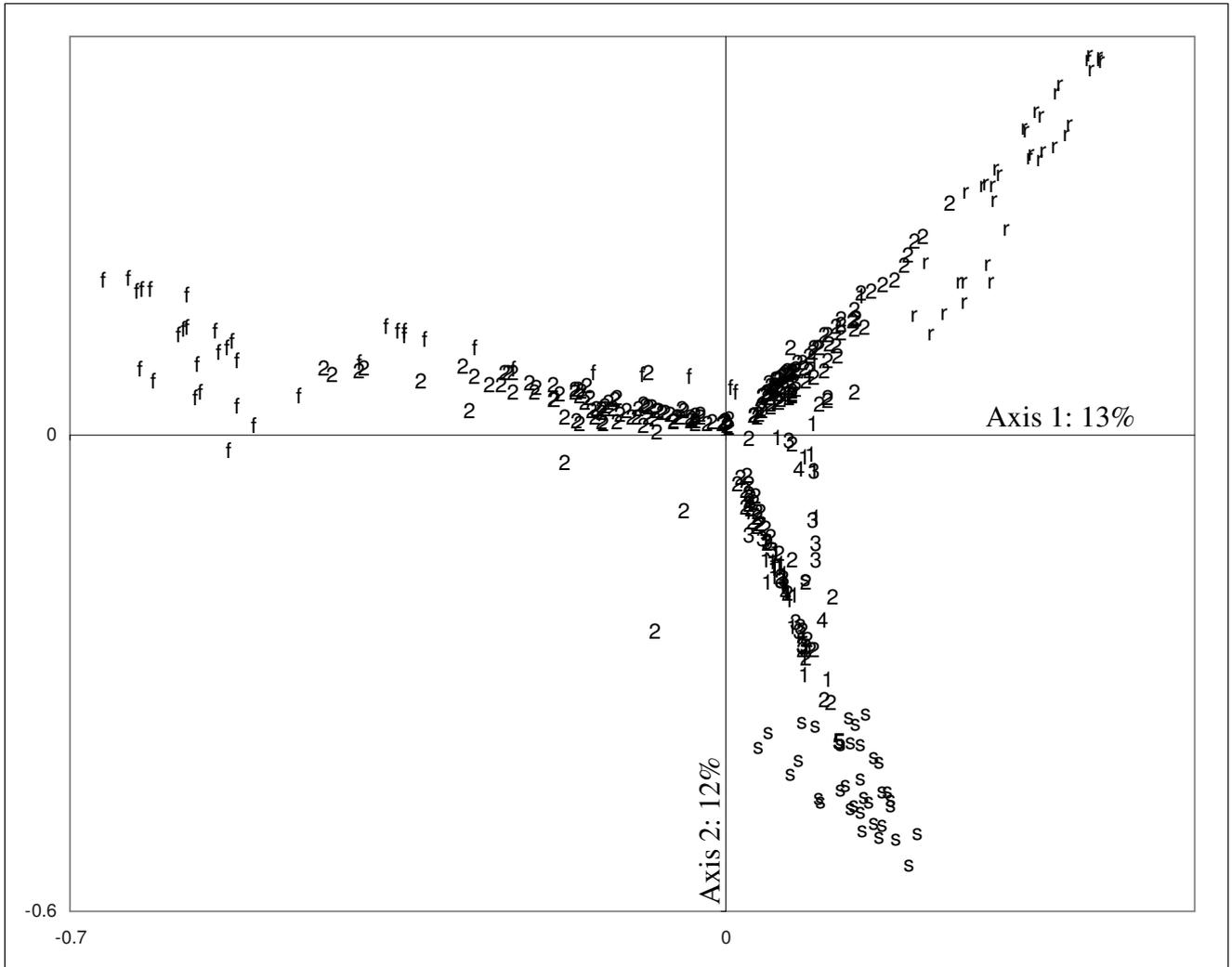


Figure 6.3 PCoA scatter diagram depicting the community composition in terms of the five PFTs of 305 species sampled in 108 (10 m x 10 m) plots. PFTs were defined based on the clustering partition of 305 species described only by the optimal trait (annual) expressing TDAP.

6.4 Discussion

By scaling up species traits to the community level and testing against the null model the assembly patterns based on these traits, this study revealed both trait-convergence (TCAP) and trait-divergence (TDAP) assembly patterns in the plant communities of the fragmented Cape lowlands, based on the environmental variables (site factors) used. Therefore, this confirmed that both TCAP and TDAP related to environmental variables could be detected in plant communities (e.g. Grime 2006; Wilson 2007; Pillar et al. 2009). Species differing in traits co-occurred in the same communities, and species composition was highly correlated to the site factors chosen. This

strongly indicated TDAP related to the site variables. The results also showed that the method used was able to separate the components reflecting TCAP from those reflecting TDAP related to the sites factors used in this study. The fact that only the trait annual expressed TDAP could be attributed to the fact that the three vegetation types investigated vary considerably in the number of annuals. Annuals are generally few in fynbos (Rebelo et al. 2006). The results also showed that the method used separated the components reflecting TCAP from those reflecting TDAP related to the sites factors used in this study. This is of particular importance for TDAP, since finding divergence patterns is more difficult than finding TCAP (Wilson 1999).

By being able to sort out TCAP and TDAP related to environmental variables, this method can be seen as a major methodological breakthrough in community ecology. The method is very flexible and can be used for both binary and quantitative traits as well as qualitative or quantitative community data. The iterative algorithm is useful for searching the subsets of traits that maximise the expression of either TCAP or TDAP. Since community components are fuzzy-weighted by traits, classifying species into functional types is not a precondition for distinguishing TCAP and TDAP (Pillar & Sosinski 2003). The method can serve as a vital tool to test hypotheses addressing links between pattern and processes, therefore, throwing light on plant community assembly rules or constraints predicting community structure and ecosystem function (Weiher & Keddy 1995).

Three main trends emerged within the plant communities of the fragmented Cape lowlands:

(1) Most of the communities sampled within the three vegetation types were grouped separately. This shows that these vegetation types are composed of predominantly distinct elements, which define their structure and function (see also Rebelo et al. 2006). However, the phylogenetic relationships among species may to some extent influence species assembly patterns in response to environmental gradients (Westoby et al. 1995; Duarte et al. 2007).

(2) Some of the communities revealed a high degree of variability in trait composition since these communities were not very close to those of the other sites of the same vegetation type as revealed by the PCoA ordination diagrams. These were the smallest Swartland Shale Renosterveld fragment and mainland, the smallest Atlantis Sand Fynbos fragment, and the largest and medium-sized Langebaan Dune Strandveld fragments. This could be due to the influence of disturbance in plant community composition of these Cape lowland vegetation types. The disturbance history of these sites indeed varied to a large degree, from absence of grazing in the Swartland Shale Renosterveld mainland and the largest and smallest fragments, a long absence of fire in the smallest Atlantis Sand Fynbos fragment, to a long history of sheep grazing in all the Langebaan Dune Strandveld fragments.

(3) Finally, there was a high degree of redundancy among traits as evident in the high variation in trait data accounted for by the first two axes of the PCoA ordination diagrams (Figures 6.1 and 6.2). This could also be attributed to the fact the classification scheme produced only two and three sets of PFTs that were significant following bootstrap analysis for cluster level of partition of species. In figure 6.3, only 35% of the variation in trait data could be explained by the first ordination axes. This could be attributed to the fact that only one trait (annual), maximised the expression of TDAP. This notwithstanding, ecological redundancy improves resilience, which is a vital element of the stability of an ecosystem (Cowling et al. 1994; Walker et al. 1999; see also discussion in Chapter 5). Hence, the functioning of the remnant communities of natural vegetation in the Cape lowlands is reasonably secured even under strong anthropogenic pressure. According to Walker (1995), the stability of an ecosystem can be enhanced considerably if each functional group is composed of several ecologically equivalent species that may respond differently to environmental factors. With the presence of many species within one PFT, there is a greater chance that if one species is lost, those with similar traits left will continue to perform its function in the ecosystem. Such compensation is impossible once the species go extinct in ecosystems wherein a PFT is composed of just one or a few species. Although ecological redundancy is helpful in fostering ecosystem

persistence, resilience of an ecosystem might also be influenced by the traits of less-abundant species (Walker et al. 1999). However, it has been noted that the level of functional redundancy exhibited by an ecological community is influenced by how many traits are used, the relationship between these traits, and their relative weighting (Rosenfeld 2002). The degree of redundancy will be higher if few traits are used because the effect of changes in species richness on functional diversity will be much less. On the other hand, the degree of redundancy will be less if more traits are used. According to Petchey and Gaston (2006), this renders the concept of redundancy rather subjective, although this may happen only when the traits used are not relevant to the ecological question being addressed (Walker et al. 1999). Although the degree of redundancy exhibited in these Cape lowland vegetation types could be due to the few traits used, Petchey and Gaston (2006) noted that emphasis should be put on the relevance of traits to the process being investigated rather than on the number of traits. The high degree of redundancy revealed in this study is not subjective since the selection of traits was based on their relevance to species' response to habitat fragmentation. These included traits related to species dispersal, pollination, and longevity.

6.5 Conclusion

Both trait-convergence and trait-divergence assembly patterns were exhibited in the Cape lowlands' plant communities in relation to environmental variables associated with human-induced habitat fragmentation. Although the three vegetation types are predominantly composed of distinct constituents, structure and function, they also exhibited a high degree of functional redundancy. Plant community composition in these vegetation types also seems to be greatly influenced by disturbance regime. Therefore any conservation effort in these vegetation types should include mimicking the prevalent natural disturbance regimes and linking fragments.

6.6 References

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Chapter 7

Habitat fragmentation in the Cape lowlands: linking knowledge to practice

Abstract

The aim of this study was to gain a better understanding of the effects of habitat fragmentation on vegetation patterns and dynamics in the Cape lowlands. The focus was on plant functional traits, which are now recognized as better predictors of ecosystem response to global change, although species were not ignored. The results showed that the three Cape lowland vegetation types studied are all susceptible to habitat fragmentation, albeit at varying degrees. Based on these findings, mitigation measures have been proposed, which could minimize the negative effects and help to promote biodiversity conservation in the region. These fragments, which are all irreplaceable should be maintained and buffer zones around them. The management of the fragments should mimic the natural disturbance regimes in the respective vegetation types. Populations of species belonging to the critical plant functional types (PFTs) identified should be regularly monitored, and such species re-introduced in patches where they are missing through local community monitoring and planting initiatives. Dispersal and pollination which are important functional attributes for the persistence of biodiversity and the functioning of fragmented ecosystems must be promoted. This can be achieved by removing barriers between patches. Studies on the synergistic interactions between fragmentation and other anthropogenic changes that may be confounding the fragmentation effect on species assemblages are required to develop sound management strategies and interventions.

Keywords: Buffer zones, disturbance regime, global change, management, plant functional traits

7.1 Introduction

This study, aimed at gaining a better understanding of the effects of habitat fragmentation (specifically habitat loss) on vegetation patterns and dynamics in the Cape lowlands, has provided insights into mitigation measures that could minimize the negative effects of fragmentation and help to promote biodiversity conservation in the region. Since the ultimate aim of this study was to provide knowledge and advice to promote biodiversity conservation in the fragmented Cape lowlands, I adopted a novel approach by focusing on plant functional traits, which are now recognized as better predictors of ecosystem response to global change (Díaz & Cabido 1997, 2001; Smith et al. 1997; Cornelissen et al. 2003). While focusing on plant traits, the species-based approach was not ignored, as species remain the concept of biodiversity that many conservation practitioners understand and upon which most management interventions are based. The study also adopted a multi-scale approach (i.e. 0.1, 1, 50 and 100 m²) bearing in mind that information gathered at one scale may not necessarily answer questions at another scale. Moreover, most ecological phenomena vary as a function of scale (Palmer & White 1994; Crawley & Harral 2001) and there is no single correct scale at which the effects of landscape changes on biodiversity and ecosystem process can be studied or at which the mitigating effects can be implemented. This implies landscape changes and the mitigation measures can occur at much larger scales than the ones used in this study.

7.2. Key findings of the study

To gain a better understanding of the full impact of habitat fragmentation in the Cape lowlands, I investigated the effect of reduced patch size on species richness and plant functional type (PFT) richness and diversity. The findings revealed different fragmentation effects on species richness and PFTs for the three vegetation types studied. The effect on PFTs was more pronounced than that on species richness. Focusing on plant traits helped to identify PFTs that need special conservation attention in these Cape lowland vegetation types, thus validating the plant trait approach.

7.2.1 Effect of reduced patch size on species richness

The effect of reduced patch size on species richness was generally weak and also varied with the scale, indicating that there was more of an area effect than a fragmentation effect *per se*. However, the fragment size effect was evident in ASF where fragments below 600 ha were much more depleted in species richness than the mainland at all scales. In contrast, the fragment size effect was masked by site factors in SSR and LDS (notably the grazing history in these vegetation types). The SSR medium-sized fragment (70 ha) with a history of grazing was much richer in species per unit area sampled, while fewer species were found in the smallest fragment (15 ha) than in the other sites. Species richness per unit area sampled in the largest LDS fragment (70 ha) with a history of sheep (and to a lesser extent cattle) grazing, was much higher than it was in the mainland that had not been grazed for over 40 years. There was some evidence of the fragment size effect as all the fragments had a grazing history but fewer species were recorded per unit area sampled in the smallest (8 ha) than in the largest and medium-sized (18 ha) fragments.

The distinctiveness of species assemblages in the respective mainlands and corresponding fragments of the different vegetation types studied was measured in terms of percentage complementarity. This was found in the study to be generally very high, due to the high number of unique species and few common species found between any two sites of the three vegetation types. Species turnover (β -diversity) was found to be generally very high among the different sites and contributed the most to overall plant species diversity in the region. The high complementary and species turnover reflect the degree of habitat heterogeneity in the region, and also indicate an abundance of habitat specialists. Therefore these fragments do contribute significantly to overall regional plant diversity and may also be the last suitable habitats for some species since they harbour several endemic species (see Appendix 16).

7.2.2. Effect of reduced patch size on plant functional type richness and diversity

An assessment of the response of the three vegetation types to habitat fragmentation (reduced patch size) using plant functional traits showed that they were all susceptible, albeit at varying degrees. I predicted that ASF would be the most susceptible since most (five) PFTs that were classified as endangered were dominated by species of this vegetation type. These were the short-distance dispersed dioecious and non-dioecious specialist- and generalist-pollinated perennial seeders. Most of the species in these PFTs belonged to the genera: *Aspalathus*, *Diastella*, *Diosma*, *Elegia*, *Erica*, *Hermannia*, *Ischyrolepis*, *Lampranthus*, *Leucadendron*, *Macrostylis*, *Muraltia*, *Passerina*, *Phyllica*, *Polygala*, *Restio*, *Roella*, *Salvia*, *Serruria*, *Sisymbrium*, *Struthiola*, *Thesium*, *Wahlenbergia*, and *Zygophyllum*. This linked well with the findings on the effect of fragmentation on species richness because the species missing from the different ASF sites belonged to the same genera and PFTs. Next was SSR with one of the PFTs classified as endangered (i.e. the short-distance dispersed specialist pollinated annual seeders *Hemimeris racemosa*) and many geophytes with highly specialised pollination systems. Based on my predictions, the least susceptible of the three vegetation types was LDS, with many fleshy-fruited generalist-pollinated and long-distance dispersed species.

To test these predictions, I investigated the effect of reduced patch size on plant functional type (PFT) richness and diversity in these three vegetation types. The results obtained did follow my predictions. LDS stood out as the least threatened of the three vegetation types. The effect of reduced patch size was more on PFT diversity than on richness. PFT richness relative to fragment size was not consistent at all scales in all three vegetation types, indicating a scale effect. There was some evidence of the negative effect of reduced patch size on PFT richness in ASF. More PFTs were lost as patch size decreased, although this was not significant among all the sites and at all scales. The fact that PFT richness was significantly higher only in the mainland (1 100 ha) than in the medium-sized fragment (37 ha), and also higher in the largest fragment (600 ha) than in the

smallest fragment (16 ha) at the 50-m² scale, highlights the sampling scale effect. In fact, up to five PFTs found in ASF were absent from the smallest fragment at the different scales sampled. PFT diversity per unit area sampled was higher in the ASF mainland and the largest fragment than in the two smaller fragments, and the mainland was equally higher in PFT diversity than the fragments combined. Similarly, PFT richness and diversity per unit area sampled was lowest in the smallest SSR fragment than in the other sites. Meanwhile, the grazed fragment was higher in PFT richness and diversity per unit area sampled than the ungrazed sites, indicating that grazing is vital for the functioning of renosterveld. Seven of the PFTs found in SSR were absent from the smallest fragment. The results actually confirmed that SSR, with over 80% transformed and less than 5% under protection, is one of the most critically endangered of the Cape lowland vegetation types (Rouget et al. 2003, 2006). There was evidence of some degree of functional redundancy particularly in LDS, as the effect of fragmentation on PFT richness and diversity in this vegetation type was minimal.

7.2.3. Critical plant functional types

By focusing on plant traits, this study highlighted some of the plant functional types that need special conservation attention in the three vegetation types studied, which makes the PFT approach so much better. These were PFTs that were missing from most of the sites of the three vegetation types. These were mostly short- or long-distance dispersed dioecious and non-dioecious seeders and resprouters, some with highly specialised pollination systems (see Chapter 5). Fynbos species within these PFTs were mostly those in the families Ericaceae, Proteaceae, Restionaceae, Rhamnaceae, Rutaceae, and Thymelaeaceae. Renosterveld species in these PFTs were dominated by species in Anacardiaceae, Apiaceae, Campanulaceae, Menispermaceae and Scrophulariaceae as well as many geophytes in Amaryllidaceae, Asphodelaceae, Geraniaceae, Hyacinthaceae, Hypoxidaceae, Iridaceae, Orchidaceae, and Oxalidaceae. Strandveld species in these PFTs were mainly in Asclepiadaceae, Asphodelaceae, Ebenaceae, Geraniaceae and Tecophilaeaceae. Most of

the seeders in these PFTs tend to allocate more resources to seed production (Rebelo et al. 2006). Some of them (mostly the fynbos species) are also myrmecochorous or ant-dispersed (Bond & Slingsby 1984; Johnson 1992), and usually have small, transient seed banks, which makes them more vulnerable to habitat fragmentation (Cowling et al. 1994a). For these and other short-distance dispersed species, the rate of re-colonisation from nearby patches is greatly reduced due to their poor dispersal ability (see also Bond et al. 1988; Bond 1994). Habitat fragmentation may also increase the separation of the sexes of dioecious species. The absence of an effective population size in such species will render the establishment of a population virtually impossible since both sexes are needed. Moreover, smaller populations are more prone to higher extinction risks due to environmental, demographic or genetic stochasticity (Franklin 1980; Shaffer 1981; Lindenmayer & Fischer 2006). The small plant population sizes in smaller fragments can also reduce the likelihood of pollination, as these small populations are often less attractive to pollinators (see also Morgan 1999; Pauw 2004). Since such populations are often made up of closely related individuals, there is an increased likelihood of loss of genetic diversity and inbreeding depression (see also Ellstrand & Elam 1993; Young et al. 1996; Matthies et al. 2004; Bruna & Oli 2005). The highly specialised pollination systems exhibited by some of these species may be disrupted by habitat fragmentation with potential ramifications for genetic diversity. For example, pollinators may visit flowers less frequently, leading to reduced fecundity and low seed set (see Bond 1994; Donaldson et al. 2002; Bruna & Oli 2005; Ward & Johnson 2005; Aguilar et al. 2006; Lawson et al. 2008). Such reduced fecundity and low seed set was observed in *Phyllica cephalantha* (Rhamnaceae) in the smallest ASF fragment (data not shown). While this species had seeds in the other ASF sites, most of the individuals of the population in this fragment were without seeds.

7.2.4 Critical patch sizes

The results of this study indicate that the critical patch sizes for effective biodiversity conservation in the three Cape lowland vegetation types investigated should not be less than 600 ha for ASF, 100

ha for SSR and 20 ha for LDS. However, since disturbance is one of the factors confounding the fragmentation effects, management in these patches should mimic the typical disturbance regimes prevalent in the respective vegetation types to render them functional.

7.2.5. Community assembly patterns

Both trait-convergence (TCAP) and trait-divergence (TDAP) assembly patterns were revealed within the plant communities sampled in relation to various site factors, some associated with habitat fragmentation. TCAP was revealed as species with different traits co-occurred in the same communities. This indicates that the composition and functioning of the plant communities in the Cape lowlands is influenced by various site factors related to habitat fragmentation such as soil fertility (vegetation type), patch size, patch distance from nearest neighbour, surrounding matrix type and disturbance regime (e.g. grazing, fire and alien infestation). These factors operate at different spatial and temporal scales and select from the regional species pool, those species with appropriate responses that can persist at any given site, resulting in assemblages with varying trait compositions. Therefore, plant communities in the Cape lowlands are composed of species with traits that enable them to cope with these different site conditions and to also coexist. The traits that revealed TCAP were: long and short distance dispersal, perennial, seeders, dioecious, and generalist pollinated. These constitute traits of the most widely distributed species in the three vegetation types studied. In contrast, TDAP was revealed by only one trait i.e. annuals. This is understandable given that there are generally very few annuals in fynbos.

Although the three vegetation types are predominantly composed of distinct constituents, structure and function, they also exhibited a high degree of functional redundancy. Community composition in these vegetation types seems to be also greatly influenced by disturbance regime. Therefore any conservation effort in the fragmented Cape lowlands should include mimicking the prevalent natural disturbance regimes and promoting ecological redundancy by linking fragments.

7.2.6 Confounding factors to the fragmentation effects

This study also revealed that the effects of habitat fragmentation on biodiversity in the Cape lowlands varied for the different vegetation types and were confounded by a number of factors: - (1) the spatial scale of sampling, (2) the temporal scale of the fragmentation event (3) the prevalent disturbance regime in a particular patch such as fire, grazing and alien invasion, and (4) the type of matrix surrounding the patch.

7.3 Proposed management interventions

It is clear from the results of this study that the remaining patches of natural vegetation in the Cape lowlands do not only contribute to regional plant diversity, but most of them are also functional ecosystems. These remnant patches are therefore 100% irreplaceable (see also Cowling & Pressey 2003) as they are all required to meet the target of about 30% of the original extent needed under conservation to represent 75% of the species in the different vegetation types (Rouget et al. 2006). However, most of these remnant patches are located on private lands (Kemper 1997; Rouget et al. 2003; von Hase et al. 2003), making private landowners the custodians of these unique habitats. It is therefore very unlikely that their conservation will be through the establishment of formal protected areas. Due to their accessibility and suitability for agriculture and urban development, these lowland habitats will remain vulnerable to competition from human land uses as well as invasion by alien plant species and therefore, are prone to further transformation. Despite the paucity of knowledge about the biology and ecology of most species in the region and given that the loss of habitat and species is happening faster than researchers can identify conservation priorities, urgent management interventions need to be developed and implemented to ensure that the unique biodiversity in the Cape lowlands continues to persist.

7.3.1 Maintaining existing fragments

There is need for a concerted effort by all stakeholders (the landowners, industries, civil society, conservation agencies, NGOs, local, provincial and national government etc) to maintain the existing fragments, which are all irreplaceable. The conservation-conscious landowners should be given incentives to conserve these remnants patches by creating buffer zones around them and forming conservancies or joining existing ones, like the CapeNature Stewardship programme. In this light, initiatives such as the “Biodiversity and Wine Initiative”³ geared towards conserving these remnants should be encouraged and emulated elsewhere by CapeNature. Furthermore, workshops should also be organised during which the results are disseminated to all stakeholders (particularly the farmers who are the custodians of these remnant patches of natural vegetation) and to raise their awareness on the value of the remnant patches. Legislation should be put in place to ensure that local and provincial governments include spatial biodiversity priorities and environmental assessment processes into their land use plans.

7.3.2 Promoting species and plant functional type diversity

In order to promote plant species and PFT diversity in these Cape lowland vegetation types, restoration initiatives geared at linking fragments should be initiated and implemented. This can be done through several ways:

(1) Removing and/or softening barriers. Landscape features that act as barriers should be identified and possibly removed. For example, alien *Acacia saligna* invasion and/or *Eucalyptus* species plantations surround all the Atlantis Sand Fynbos sites in this study. These matrices have a resistance value of 50 and 75 respectively (Jonas et al. 2006), with serious ramifications for the movement of plant propagules and pollinators between patches. The alien clearing activity that is currently taking place in the mainland (i.e. the Riverlands Nature Reserve) should be extended to

³ The Biodiversity and Wine Initiative (BWI) is a pioneering partnership between the South African wine industry and the conservation sector. The goals are to minimise the further loss of threatened natural habitat, and to contribute to sustainable wine production, through the adoption of biodiversity guidelines by the South African wine industry is (<http://www.bwi.co.za/>)

the smaller fragments or the landowners of these patches should be given incentives to remove these alien species and replace them with native species. Natural vegetation will also attract other indigenous animal species (birds, insects and mammals) that will facilitate the movement of seed and pollen between patches. There is an urgent need to clear the alien *Acacia saligna* that has severely infested the Atlantis Sand Fynbos medium-sized fragment and may soon out compete most of the indigenous species. The clearing of alien species around these patches will also greatly improve their connectivity. The alien-clearing programme should also involve regular monitoring as well as repeat treatments where necessary to ensure success, since these species usually have large seed banks. Inhabitants around all these fragments (especially fragments surrounded by urban and suburban settlement) should be encouraged (through the supply of planting materials), to practice gardening with indigenous plants (trees, shrubs and herbs). Such gardens will serve as stepping-stones and also help to soften the matrix, allowing for the movement of indigenous birds and insects between fragments, thus facilitating dispersal and pollination. This will improve connectivity between fragments and facilitate pollen and seed inflow from one population to another, particularly for those species of the critical plant functional types in 7.3.3 below. This will help to preserve and enhance genetic diversity and reduce inbreeding, thereby rescuing populations from extinction (see also Richards 2000; Ingvarsson 2001). The removal of barriers between will also help to increase the variety of microhabitats and also ensure that whole metapopulations may persist, even if local populations have some probability of going extinct.

(2) Change in farming practices. Farmers should be encouraged to use indigenous trees for wind breaks instead. Instead of completely replacing natural vegetation by agricultural crops, farmers should be encouraged to practice the strip-plough technique that is common in the West Coast (Rocherpan area) region. This will help to improve movement of invertebrates between fragments. Moreover, the insects that will harbour and visit these patches of natural vegetation will also pollinate the farmers' crops. These natural patches will also attract other animal species, which may help to control many insect pests in the farms. In addition, farmers should be given incentives and

be encouraged to minimise the use chemicals in farms immediately surrounding these fragments. Pesticides negatively impact on indigenous plant and insect species, reducing pollination and pest control services, while fertilizers facilitate invasion by alien species by changing the soil chemistry, (see Rebelo et al. 2006).

7.3.3 Monitoring and re-introducing populations of threatened taxa

Local communities should be encouraged to set up community nurseries that can be used to augment small or re-introduce populations in fragments where they were found missing. For example the “Friends of the Tygerberg Hills”⁴, who are very helpful in monitoring plant populations in the various patches around the Tygerberg (Swartland) area, could be helpful in this regard. This association should be given the mandate to clear some of the *Otholobium hirtum* that dominate the smallest Swartland Shale Renosterveld fragment and hand plant (re-introduce) some of the species (especially the geophytes) that are missing from this patch. More of such associations should be created in the region and mandated to monitor the populations and also re-introduce species of the critical PFTs in patches where these species are missing. Conservation-conscious landowners should also be encouraged to do the same. In this regard, farmers could contact their local nursery, nearest botanical garden or check on www.plantzafrica.com for species suitable to their area. These monitoring and re-introduction programmes should pay particular attention to species of the endangered and vulnerable PFTs. The endangered PFTs that need special attention are the short distance dispersed, specialist- and generalist-pollinated, dioecious and non-dioecious, perennial seeders, and the short-distance dispersed specialist-pollinated, annual seeders. The fynbos species belonging to these PFTs and absent from the largest and smallest fragments are *Leucadendron cinereum*, *Diastella proteoides*, *Polygala garcinii* and *Muraltia* species The

⁴ Friends of Tygerberg Hills are concerned people who work for the preservation of the Tygerberg Nature Reserve, organise regular walks and clearing of alien vegetation, and who share their knowledge with visitors and other Friends Groups. They participate in the CREW (Custodians for Rare and Endangered Wildflowers) Programme coordinated by the South African National Biodiversity Institute (SANBI), as well as present environmental talks and educational programmes at the Kristo Pienaar EE Centre in the Tygerberg Nature Reserve. The Friends of Tygerberg Hills produce a quarterly newsletter. Contact: Jürg Zimmermann – E-mail: jurgz@mweb.co.za

renosterveld species of these PFTs are *Hemimeris racemosa* and *Salvia africana-caerulea*, all absent from the smallest Swartland Shale Renosterveld fragment.

The vulnerable PFTs needing special attention are the:

(1) Long-distance dispersed, dioecious, specialist-pollinated resprouters, with only one species, *Leucadendron lanigerum subsp. lanigerum*, which was absent from the Atlantis Sand Fynbos smallest fragment;

(2) Long-distance dispersed, dioecious, perennial, specialist-pollinated seeders, such as two strandveld species, *Diospyros glabra* and *Euclea racemosa* (absent from the Langebaan dune Strandveld largest and medium-sized fragments);

(3) Long-distance dispersed, generalist-pollinated, dioecious, perennial seeders with species such as *Arctopus echinatus*, *Cissampelos capensis* and *Rhus* species (all absent from the Swartland Shale Renosterveld smallest fragment);

(4) Long-distance dispersed, non-dioecious, specialist-pollinated, perennial seeders with species such as *Pelargonium oenothera* (absent from the ASF mainland, and the medium-sized and smallest fragments), and *Microloma sagittatum* (absent from the LDS largest and smallest fragments);

(5) Long-distance dispersed, specialist-pollinated, annual seeders such as *Pelargonium senecioides* (absent from the ASF mainland and the largest and medium-sized fragments as well as from the LDS mainland), and *Crassula strigosa* (absent from the SSR mainland and smallest patch);

(6) Short-distance dispersed specialist-pollinated non-dioecious resprouters. This PFT was composed of species such as *Babiana* species and *Muraltia filiformis* (missing from the largest ASF fragment), many geophytes including *Babiana stricta*, *Cyphia*, *Geissorhiza aspera*, *Spiloxene capensis*, *S. flaccida*, *Wachendorfia multiflora*, *Ixia* and *Moraea* species, as well as *Salvia africana-lutea* (all absent from the smallest SSR fragment); *Bulbine praemorsa*, *Caesia* sp., *Cyanella hyacinthiodes*, and *Trachyandra chlamydophylla* (absent from the LDS mainland);

(7) Short-distance dispersed, generalist-pollinated, annual seeders composed of *Nemesia affinis* and *Wahlenbergia androsacea* (both missing from the ASF medium-sized and smallest fragments) and *Cysticapnos cracca*, *Nemesia barbata*, *Sebaea exacoides* (all not present in the smallest SSR fragment).

7.3.4. Mimicking natural disturbance regimes

Conservation planning initiatives and management plans should be made for these sites taking into consideration the current and future land use pressures and as well as the prevalent natural disturbance regimes. Changes in disturbance regimes affect species abundances and composition (Pickett & Thompson 1979; Hobbs & Yates 2003; Rebelo et al. 2006). Fire constitutes the major disturbance in fynbos (Le Maitre & Midgley 1992) and occurs at regular intervals of 5–50 years (Rebelo et al. 2006). This study showed that one of the reasons why the smaller ASF fragments were lower in species richness was the changes in the fire regime in these fragments. Fire frequency was greatly reduced in the smallest fragment (16 ha), which had not burnt for over 40 years, while fire intensity was significantly increased in the medium-sized fragment (37 ha) due to the increased fuel load from the alien *Acacia saligna* that has invaded this fragment. In contrast, the mainland (1 100 ha) and the largest fragment (600 ha) burnt on average, once every seven years, with minimum and maximum burn periods of four and 25 years respectively (Brownlie & Mustart 1988). Therefore, to increase plant species diversity in the smaller fragments and render them more functional, management interventions should mimic the natural fire regimes through prescribed burning. Many fynbos species are dependent on fire for regeneration, since it is a fire-prone ecosystem. For example, serotinous species, (mainly Proteaceae), retain their seeds in fireproof seed heads on the plants and release them only after a fire when conditions for germination are favourable (Le Maitre & Midgley 1992; Rebelo et al. 2006). Some fynbos and renosterveld species rely on smoke to break dormancy (De Lange & Boucher 1990; Dixon et al. 1995). In LDS, and more especially in SSR, grazing is also vital for promoting species richness and the maintenance of

ecosystem functions. The fragments of these vegetation types that had been grazed were higher in species richness per unit area sampled than the ungrazed sites. This was particularly evident in SSR, where the medium-sized fragment (70 ha) that was grazed by large indigenous herbivores was significantly richer in species per unit area sampled than all the ungrazed sites. PFT richness and diversity was also higher in this fragment, and significantly so than in the smallest fragment. Renosterveld is sustained by an intermediate level of disturbance (Boucher 1983) and usually fluctuates between a grass- and a shrub-dominated state depending on the fire and grazing patterns (Rebello et al. 2006). Being a fire-prone ecosystem, management interventions in the renosterveld patches should therefore aim to mimic the natural fire regime of 2–10 years (Rebello et al. 2006) or 3–40 years (Rebello 1992) depending on the grazing intensity in the patch. As shown in this study, some level of grazing is required in the renosterveld and strandveld vegetation types studied, to increase plant species diversity and also render these ecosystems functional. Therefore some of these patches (especially the mainland and larger patches) should be used for grazing. However, this has to be done sustainably with the appropriate stocking densities. Local Agricultural Extension Officers should be able to give advice on appropriate stocking densities for particular patches.

7.4 Research recommendations

Although the Fynbos Biome has been studied for decades, knowledge gaps still exist. Given that proper management interventions are often based on sound knowledge, there is need for more research in the region, particularly in the present context of global changes such as habitat fragmentation, invasion by alien plants and climate change.

(1) More vegetation inventories and detailed studies on the taxonomy, general biology and ecology of the species in the region are urgently needed as this information is largely lacking. For example, information is needed on the habitat requirements of species, their pollinators and seed dispersers as well as the disturbances to which the plant species and their animal mutualists are adapted.

- (2) There is dire need for a proper documentation of the land use histories of the sites to guide management intervention and future studies.
- (3) There is a need for more detailed studies on the long-term effects of habitat fragmentation. Such studies should focus on plant traits to ascertain the species, plant functional types and associated ecological processes most threatened by fragmentation. Studies that focus on plant traits will improve our understanding of the mechanisms behind the observed patterns at the population, community and landscape levels. Such studies will help tease out patches that are still functional and indispensable from those that have irreversibly lost their functionality, and are thus expendable. With more of such studies in other Cape lowland vegetation types, results can be reliably extrapolated to the entire lowland fynbos, renosterveld and strandveld.
- (4) Detailed studies on the role of corridors are also required to help identify those that might also be conducive to alien plant invasion and therefore need to be avoided.
- (5) Regular monitoring of critical populations is necessary. In this respect the work carried out by CREW (Custodians of Rare and Endangered Wildflowers) and the Friends of the Tygerberg Hills is commendable. More such programmes need to be put in place to assess the status of plant populations within fragments. Such monitoring should provide information on whether these populations are stable, decreasing or increasing, and whether there is effective movement of pollinators and dispersers between patches. Such regular monitoring will also provide valuable information on the general biology and ecology of the species, their habitat types, their pollinators and seed dispersers, the type and changes in the surrounding matrix and how these affect movement of pollinators and dispersers, the presence or absence of corridors etc.
- (6) Since these lowlands are highly fragmented and are often altered by other anthropogenic changes, the species that they harbour are under a modified environment of reduced area, increased isolation, novel ecological boundaries and changes in disturbance regimes. There is a need for detailed studies of the synergistic interactions between fragmentation and these human-induced changes, which may be confounding the fragmentation effect.

(7) Although considerable effort is being made to control and manage alien plant invasion, there is still need for more research on the impact and control of all alien invasive plants, including alien grasses that are becoming more and more invasive in the Cape lowlands.

(8) Given that this region is not spared from the effects of global climate change, there is also need for studies that focus on the magnitude of habitat transformation that climate change will cause. Such studies should be aimed at identifying the plant and animal taxa as well as the vegetation types that will be most affected and also provide mitigation measures.

7.5 References

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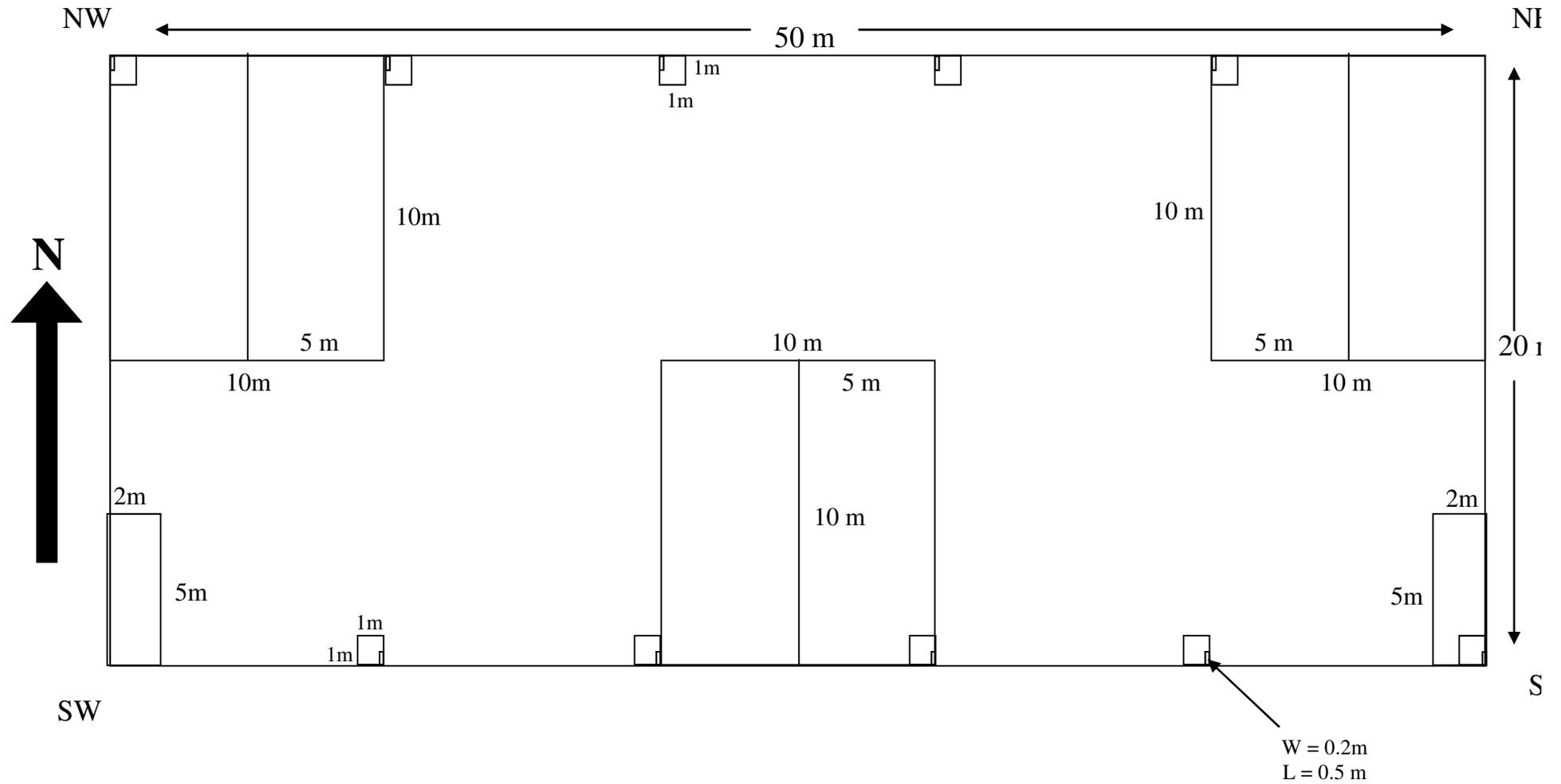
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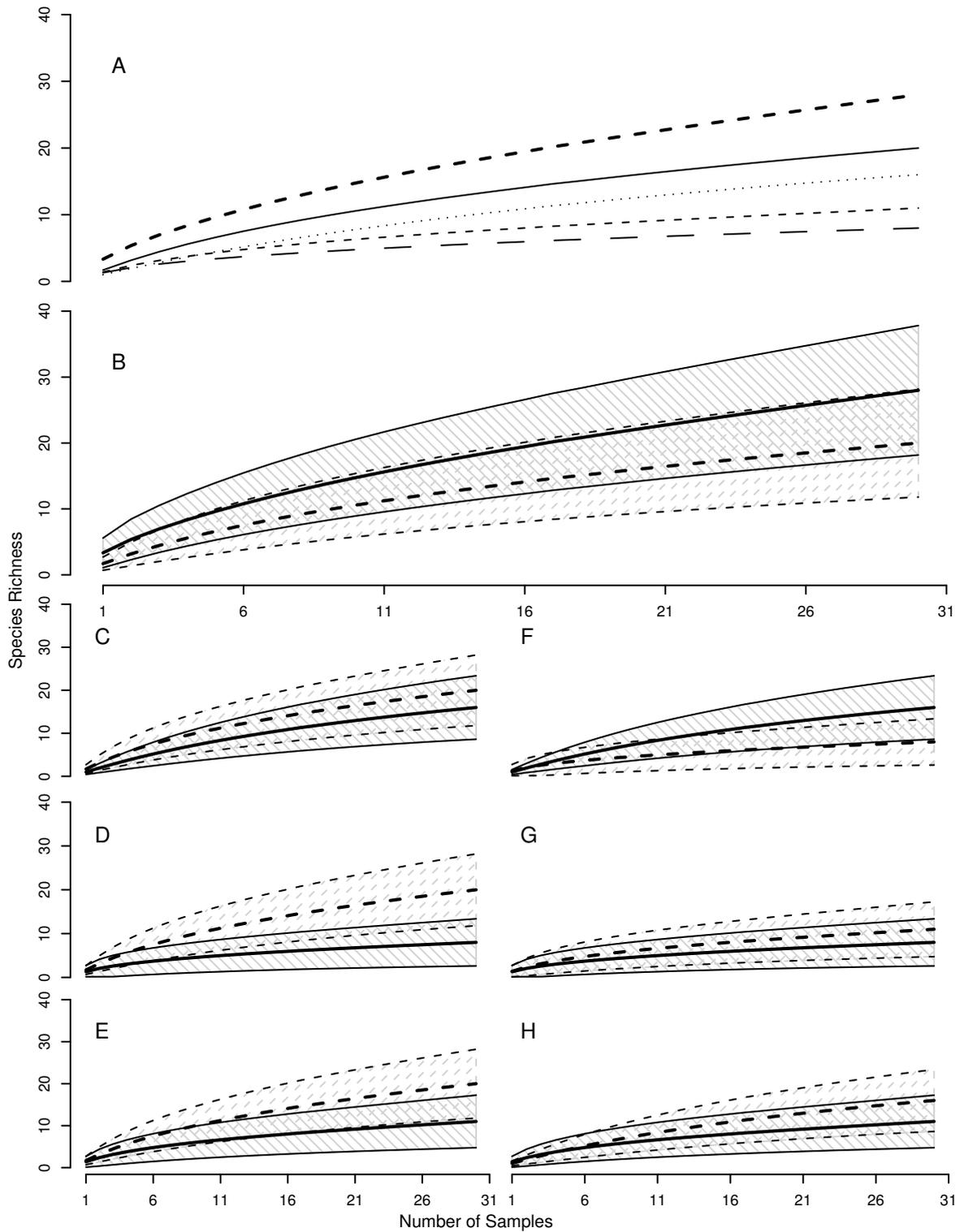
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Appendices

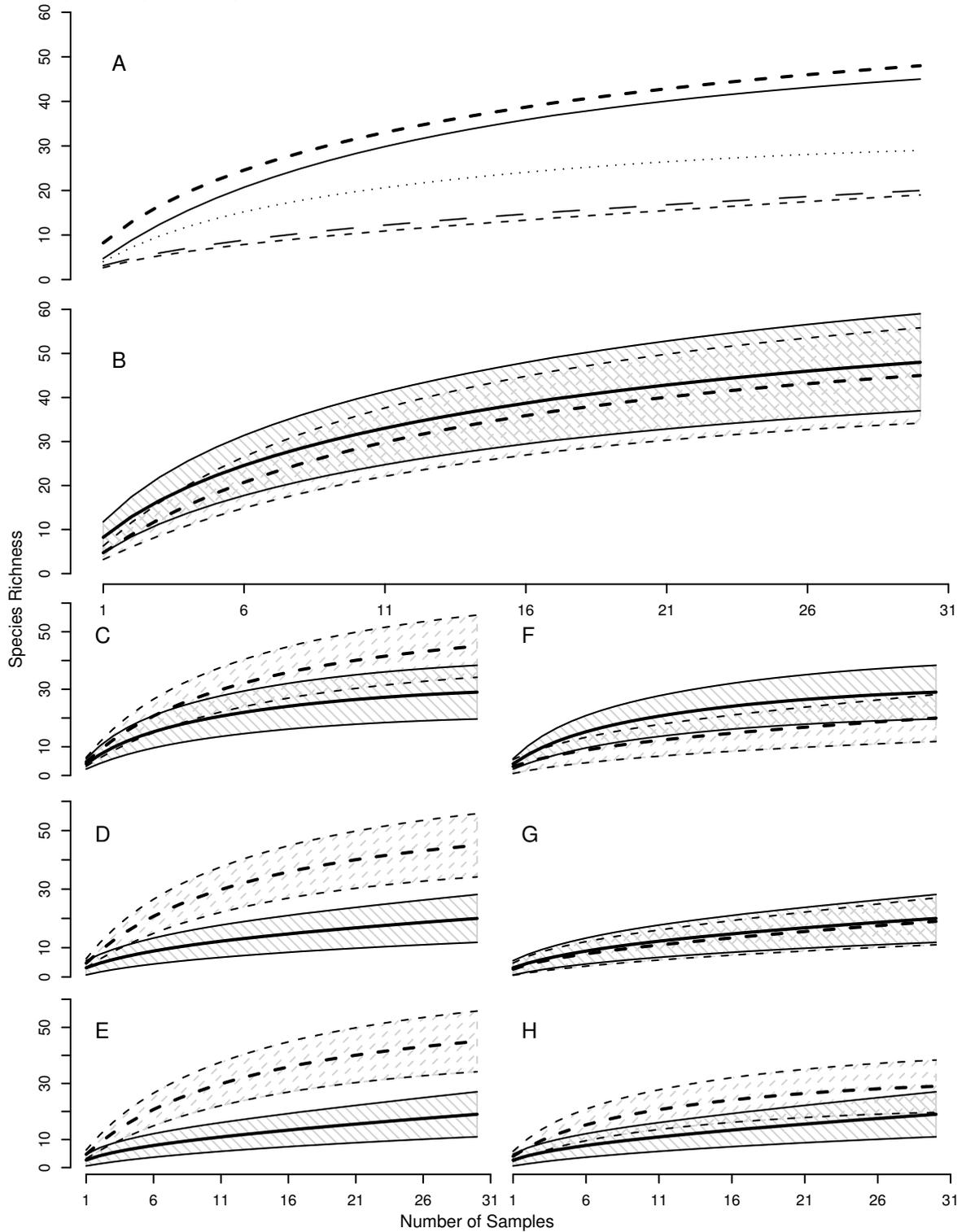
Appendix 1: Modified Whittaker plot design showing layout of sampling grains (quadrats) within the 50 m x 20 m relevés (N.B. only the two 2m x 5m as indicated were sampled but the data was not included in the analyses)



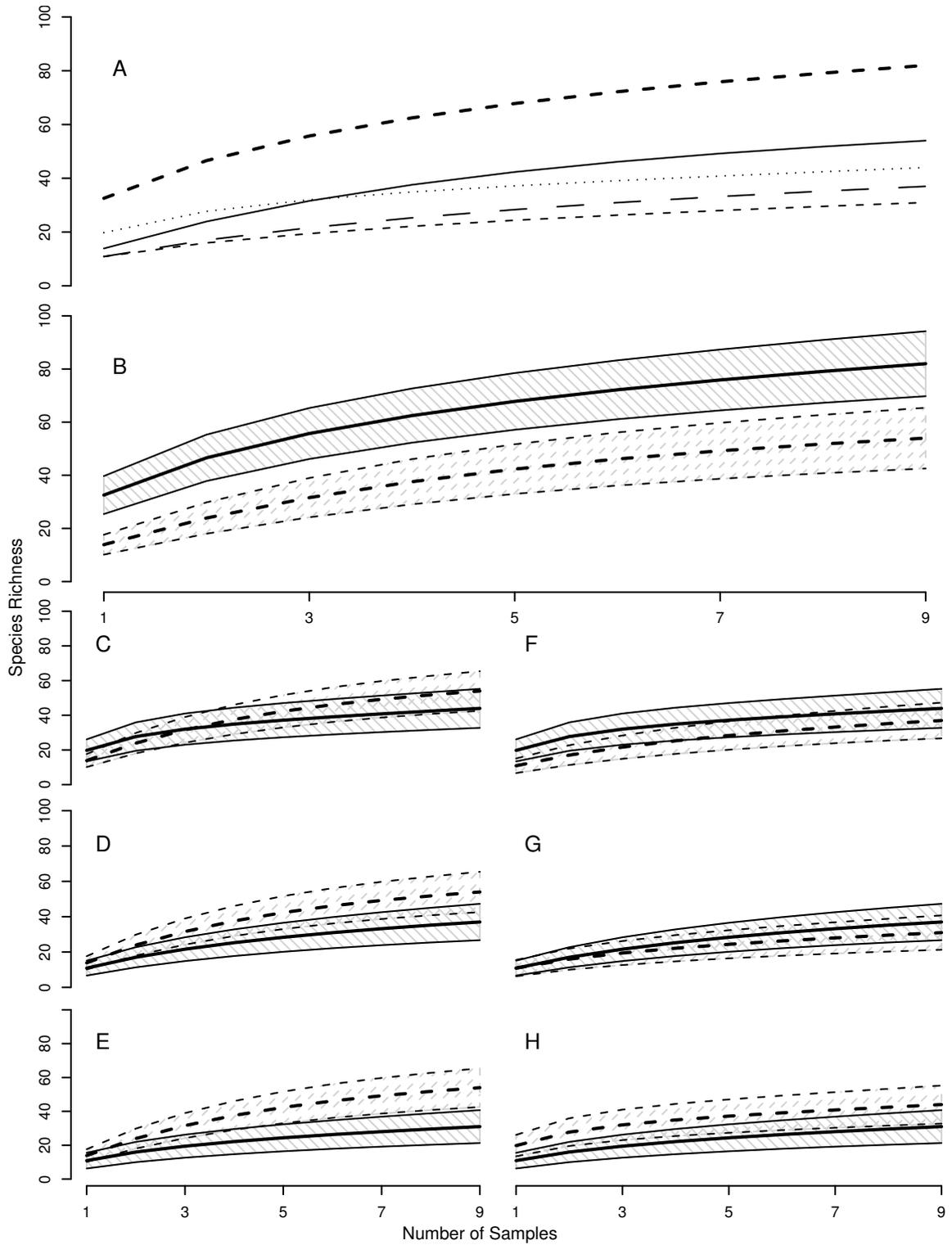
Appendix 2: Comparisons of Atlantis Sand Fynbos species accumulation curves at 0.1 m² : **A**) Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B**) ML (dashed-lines) vs. CF (solid lines); **C**) ML (dashed-lines) vs. LF (solid lines); **D**) ML (dashed-lines) vs. MF (solid lines); **E**) ML (dashed-lines) vs. SF (solid lines); **F**) MF (dashed-lines) vs. LF (solid lines); **G**) SF (dashed-lines) vs. MF (solid lines); and **H**) LF (dashed-lines) vs. SF (solid lines).



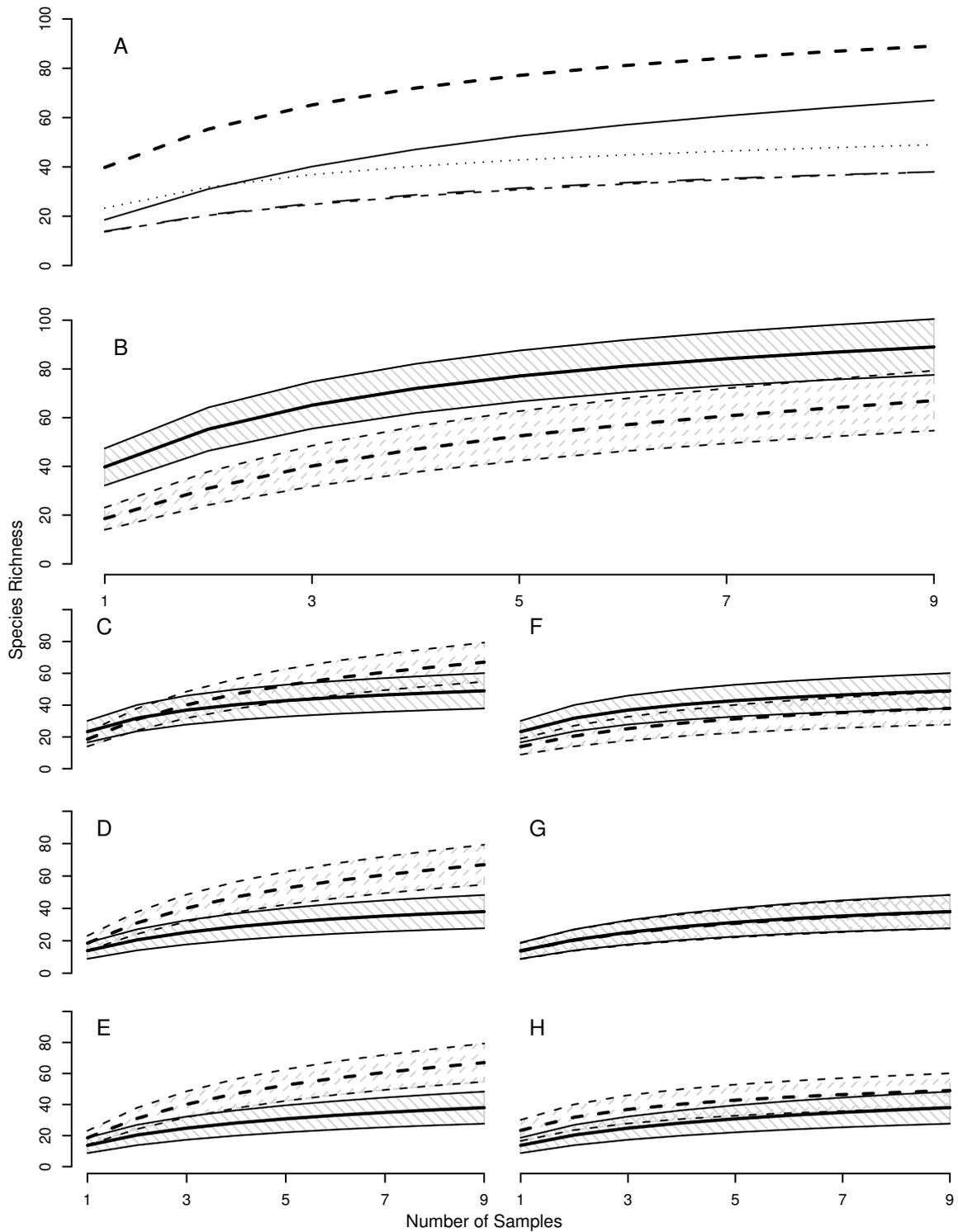
Appendix 3: Comparisons of Atlantis Sand Fynbos species accumulation curves at 1 m² : **A**) Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B**) ML (dashed-lines) vs. CF (solid lines); **C**) ML (dashed-lines) vs. LF (solid lines); **D**) ML (dashed-lines) vs. MF (solid lines); **E**) ML (dashed-lines) vs. SF (solid lines); **F**) MF (dashed-lines) vs. LF (solid lines); **G**) SF (dashed-lines) vs. MF (solid lines); and **H**) LF (dashed-lines) vs. SF (solid lines).



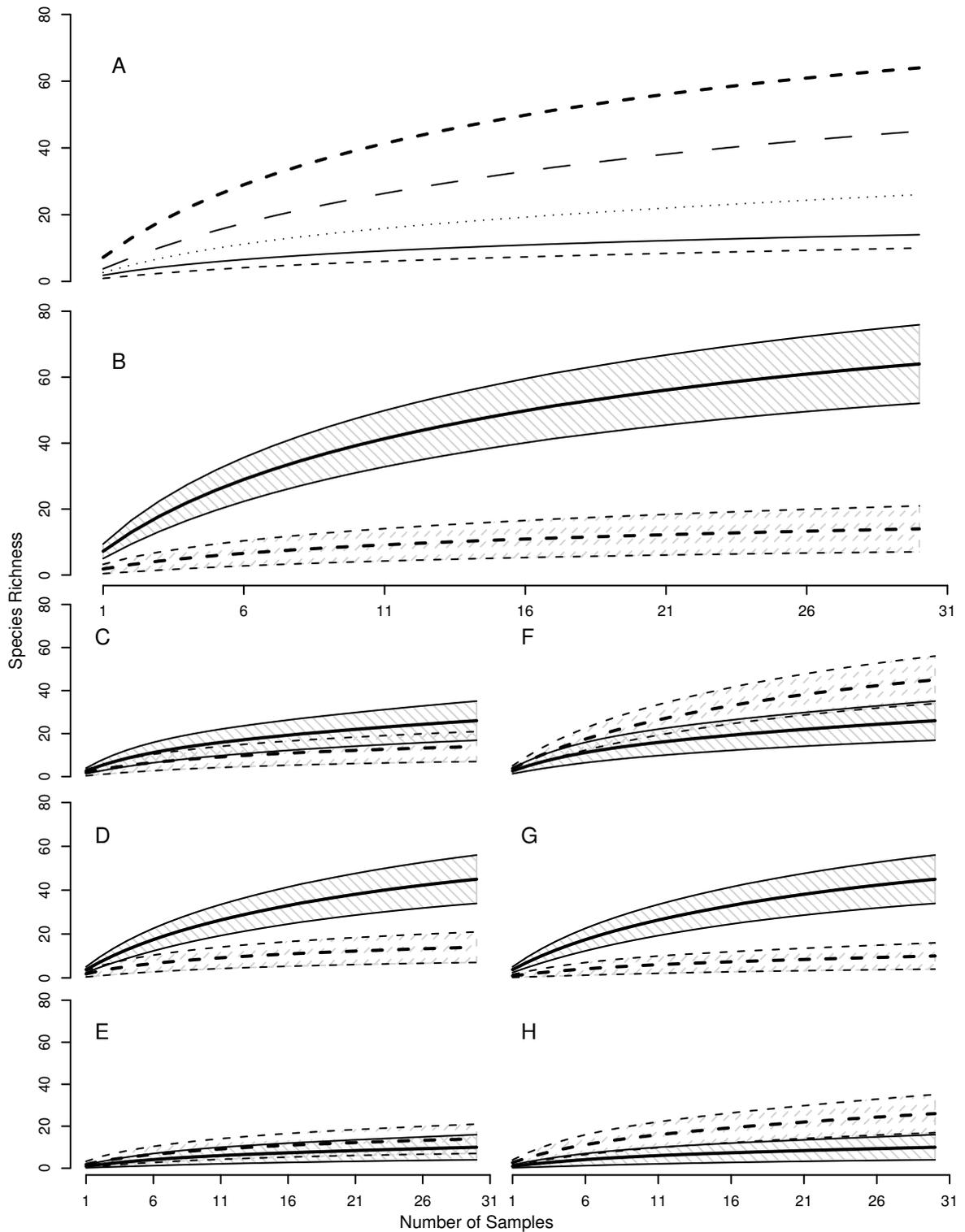
Appendix 4: Comparisons of Atlantis Sand Fynbos species accumulation curves at 50 m² : **A**) Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B**) ML (dashed-lines) vs. CF (solid lines); **C**) ML (dashed-lines) vs. LF (solid lines); **D**) ML (dashed-lines) vs. MF (solid lines); **E**) ML (dashed-lines) vs. SF (solid lines); **F**) MF (dashed-lines) vs. LF (solid lines); **G**) SF (dashed-lines) vs. MF (solid lines); and **H**) LF (dashed-lines) vs. SF (solid lines).



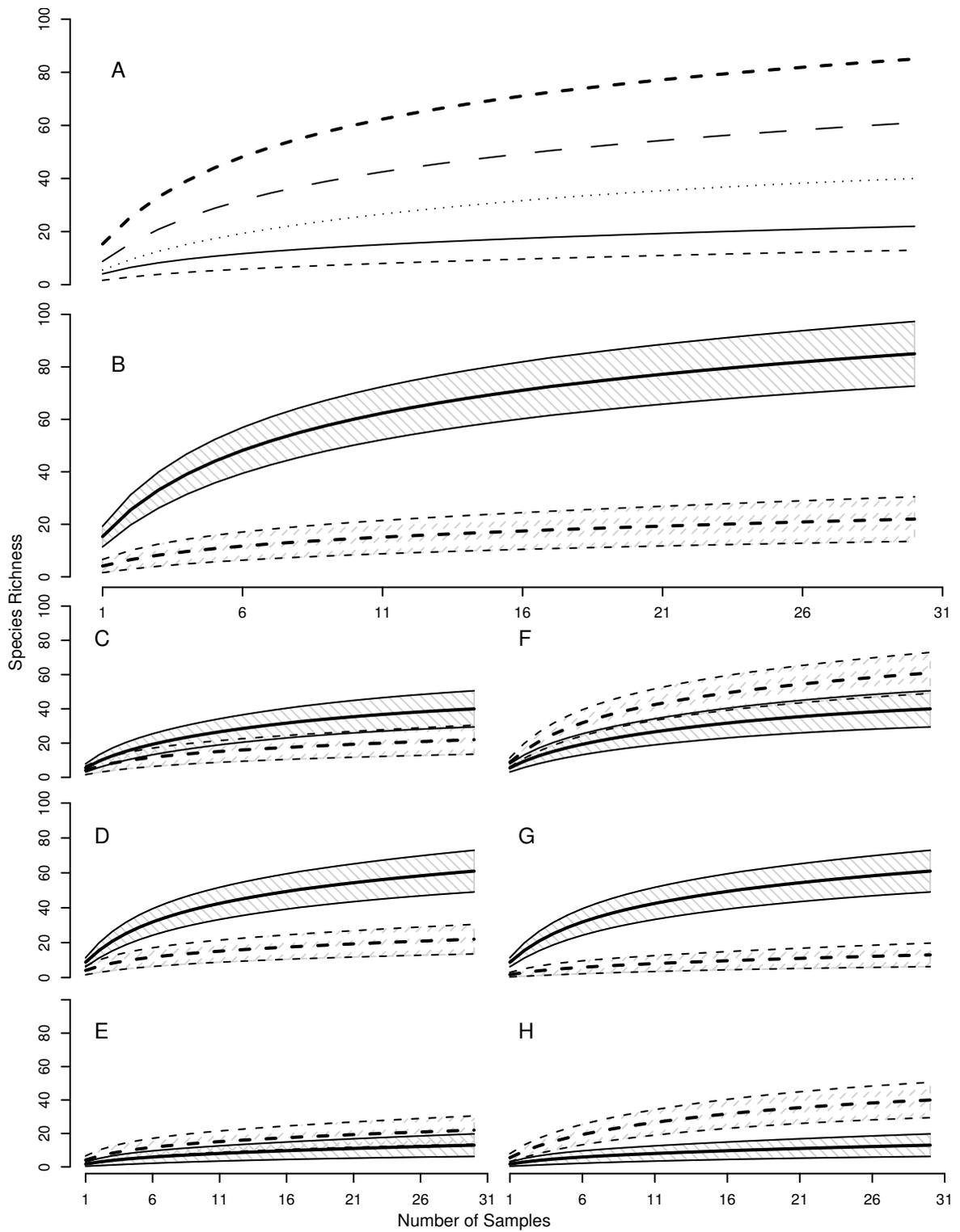
Appendix 5: Comparisons of Atlantis Sand Fynbos species accumulation curves at 100 m² : **A**) Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B**) ML (dashed-lines) vs. CF (solid lines); **C**) ML (dashed-lines) vs. LF (solid lines); **D**) ML (dashed-lines) vs. MF (solid lines); **E**) ML (dashed-lines) vs. SF (solid lines); **F**) MF (dashed-lines) vs. LF (solid lines); **G**) SF (dashed-lines) vs. MF (solid lines); and **H**) LF (dashed-lines) vs. SF (solid lines).



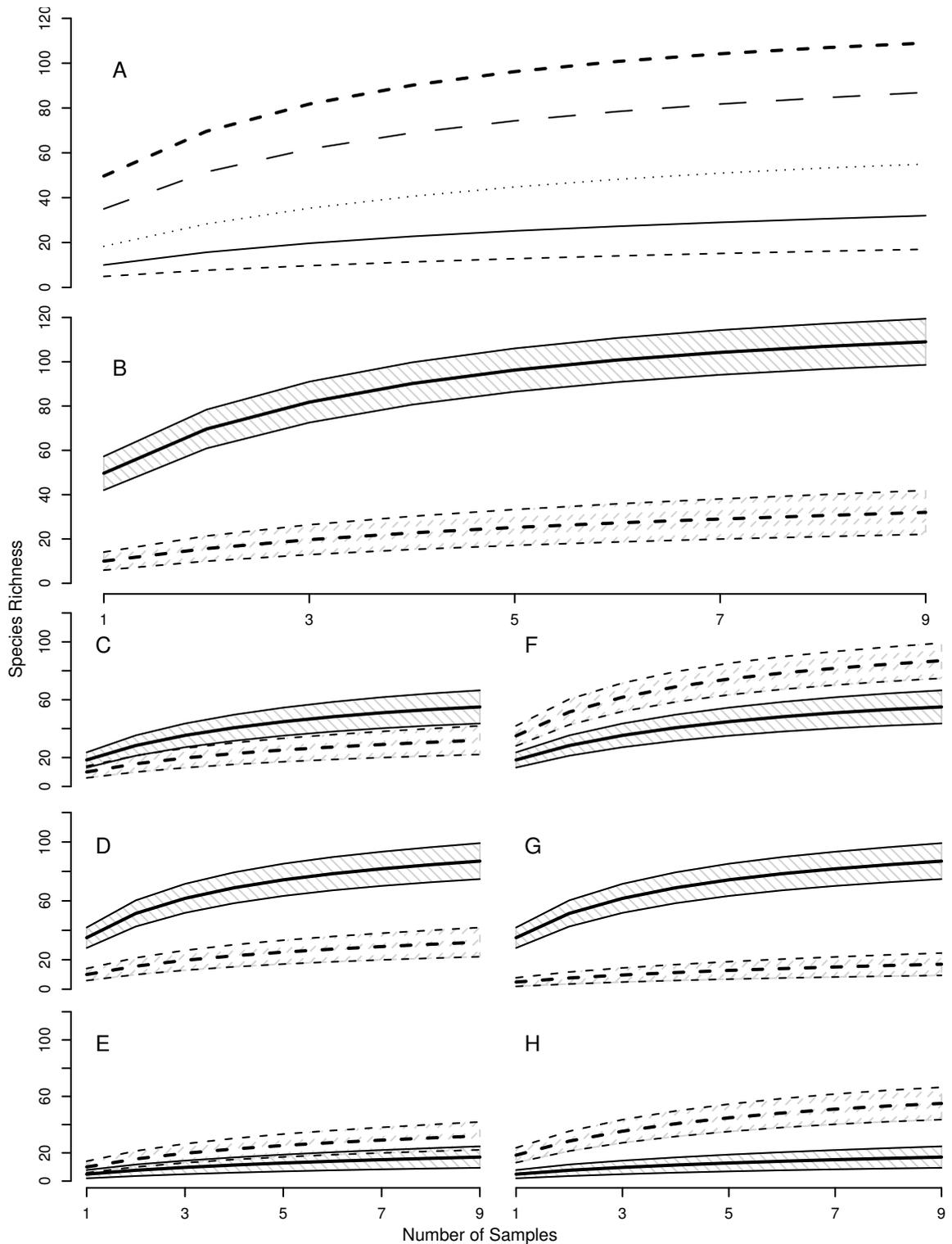
Appendix 6: Comparisons of Swartland Shale Renosterveld species accumulation curves at 0.1 m² : **A)** Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B)** ML (dashed-lines) vs. CF (solid lines); **C)** ML (dashed-lines) vs. LF (solid lines); **D)** ML (dashed-lines) vs. MF (solid lines); **E)** ML (dashed-lines) vs. SF (solid lines); **F)** MF (dashed-lines) vs. LF (solid lines); **G)** SF (dashed-lines) vs. MF (solid lines); and **H)** LF (dashed-lines) vs. SF (solid lines).



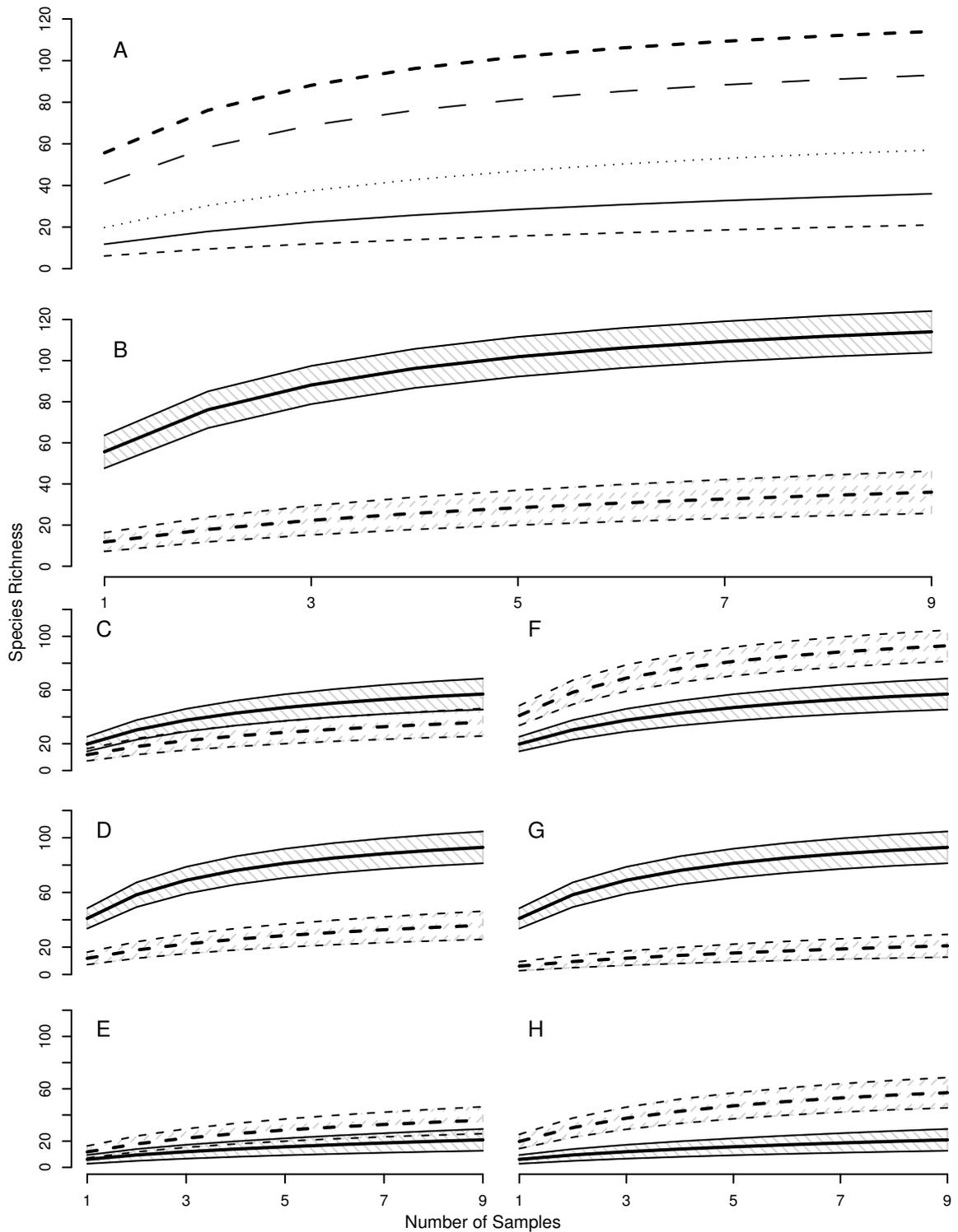
Appendix 7: Comparisons of Swartland Shale Renosterveld species accumulation curves at 1 m² : **A**) Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B**) ML (dashed-lines) vs. CF (solid lines); **C**) ML (dashed-lines) vs. LF (solid lines); **D**) ML (dashed-lines) vs. MF (solid lines); **E**) ML (dashed-lines) vs. SF (solid lines); **F**) MF (dashed-lines) vs. LF (solid lines); **G**) SF (dashed-lines) vs. MF (solid lines); and **H**) LF (dashed-lines) vs. SF (solid lines).



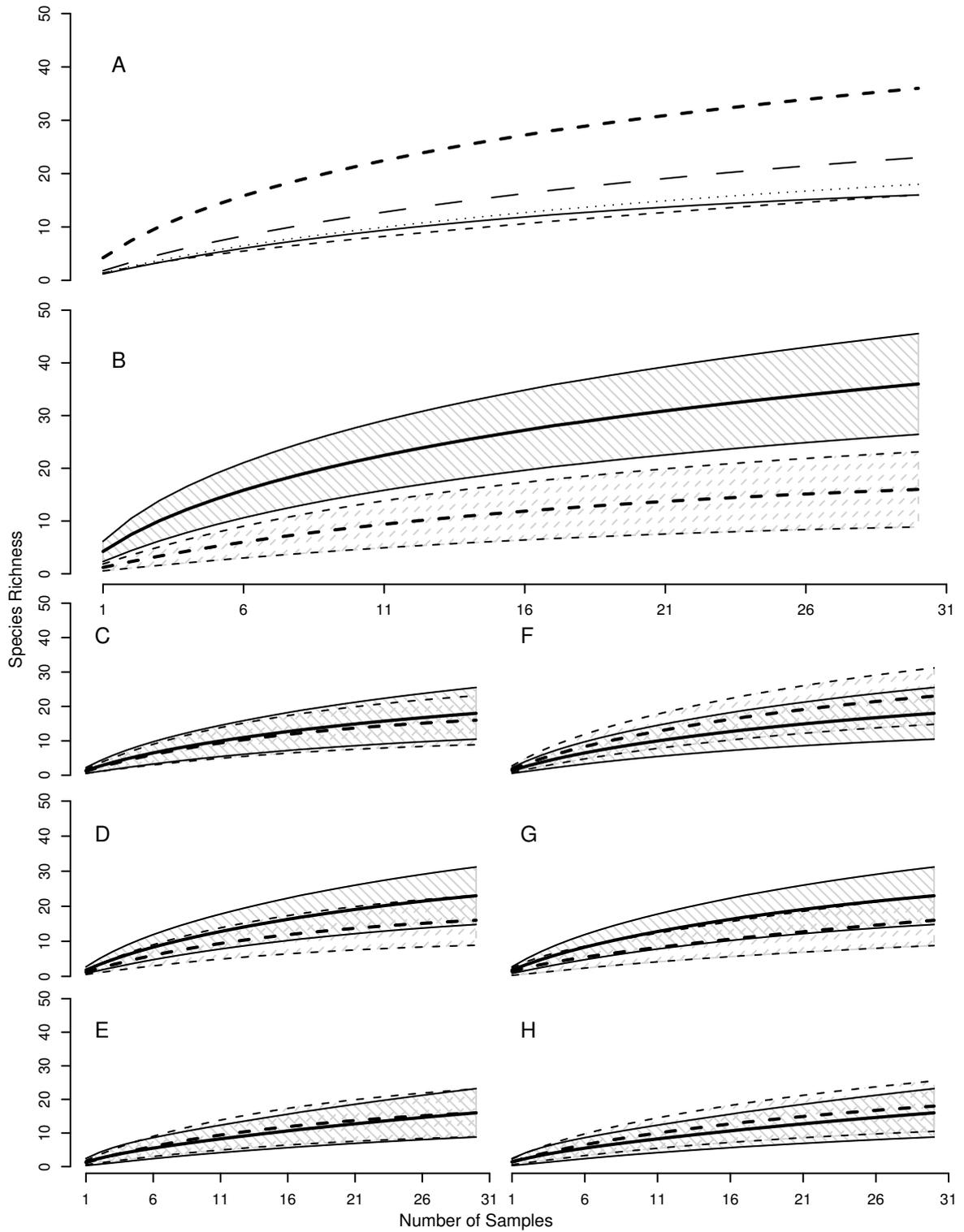
Appendix 8: Comparisons of Swartland Shale Renosterveld species accumulation curves at 50 m² : **A)** Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B)** ML (dashed-lines) vs. CF (solid lines); **C)** ML (dashed-lines) vs. LF (solid lines); **D)** ML (dashed-lines) vs. MF (solid lines); **E)** ML (dashed-lines) vs. SF (solid lines); **F)** MF (dashed-lines) vs. LF (solid lines); **G)** SF (dashed-lines) vs. MF (solid lines); and **H)** LF (dashed-lines) vs. SF (solid lines).



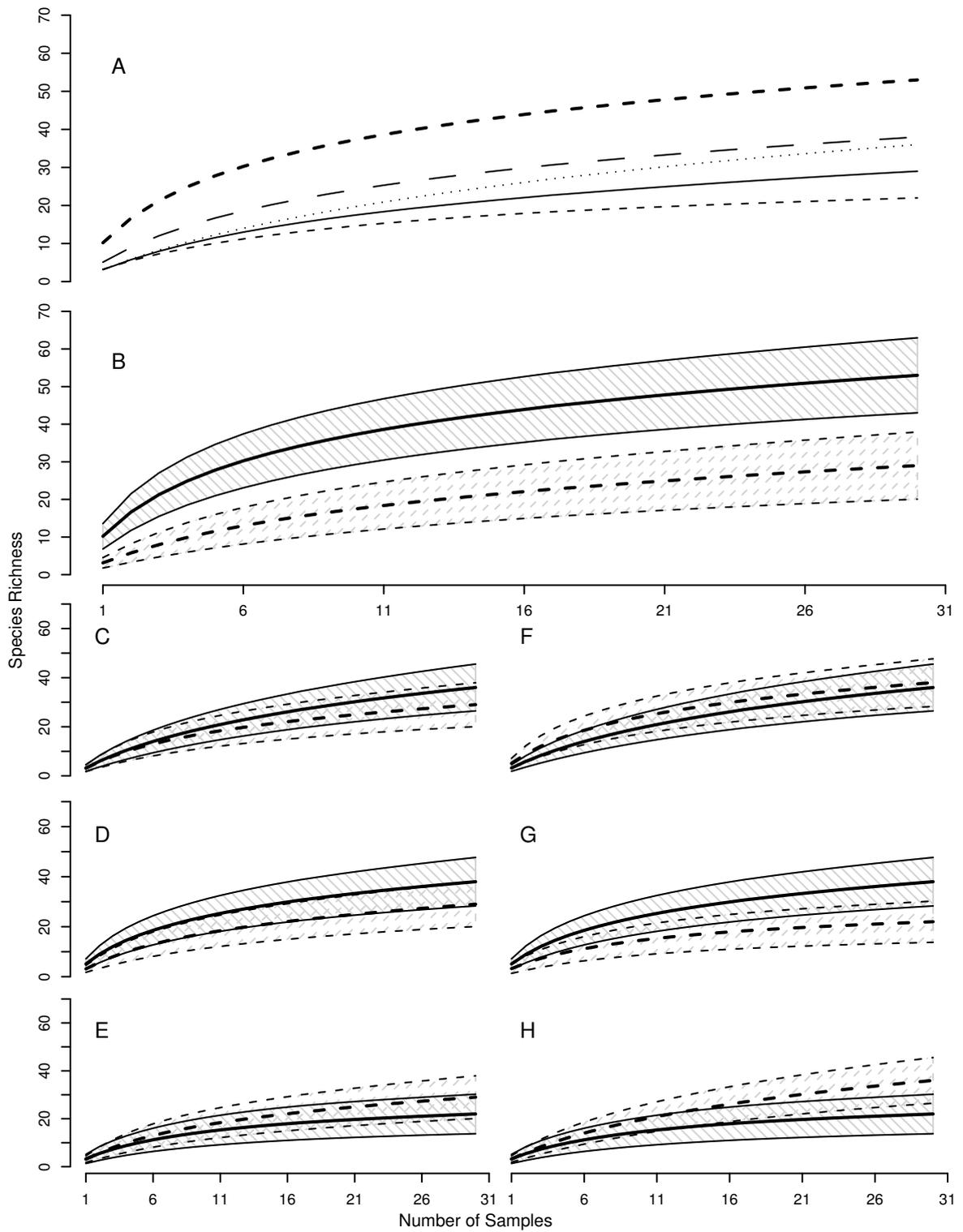
Appendix 9: Comparisons of Swartland Shale Renosterveld species accumulation curves at 100 m² : **A)** Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B)** ML (dashed-lines) vs. CF (solid lines); **C)** ML (dashed-lines) vs. LF (solid lines); **D)** ML (dashed-lines) vs. MF (solid lines); **E)** ML (dashed-lines) vs. SF (solid lines); **F)** MF (dashed-lines) vs. LF (solid lines); **G)** SF (dashed-lines) vs. MF (solid lines); and **H)** LF (dashed-lines) vs. SF (solid lines).



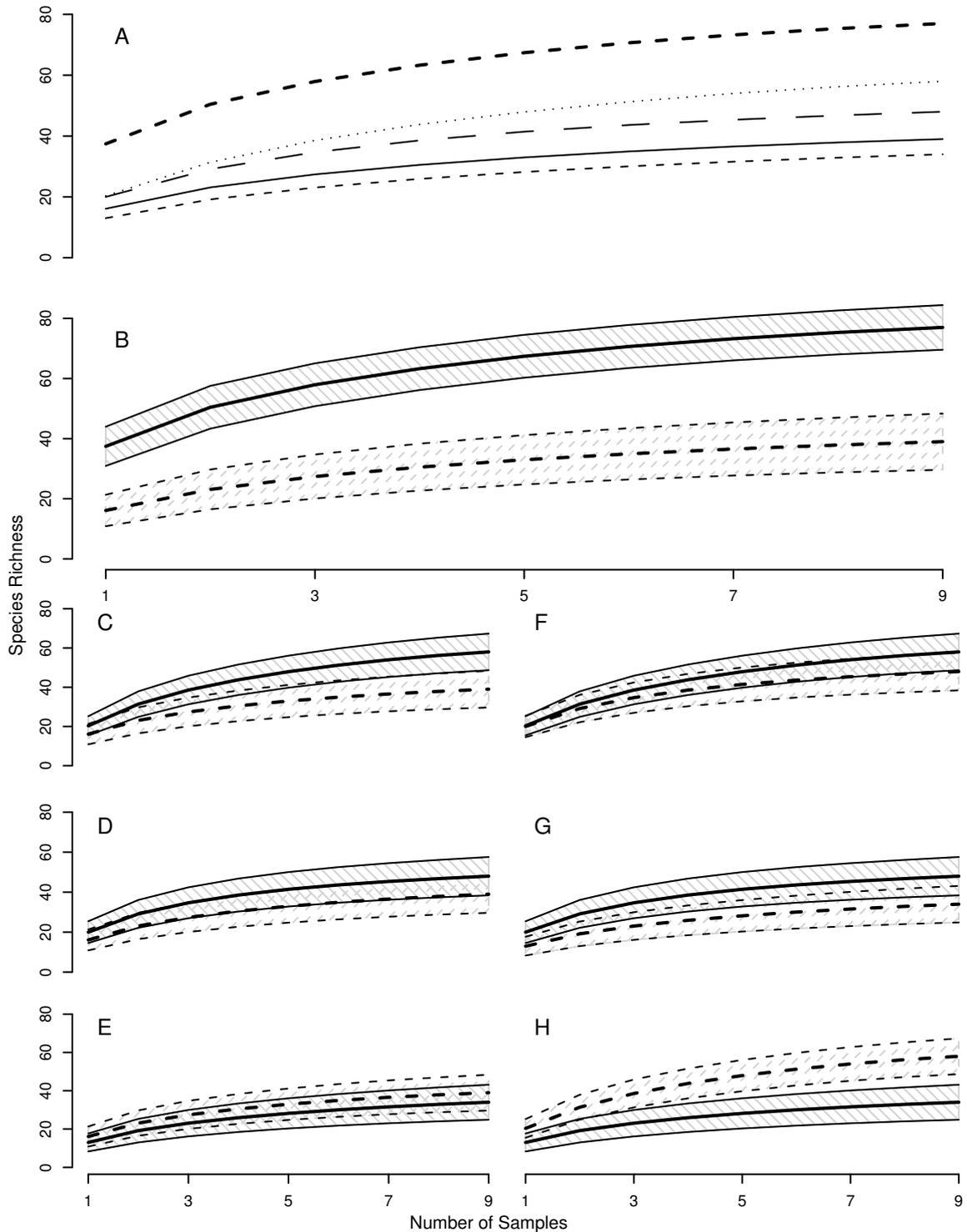
Appendix 10: Comparisons of Langebaan Dune Strandveld species accumulation curves at 0.1 m²: **A)** Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B)** ML (dashed-lines) vs. CF (solid lines); **C)** ML (dashed-lines) vs. LF (solid lines); **D)** ML (dashed-lines) vs. MF (solid lines); **E)** ML (dashed-lines) vs. SF (solid lines); **F)** MF (dashed-lines) vs. LF (solid lines); **G)** SF (dashed-lines) vs. MF (solid lines); and **H)** LF (dashed-lines) vs. SF (solid lines).



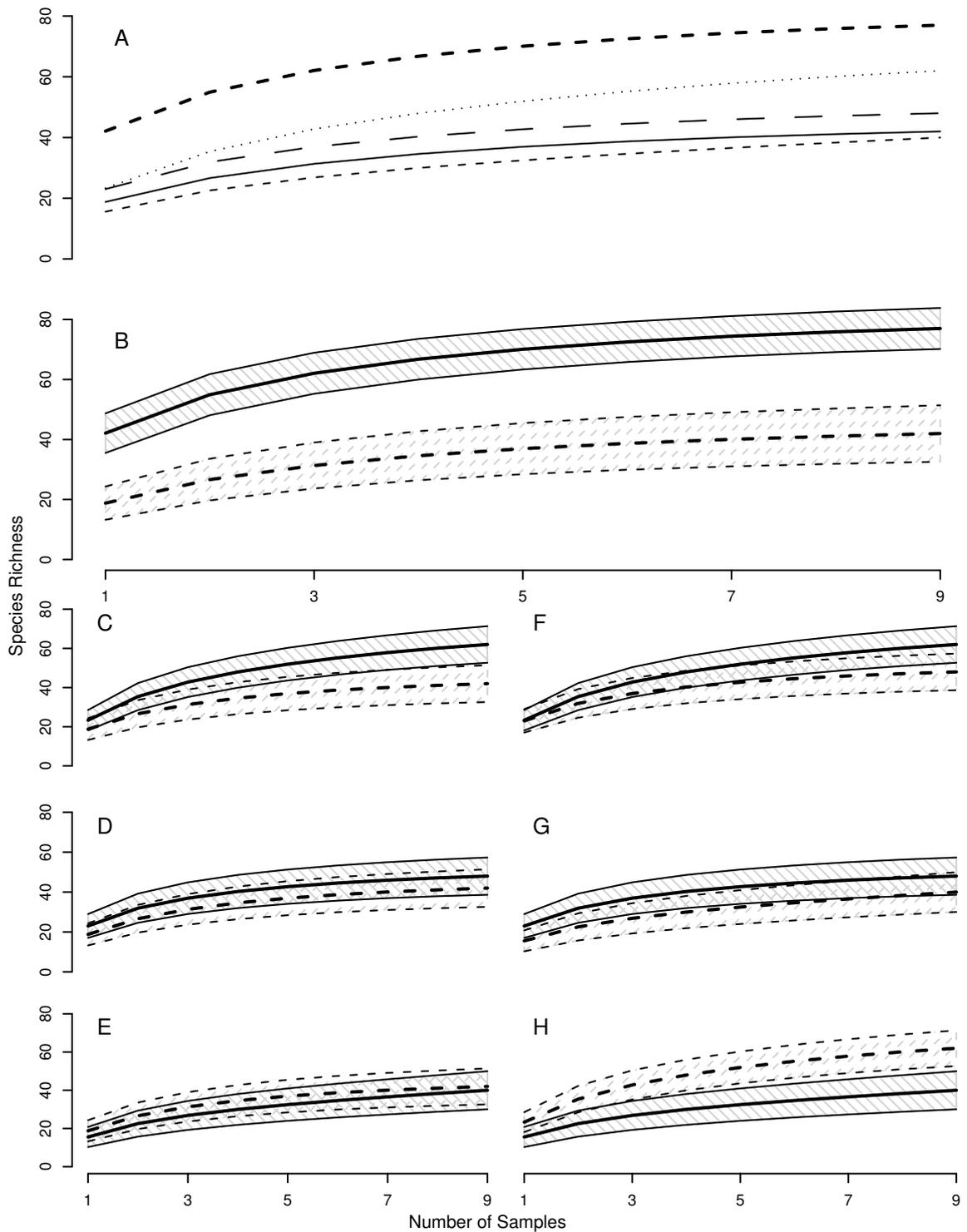
Appendix 11: Comparisons of Langebaan Dune Strandveld species accumulation curves at 1 m²: **A**) Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B**) ML (dashed-lines) vs. CF (solid lines); **C**) ML (dashed-lines) vs. LF (solid lines); **D**) ML (dashed-lines) vs. MF (solid lines); **E**) ML (dashed-lines) vs. SF (solid lines); **F**) MF (dashed-lines) vs. LF (solid lines); **G**) SF (dashed-lines) vs. MF (solid lines); and **H**) LF (dashed-lines) vs. SF (solid lines).



Appendix 12: Comparisons of Langebaan Dune Strandveld species accumulation curves at 50 m²: **A)** Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B)** ML (dashed-lines) vs. CF (solid lines); **C)** ML (dashed-lines) vs. LF (solid lines); **D)** ML (dashed-lines) vs. MF (solid lines); **E)** ML (dashed-lines) vs. SF (solid lines); **F)** MF (dashed-lines) vs. LF (solid lines); **G)** SF (dashed-lines) vs. MF (solid lines); and **H)** LF (dashed-lines) vs. SF (solid lines).



Appendix 13: Comparisons of Langebaan Dune Strandveld species accumulation curves at 100 m²: **A)** Overview: ML (solid line), CF (bold dashed-line), LF (dotted line), MF (broken line), and SF (regular dashed-line); **B)** ML (dashed-lines) vs. CF (solid lines); **C)** ML (dashed-lines) vs. LF (solid lines); **D)** ML (dashed-lines) vs. MF (solid lines); **E)** ML (dashed-lines) vs. SF (solid lines); **F)** MF (dashed-lines) vs. LF (solid lines); **G)** SF (dashed-lines) vs. MF (solid lines); and **H)** LF (dashed-lines) vs. SF (solid lines).



Appendix 14: Significant results of PFT diversity based on the effective number of species for the Gini-Simpson Index

a) Diversity of the eight objectively defined PFTs

Atlantis Sand Fynbos

There were no significant results at the 0.2 m x 0.5 m and 5 m x 10 m scales (data not shown).

At the 1 m x 1 m scale, PFT diversity differed significantly with fragment size (Kruskal-Wallis ANOVA: $H_{3,120} = 9.003721$, $p = 0.0292$).

- The largest fragment was higher in PFT diversity than the medium-sized and smallest fragments (Mann-Whitney $U = 2.592631$, $p = 0.0095$) and (Mann-Whitney $U = 2.255049$, $p = 0.02413$) respectively.

At the 10 m x 10 m scale, PFT diversity also differed significantly with fragment size (One-way ANOVA: $F_{3,32} = 3.5187$, $p = 0.02602$)

- The post hoc (Bonferroni) test showed that the mainland was slightly more diverse in PFT than the smallest fragment ($MS = 0.42705$, $df = 32$, $p = 0.025384$)
- The mainland was also more diverse in PFT than the combined fragments ($t = 2.770404$, $df = 34$, $p = 0.009008$).

Swartland Shale Renosterveld

PFT diversity differed significantly with fragment size at all the four scales based on both the effective number of species per PFT for the Gini-Simpson Index.

At the 0.2 m x 0.5 m scale, PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,111} = 33.37729$, $p < 0.00001$).

- The mainland was less diverse in PFT than the largest and medium-sized fragments (Mann-Whitney $U = -2.95318$, $p = 0.003145$), and (Mann-Whitney $U = -3.07274$, $p = 0.002121$), respectively.
- The mainland was also slightly less diverse in PFT than the combined fragments (Mann-Whitney $U = -1.97067$, $p = 0.048763$).
- The largest and medium-sized fragments were much more diverse in PFT than the smallest fragment (Mann-Whitney $U = 4.626252$, $p < 0.00001$) and (Mann-Whitney $U = 5.052648$, $p < 0.00001$), respectively.

Results at the 1 m x 1 m scale were also significant (Kruskal-Wallis ANOVA: $H_{3,118} = 57.02758$, $p < 0.00001$)

- PFT diversity was lower in the mainland than in the largest and medium-sized fragments (Mann-Whitney $U = -3.42727$, $p = 0.000610$) and (Mann-Whitney $U = -4.23583$, $p = 0.000023$) respectively but,
- The mainland was more diverse in PFT than the smallest fragment (Mann-Whitney $U = 3.323227$, $p = 0.000890$).

- The largest and medium-sized fragments were also much more diverse in PFT diversity than the smallest fragment (Mann-Whitney $U = 5.764940$, $p < 0.00001$) and (Mann-Whitney $U = 6.478110$, $p < 0.00001$) respectively.

At the 5 m x 10 m scale, PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 15.82089$, $p = 0.0012$).

- The mainland was slightly more diverse in PFT than the smallest fragment (Mann-Whitney $U = 2.386622$, $p = 0.017005$),
- The largest and medium-sized fragments were also much more diverse in PFT than the smallest fragment (Mann-Whitney $U = 3.003824$, $p = 0.002666$) and (Mann-Whitney $U = 3.445562$, $p = 0.000570$) respectively.

Results at the 10 m x 10 m scale were also significant (Kruskal-Wallis ANOVA: $H_{3,36} = 16.09116$, $p = 0.0011$).

- PFT diversity was higher in the mainland than in the smallest fragment (Mann-Whitney $U = 2.297042$, $p = 0.021617$),
- PFT diversity was higher in the largest and medium-sized fragments than in the smallest one (Mann-Whitney $U = 3.003824$, $p = 0.002666$) and (Mann-Whitney $U = 3.445562$, $p = 0.000570$), respectively.

Langebaan Dune Strandeveld

In Langebaan Dune Strandeveld, PFT diversity did not differ significantly with fragment size at the all four scales (data not shown).

b) Diversity of the 19 subjectively defined PFTs

Atlantis Sand Fynbos

At the 0.2 m x 0.5m scale, PFT diversity based on the effective number of species for the Gini-Simpson Index did not differ significantly with fragment size (details not shown).

At the 1 m x 1 m scale, PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,120} = 22.31807$, $p = 0.0001$).

- PFT diversity was significantly higher in the mainland than in the medium-sized fragment (Mann-Whitney $U = 4.134507$, $p = 0.000036$), the smallest fragment (Mann-Whitney $U = 3.143414$, $p = 0.001670$) and in the combined fragments (Mann-Whitney $U = 3.699910$, $p = 0.000216$), respectively.
- PFT diversity was also higher in the largest fragment than in the medium-sized one (Mann-Whitney $U = 3.129965$, $p = 0.001748$).

At the 5 m x 10 m scale, PFT diversity differed slightly between the mainland and the three fragments (One-way ANOVA: $F_{3,32} = 2.9238$, $p = 0.04880$).

- The Bonferroni test showed that the mainland was slightly more diverse in PFT than the medium-sized fragment ($MS = 1.2660$, $df = 32$, $p = 0.044018$).
- The t-test showed that PFT diversity was marginally higher in the mainland than in the combined fragments ($t = 2.014468$, $df = 34$, $p = 0.05$).

At the 10 m x 10 m scale, PFT diversity differed with fragment size (One-way ANOVA: $F_{3,32} = 3.4149$, $p = 0.02900$).

- The post hoc test revealed that PFT diversity was slightly higher in the mainland than in the medium-sized fragment ($MS = 2.6111$, $df = 32$, $p = 0.038448$) and,
- The t-test also showed that PFT diversity was higher in the mainland and than in the combined fragments ($t = 2.230768$, $df = 34$, $p = 0.032400$).

Swartland Shale Renosterveld

In Swartland Shale Renosterveld, PFT diversity based on the effective number of species for the Gini-Simpson Index differed very significantly with fragment size at all four scales, for the 19 subjectively defined PFTs.

At the 0.2 m x 0.5 m scale, the result obtained was highly significant: (Kruskal-Wallis ANOVA: $H_{3,111} = 44.90176$, $p < 0.00001$).

- The mainland was less diverse in PFT than in the largest and medium-sized fragments (Mann-Whitney $U = -2.95868$, $p = 0.003090$), and (Mann-Whitney $U = -4.63514$, $p < 0.00001$) respectively,
- The mainland was also less diverse in PFT than the the combined fragments (Mann-Whitney $U = -2.58926$, $p = 0.009619$),
- The mainland was more diverse than in the smallest fragment (Mann-Whitney $U = 2.731809$, $p = 0.006299$),
- The largest and medium-sized fragments were both much more diverse in PFT than the smallest one (Mann-Whitney $U = 4.535826$, $p < 0.00001$), and (Mann-Whitney $U = 5.669375$, $p < 0.00001$) respectively.

At the 1 m x 1 m scale, the result was also highly significant (Kruskal-Wallis ANOVA: $H_{3,118} = 65.21664$, $p < 0.00001$).

- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -5.07293$, $p < 0.00001$) but,
- Much higher in the mainland than the smallest fragment (Mann-Whitney $U = 5.132248$, $p < 0.00001$).
- PFT diversity was also lower in the largest fragment than in the medium-sized one (Mann-Whitney (Mann-Whitney $U = -3.19168$, $p = 0.001415$) but,
- Much higher in the largest fragment than in the smallest one (Mann-Whitney $U = 5.489016$, $p < 0.00001$),
- PFT diversity was much higher in the medium-sized fragment than in the smallest one (Mann-Whitney $U = 6.392610$, $p < 0.00001$).

At the 5 m x 10 m scale, PFT diversity also differed significantly with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 31.83312$, $p < 0.00001$).

- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -3.59189$, $p = 0.000328$), and also
- Lower in the largest fragment than in the medium-sized one (Mann-Whitney $U = -3.47392$, $p = 0.000513$),
- PFT diversity was higher in the largest and medium-sized fragments than in the smallest one (Mann-Whitney $U = -3.597657$, $p = 0.000321$) and (Mann-Whitney $U = 3.611215$, $p = 0.000305$) respectively.

Results at the 10 m x 10 m scale were equally highly significant (Kruskal-Wallis ANOVA: $H_{3,36} = 30.87005$, $p < 0.00001$).

- The mainland was less diverse in PFT than the largest and medium-sized fragments (Mann-Whitney $U = -2.56196$, $p = 0.010409$), and (Mann-Whitney $U = -3.58045$, $p = 0.000343$), respectively,
- The largest and medium-sized fragments were both much more diverse in PFT than in the smallest one (Mann-Whitney $U = -3.617072$, $p = 0.000298$), and (Mann-Whitney $U = 3.628874$, $p = 0.000285$), respectively,
- The largest fragment was less diverse in PFT diversity than the medium-sized fragment (Mann-Whitney $U = -3.57666$, $p = 0.000348$).

Langebaan Dune Strandveld

In Langebaan Dune Strandveld PFT diversity also differed with fragment size at all four scales.

At the smallest scale (0.2 m x 0.5 m), the result was (Kruskal-Wallis ANOVA: $H_{3,116} = 8.988464$, $p = 0.0294$):

- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -2.45726$, $p = 0.014001$), and also
- Lower in the largest fragment than in the medium-sized one (Mann-Whitney $U = -2.41205$, $p = 0.015864$).

At the 1 m x 1 m scale, the result was also significant (Kruskal-Wallis ANOVA: $H_{3,120} = 20.69605$, $p = 0.0001$):

- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -4.02390$, $p = 0.000057$), and
- Slightly lower in the mainland than in the combined fragments (Mann-Whitney $U = -2.50337$, $p = 0.012302$),
- PFT diversity was lower in the largest than in the medium-sized fragment (Mann-Whitney $U = -3.12882$, $p = 0.001755$),
- The medium-sized fragment was more diverse in PFT than the smallest fragment (Mann-Whitney $U = 3.551137$, $p = 0.000384$).

At the 5 m x 10 m scale, PFT diversity differed with fragment size (One-way ANOVA: $F_{3,32} = 6.7204$, $p = 0.00121$): The post hoc test revealed that,

- PFT diversity was higher in the largest than in the smallest fragment ($MS = 2.5833$, $df = 32$, $p = 0.011760$) and,
- Higher in the medium-sized fragment than in the smallest one ($MS = 2.5833$, $df = 32$, $p = 0.002355$).

Results at the 10 m x 10 m scale were also significant (Kruskal-Wallis ANOVA: $H_{3,36} = 12.67994$, $p = 0.0054$):

- PFT diversity was slightly lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -2.02152$, $p = 0.043227$), and
- Slightly higher in the largest and medium-sized fragments than in the smallest one (Mann-Whitney $U = 2.431023$, $p = 0.015057$) and (Mann-Whitney $U = 2.984085$, $p = 0.002844$) respectively.

Appendix 15: Significant results of PFT diversity based on the Shannon-Wiener Index and the effective number of species

a) Diversity of the eight objectively defined PFTs

Atlantis Sand Fynbos results

At the 0.2 m x 0.5 m and 5 m x 10 m scales, PFT diversity did not differ significantly with fragment size in Atlantis Sand Fynbos for both the Shannon-Wiener Index and the effective number of species per PFT (statistics not shown).

At the 1 m x 1 m scale, PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,120} = 9.464408$, $p = 0.0237$ for both the Shannon-Wiener Index and the effective number of species):

- PFT diversity was slightly higher in the largest fragment than in the medium-sized one (Mann-Whitney $U = 2.547930$, $p = 0.010837$), and
- Also higher in the largest fragment than in the smallest one (Mann-Whitney $U = 2.210098$, $p = 0.027099$).

At the 10 m x 10 m scale, PFT diversity also differed with fragment size (One-way ANOVA: $F_{3,32} = 6.6037$, $p = 0.00134$, for the Shannon-Wiener Index). The Bonferroni test revealed that:

- PFT diversity was higher in the mainland than in the medium-sized fragment (MS = 0.01548, $df = 32$, $p = 0.017978$), and
- Also higher in the mainland than in the smallest fragment (MS = 0.01548, $df = 32$, $p = 0.001670$).

Similarly, PFT diversity differed significantly with fragment size based on the effective number of species per PFT (One-way ANOVA: $F_{3,32} = 7.2512$, $p = 0.00076$):

- The post hoc test showed that PFT diversity was higher in the mainland than in the medium-sized fragment (MS = 0.34844, $df = 32$, $p = 0.010815$), and
- Also higher in the mainland than in the smallest fragment (MS = 0.34844, $df = 32$, $p = 0.000870$).
- PFT diversity was significantly higher in the mainland than in the combined fragments ($t = 3.352007$, $df = 34$, $p = 0.001978$ for both the Shannon-Wiener Index, and $t = 3.600317$, $df = 34$, $p = 0.001001$ based on the effective number of species).

Swartland Shale Renosterveld results

At the 0.2 m x 0.5 m scale in Swartland Shale Renosterveld, PFT diversity differed very significantly with fragment size (Kruskal-Wallis ANOVA: $H_{3,111} = 33.75110$, $p < 0.00001$ for both the Shannon-Wiener Index and the effective number of species):

- PFT diversity was slightly lower in the mainland than in the combined fragments (Mann-Whitney $U = -2.00798$, $p = 0.044646$ based on the Shannon-Wiener Index), but was not significantly different (Mann-Whitney $U = -1.86667$, $p = 0.061948$ based on the effective number of species per PFT).
- PFT diversity was lower in the mainland than in the largest fragment (Mann-Whitney $U = -2.95318$, $p = 0.003145$ based on the Shannon-Wiener Index), and (Mann-Whitney $U = -2.83743$, $p = 0.004548$, based on the effective number of species per PFT).
- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -3.16990$, $p = 0.001525$ for the Shannon-Wiener Index), and (Mann-Whitney $U = -3.03935$, $p = 0.002371$ based on the effective number of species per PFT).

- PFT diversity was slightly higher in the mainland than in the smallest fragment (Mann-Whitney U = 2.523870, p = 0.011608, based on the Shannon-Wiener Index), and (Mann-Whitney U = 2.601615, p = 0.009279, based on the effective number of species per PFT).
- Based on both the Shannon-Wiener Index and the effective number of species, PFT diversity was much higher in the largest fragment than in the smallest one (Mann-Whitney U = 4.626252, p < 0.00001), and
- Also higher in the medium-sized than in the smallest fragment (Mann-Whitney U = 5.069664, p < 0.00001).

At the 1 m x 1 m scale, results based on both the Shannon-Wiener Index and the effective number of species per PFT showed that PFT differed very significantly with fragment size (Kruskal-Wallis ANOVA: $H_{3,118} = 59.29119$, p < 0.00001):

- PFT diversity was significantly lower in the mainland than in the largest fragment (Mann-Whitney U = -3.63381, p = 0.000279), and
- Lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -4.50907, p < 0.00001).
- PFT diversity was much higher in the mainland than in the smallest fragment (Mann-Whitney U = 3.323227, p = 0.000890).
- The mainland was also slightly lower in PFT diversity than the combined fragments (Mann-Whitney U = -2.13025, p = 0.033152).
- The largest and medium-sized fragments were much more diverse in PFT than the smallest fragment (Mann-Whitney U = 5.816666, p < 0.00001) and (Mann-Whitney U = 6.477700, p < 0.00001) respectively.

At the 5 m x 10 m, PFT diversity also varied with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 20.12371$, p = 0.0002 for both the Shannon-Wiener Index and the effective number of species).

- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -2.64906, p = 0.008072), but
- Slightly higher in the mainland than in the smallest fragment (Mann-Whitney U = 2.562085, p = 0.010405), for both the Shannon-Wiener Index and the effective number of species.
- PFT diversity was higher in the largest and medium-sized fragments than in the smallest one (Mann-Whitney U = 3.092171, p = 0.001987) and (Mann-Whitney U = 3.533910, p = 0.000410) respectively.

At the 10 m x 10 m scale, the results were the also the also the same for both the Shannon-Wiener Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,36} = 20.24184$, p = 0.0002).

- PFT diversity was slightly lower in the mainland than in the largest fragment (Mann-Whitney U = -2.20755, p = 0.027276),
- Lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -2.29586, p = 0.021685), but
- Slightly higher in the mainland than in the smallest fragment (Mann-Whitney U = 2.562085, p = 0.010405).
- PFT diversity was significantly higher in the largest and medium-sized fragments than in the smallest one (Mann-Whitney U = 3.180519, p = 0.001470) and (Mann-Whitney U = 3.533910, p = 0.000410) respectively.

Langebaan Dune Strandveld results

At the 0.2 m x 0.5 m scale, although PFT diversity did not differ significantly with fragment size in Langebaan Dune Strandveld (Kruskal-Wallis ANOVA: $H_{3,116} = 4.403385$, p = 0.2211), the Mann-Whitney U test showed that

- PFT diversity was slightly lower in the mainland than in the medium-sized fragment (Mann-Whitney $U = -1.99056$, $p = 0.046530$ for both the Shannon-Wiener Index and the effective number of species per PFT).

At the 1 m x 1 m, 5 m x 10 m, and 10 m x 10 m scales, PFT diversity did not differ significantly with fragment size (statistic not shown)

b) Diversity of the 19 subjectively defined PFTs

Atlantis Sand Fynbos results

At the 0.2 m x 0.5 m and 5 m x 10 m scales, PFT diversity based on both the Shannon-Wiener Index and the effective number of species per PFT did not differ with fragment size in Atlantis Sand Fynbos (statistic not shown).

At the 1 m x 1 m scale, PFT diversity differed with fragment size for both the Shannon-Wiener Index and the effective number of species per PFT (Kruskal-Wallis ANOVA: $H_{3,120} = 22.39387$, $p = 0.0001$). For both the Shannon-Wiener Index and the effective number of species per PFT,

- PFT diversity was significantly higher in the mainland than in the medium-sized (Mann-Whitney $U = 4.134507$, $p = 0.000036$), and
- Also higher in the mainland than in the smallest fragment (Mann-Whitney $U = 3.186588$, $p = 0.001440$).
- PFT diversity was significantly in the mainland higher than in the combined fragments (Mann-Whitney $U = 3.673679$, $p = 0.000239$).
- PFT diversity was also higher in the largest fragment than in the medium-sized one (Mann-Whitney $U = 3.135425$, $p = 0.001716$).

At the 10 m x 10 m scale, PFT diversity varied between the mainland and the three fragment (One-way ANOVA: $F_{3,32} = 3.4149$, $p = 0.02900$ for the effective numbers of species per PFT).

- The Bonferroni test showed that PFT diversity was slightly higher in the mainland than in the medium-sized fragment ($MS = 2.6111$, $df = 32$, $p = 0.038448$).
- PFT diversity was also higher in the mainland than in the combined fragments ($t = 2.230768$, $df = 34$, $p = 0.032400$).

Based on the Shannon-Wiener Index, PFT diversity differed only marginally between the mainland and the three fragments (Kruskal-Wallis ANOVA: $H_{3,36} = 7.702426$, $p = 0.05$). The Mann-Whitney U test showed that,

- PFT diversity was slightly higher in the mainland than in the medium-sized fragment (Mann-Whitney $U = 2.231871$, $p = 0.025624$) and
- Also higher in the mainland than in the combined fragments (Mann-Whitney $U = 2.058963$, $p = 0.039499$).

Swartland Shale Renosterveld results

PFT diversity differed very significantly with fragment size in Swartland Shale Renosterveld at all the four scales.

At the 0.2 m x 0.5 m scale, the difference in PFT diversity was highly significant for both the Shannon-Wiener Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,111} = 44.90176$, $p < 0.00001$). Based on both the Shannon-Wiener Index and the effective number of species,

- PFT diversity was lower in the mainland than in the largest fragment (Mann-Whitney U = -2.95868, p = 0.003090) and
- Also significantly lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -4.63514, p < 0.00001).
- PFT diversity was higher in the mainland than in the smallest fragment (Mann-Whitney U = 2.731809, p = 0.006299).
- PFT diversity was lower in the mainland than in the combined fragments (Mann-Whitney U = -2.58926, p = 0.009619).
- PFT diversity was much higher in the largest fragment than in the smallest one (Mann-Whitney U = 4.535826, p < 0.00001).
- PFT diversity was also much higher in the medium-sized fragment than in the smallest one (Mann-Whitney U = 5.669375, p < 0.00001).

At the 1 m x 1 m scale, PFT diversity also differed significantly with fragment size for both the Shannon-Wiener Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,118} = 67.94456$, p < 0.00001), with the Mann-Whitney U test showing that:

- PFT diversity was slightly lower in the mainland than in the largest fragment (Mann-Whitney U = -2.05987, p = 0.039412)
- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -5.41689, p < 0.00001)
- PFT diversity was much higher in the mainland than in the smallest fragment (Mann-Whitney U = 5.132248, p < 0.00001)
- PFT diversity was lower in the largest fragment than in the medium-sized one (Mann-Whitney U = -3.39557, p = 0.000685)
- The largest and the medium-sized fragments were much more diverse in PFT than the smallest one (Mann-Whitney U = 5.547561, p < 0.00001) and (Mann-Whitney U = 6.391008, p < 0.00001) respectively

PFT diversity also differed very significantly with fragment size at the 5 m x 10 m scale (Kruskal-Wallis ANOVA: $H_{3,36} = 31.83312$, p < 0.00001 for both the Shannon-Wiener Index and the effective number of species).

- The mainland was less diverse in PFT than the largest and the medium-sized fragments (Mann-Whitney U = -3.40323, p = 0.000666) and (Mann-Whitney U = -3.59189, p = 0.000328) respectively.
- The mainland was much more diverse in PFT than the smallest fragment (Mann-Whitney U = 3.140182, p = 0.001689)
- PFT diversity was lower in the largest than in the medium-sized fragment (Mann-Whitney U = -3.47392, p = 0.000513).
- The largest and medium-sized fragments were both much more diverse in PFT than the smallest (Mann-Whitney U = -3.597657, p = 0.000321), and (Mann-Whitney U = 3.611215, p = 0.000305) respectively.
- All other comparisons were not significant (statistics not shown)

At the 10 m x 10 m scale, PFT diversity also differed considerably with fragment size (Kruskal-Wallis ANOVA: $H_{3,36} = 30.87005$, p < 0.00001 for both the Shannon-Wiener Index and the effective number of species). The Mann-Whitney U test showed that,

- The mainland was less diverse in PFT than the largest fragment (Mann-Whitney U = -2.56196, p = 0.010409).
- PFT diversity was lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -3.58045, p = 0.000343)

- PFT diversity was lower in the largest than in the medium-sized fragment (Mann-Whitney U = -3.57666, p = 0.000348)
- The largest and medium-sized fragment fragments were much more diverse in PFT than the smallest (Mann-Whitney U = -3.617072, p = 0.000298) and (Mann-Whitney U = 3.628874, p = 0.000285) respectively.

Langebaan Dune Strandveld results

Results for Langebaan Dune Strandveld at the 0.2 m x 0.5 m scale showed that PFT diversity differed with fragment size (Kruskal-Wallis ANOVA: $H_{3,116} = 9.365604$, p = 0.0248 for both the Shannon-Wiener Index and the effective number of species per PFT). Following the Mann-Whitney U test, based on both the Shannon-Wiener Index and the effective number of species per PFT

- PFT diversity was lower in the mainland was than in the medium-sized fragment for the (Mann-Whitney U = -2.58161, p = 0.009835)
- PFT diversity was lower in the largest than in the medium-sized fragment (Mann-Whitney U = -2.41205, p 0.015864)

At the 1 m x 1 m scale, PFT diversity differed with fragment size for the Shannon-Wiener Index and the effective number of species (Kruskal-Wallis ANOVA: $H_{3,120} = 20.19850$, p = 0.0002):

- PFT diversity was significantly lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -3.94738, p < 0.0001)
- The mainland to be lower in PFT diversity than the combined fragments (Mann-Whitney U = -2.63133, p = 0.008505)
- PFT diversity was lower in the largest than in the medium-sized fragment (Mann-Whitney U = -3.19460, p = 0.001400)
- The medium-sized fragment being much more diverse in PFT than the smallest fragment (Mann-Whitney U = 3.307272, p = 0.000942)

At the 5 m x 10 m scale, PFT diversity based on the effective number of species per differed between the mainland and the three fragments (One-way ANOVA: $F_{3,32} = 6.7204$, p=0.00121). The post hoc test revealed that,

- PFT diversity was higher in the largest than in the smallest fragment with (MS = 2.5833, df = 32, p = 0.011760), and
- PFT diversity was also higher in the medium-sized than in the smallest fragment (MS = 2.5833, df = 32, p = 0.002355).

For the the Shannon-Wiener Index, PFT diversity also differed with fragment (Kruskal-Wallis ANOVA: $H_{3,36} = 13.81175$, p = 0.0032), with the Mann-Whitney U test showing that

- The mainland was slightly less diverse in PFT than the medium-sized fragment (Mann-Whitney U = -2.18723, p = 0.028726), while
- The largest and the medium-sized fragments were more diverse in PFT than the smallest one (Mann-Whitney U = 2.633607, p = 0.008449) and (Mann-Whitney U = 3.139558, p = 0.001692) respectively.

At the 10 m x 10 m scale, PFT diversity also varied with fragment size for both the Shannon-Wiener Index and the effective number of species per (Kruskal-Wallis ANOVA: $H_{3,36} = 12.67994$, p = 0.0054):

- PFT diversity was slightly lower in the mainland than in the medium-sized fragment (Mann-Whitney U = -2.02152, p = 0.043227), while
- The largest and the medium-sized fragments were slightly more diverse in PFT than the smallest one (Mann-Whitney U = 2.431023, p = 0.015057) and (Mann-Whitney U = 2.984085, p = 0.002844) respectively.

Appendix 16. List of indigenous species and their traits for the three Cape lowland vegetation types studied. **Veg** = vegetation type, ASF = Atlantis Sand Fynbos, LDS = Langebaan Dune Strandveld, SSR = Swartland Shale Renosterveld; **Ht** = Average height of at least five species; **DD** = Dispersal distance based on dispersal mode; **Poll** = Pollination (Gen = Generalist- and Spec = Specialist-pollinated); **DV** = Dispersal versatility; **PV** = Pollination versatility; **Spine** = Spinescence.

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Agathosma cf. bisulca</i>	LDS	Low shrub	0.95	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Agathosma imbricate</i>	ASF	Low shrub	0.65	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Aizoon sarmentosum</i>	SSR	Succulent herb	0.50	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Albuca cooperi</i>	ASF	Geophytic herb	0.40	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Anisodontia cf. scabrosa</i>	LDS	Low shrub	0.72	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Anthospermum aethiopicum</i>	SSR	Low shrub	1.50	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Native
<i>Anthospermum galiodes</i>	SSR	Dwarf shrub	0.5	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Native
<i>Anthospermum hirtum</i>	SSR	Low shrub	0.60	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Anthospermum spatulatum</i>	ASF, LDS	Low shrub	1.60	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Native
<i>Apatesia pillansii</i>	LDS	Succulent herb	0.44	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Arctopus echinatus</i>	SSR	Herb	0.15	Long	Perennial	Seeder	Dioecious	Gen	Poly	Mono	Yes	Native
<i>Arctotheca calendula</i>	SSR	Herb	0.20	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Arctotis acaulis</i>	SSR	Herb	0.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Arctotis angustifolia</i>	ASF	Herb	0.30	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Arctotis sp.</i>	SSR	Herb	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Argyrobium velutinum</i>	ASF, LDS	Dwarf shrub	0.45	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Aristea africana</i>	SSR	Geophytic herb	0.15	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Aristida diffusa</i>	ASF	Graminoid	0.7	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Aspalathus acanthophylla</i>	SSR	Dwarf shrub	0.5	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Endemic
<i>Aspalathus cf. acuminata</i>	SSR	Low shrub	0.60	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Aspalathus cf. albens</i>	ASF	Dwarf shrub	0.42	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Aspalathus cf. cuspidata</i>	LDS	Low shrub	0.64	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Aspalathus cf. divaricata</i>	ASF	Dwarf shrub	0.40	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Aspalathus cf. ericifolia</i>	ASF	Low shrub	0.55	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Aspalathus cf. flexuosa</i>	SSR	Dwarf shrub	0.35	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Aspalathus cf. hispida</i>	LDS	Low shrub	1.48	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Aspalathus quinquefolia</i>	ASF, LDS	Low shrub	0.45	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Aspalathus ternata</i>	LDS	Low shrub	1.00	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Asparagus aethiopicus</i>	LDS	Woody climber	2.50	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Asparagus capensis</i>	SSR	Low shrub	0.95	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Asparagus declinatus</i>	LDS	Woody climber	1.00	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Asparagus retrofractus</i>	SSR	Woody climber	1.60	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Asparagus rubicundus</i>	All	Low shrub	0.87	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Athanasia rugulosa</i>	ASF	Low shrub	0.90	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Athanasia trifucata</i>	SSR	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Babiana cf. tubulosa</i>	LDS	Geophytic herb	0.12	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Babiana nana</i>	ASF	Geophytic herb	0.15	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Babiana stricta</i>	SSR	Geophytic herb	0.20	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Babiana villosula</i>	ASF	Geophytic herb	0.40	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Berkheya armata</i>	ASF, SSR	Herb	0.12	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	Yes	Endemic
<i>Berkheya rigida</i>	SSR	Herb	0.50	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	Yes	Endemic
<i>Berzelia abrotanoides</i>	ASF	Low shrub	1.30	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Brunsvigia cf. bosmaniae</i>	SSR	Geophytic herb		Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Brunsvigia cf. marginata</i>	SSR	Geophytic herb	0.20	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Bulbine praemorsa</i>	SSR	Geophytic herb	0.50	Short	Perennial	Resprouter	Non-dioecious	Spec	Poly	Mono	No	Native
<i>Bulbinella sp.</i>	SSR	Geophytic herb	0.51	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Caesia sp.</i>	LDS	Geophytic herb	0.35	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Calopsis viminea</i>	ASF	Graminoid	0.52	Long	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Cannomois parviflora</i>	ASF	Graminoid	0.80	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Chaetobromus dregeanus</i>	LDS	Graminoid	0.35	Long	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Chasmanthe floribunda</i>	SSR	Geophytic herb	0.70	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Cheilanthes capensis</i>	SSR	Geophytic herb	0.15	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	n/a	No	Native
<i>Chironia linoides</i>	ASF	Low shrub	0.65	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Chlorophytum triflorum</i>	LDS	Geophytic herb	1.00	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Chlorophytum viscosum</i>	LDS	Geophytic herb	0.60	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Chondropetalum nudum</i>	ASF	Graminoid	0.70	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Chrysanthemoides monilifera</i>	LDS	Low shrub	1.35	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Chrysocoma ciliata</i>	SSR	Dwarf shrub	0.5	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Cissampelos capensis</i>	SSR, LDS	Climber (herb)	0.96	Long	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Native
<i>Conicosia pugioniformis</i>	ASF, LDS	Succulent herb	0.30	Long	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Conyza scabrida</i>	SSR	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Corycium cf. orobanchoides</i>	SSR	Geophytic herb	0.42	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Cotula turbinata</i>	SSR	Herb	0.15	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Cotyledon orbiculata var. orbiculata</i>	LDS	Succulent shrub	0.55	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Crassula capensis</i>	SSR	Geophytic herb	0.13	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Crassula strigosa</i>	SSR	Herb	0.12	Long	Annual	Seeder	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Cyanella hyacinthioides</i>	LDS	Geophytic herb	0.54	Short	Perennial	Resprouter	Non-dioecious	Spec	Poly	Mono	No	Native
<i>Cyanella lutea</i>	SSR	Geophytic herb	0.19	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Cynanchum africanum</i>	LDS	Climber (herb)	0.60	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Cyperus sp.</i>	SSR	Graminoid		Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Cyphia bulbosa</i>	SSR	Geophytic herb	0.30	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Cyphia digitata</i>	SSR	Climber (herb)		Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Cysticapnos cracca</i>	SSR	Climber (herb)	1.00	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Diastella proteoides</i>	ASF	Dwarf shrub	0.50	Short	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Elytropappus rhinocerotis</i>	SSR	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Dimorphotheca pluvialis</i>	SSR	Herb	0.20	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Diosma aspalathoides</i>	ASF	Low shrub	0.55	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Diosma dichotoma</i>	ASF	Low shrub	0.65	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Diosma oppositifolia</i>	ASF	Low shrub	0.75	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Diospyros cf. glabra</i>	LDS	Tall shrub	2.20	Long	Perennial	Seeder	Dioecious	Spec	Poly	Mono	No	Native
<i>Drimia capensis</i>	SSR	Geophytic herb		Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Drimia sp.</i>	LDS	Geophytic herb	0.86	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Ehrharta brevifolia</i>	LDS	Graminoid	0.50	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ehrharta calycina</i>	All	Graminoid	0.75	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ehrharta longiflora</i>	SSR	Graminoid	0.60	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ehrharta villosa</i>	LDS	Graminoid	0.96	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Elegia filacea</i>	ASF	Graminoid	0.70	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Elegia neesii</i>	ASF	Graminoid	0.65	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Erica mammosa</i>	ASF	Low shrub	1.30	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Erica plumosa</i>	ASF	Low shrub	0.70	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Erica sp. 1</i>	ASF	Low shrub	0.85	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Erica sp. 2</i>	ASF	Low shrub	0.65	Short	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Ericephalus africanus</i>	SSR	Low shrub	0.85	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Ericephalus racemosus</i>	LDS	Low shrub	1.34	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Euclea racemosa</i>	LDS	Low shrub	1.80	Long	Perennial	Seeder	Dioecious	Spec	Poly	Mono	No	Native
<i>Euphorbia arceuthoboides</i>	LDS	Succulent shrub	0.95	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Native
<i>Euphorbia burmanii</i>	LDS	Succulent shrub	1.10	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Native
<i>Euphorbia caput-medusae</i>	LDS	Succulent shrub	0.77	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Euphorbia genistoides</i>	SSR	Low shrub	0.70	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Euryops thunbergii</i>	SSR	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Exomis microphylla</i>	LDS	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Felicia fruticosa</i>	SSR	Low shrub	0.90	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Felicia tenella</i>	All	Herb	0.82	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Festuca scabra</i>	SSR	Graminoid	0.45	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ficina cf. trichodes</i>	SSR	Graminoid	0.20	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ficina bulbosa</i>	ASF	Graminoid	0.40	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ficina cf. indica</i>	LDS	Graminoid	0.30	Long	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Ficina oligantha</i>	SSR	Graminoid	0.25	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Ficina sp.</i>	SSR	Graminoid	0.15	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Geissorhiza aspera</i>	SSR	Geophytic herb	0.23	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Gorteria personata</i>	SSR	Herb	0.10	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Gymnodiscus capillaris</i>	ASF	Herb	0.25	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Gymnosporia buxifolia</i>	SSR	Low shrub	1.30	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	Yes	Native
<i>Hebenstretia sp. 1</i>	LDS	Herb	0.45	Long	Annual	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Hebenstretia sp. 2</i>	LDS	Herb		Long	Annual	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Helichrysum asperum</i>	ASF, SSR	Dwarf shrub	0.40	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helichrysum cf. rosum</i>	SSR	Low shrub	0.85	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helichrysum cylindriflorum</i>	ASF	Dwarf shrub	0.25	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helichrysum cymosum</i>	SSR	Low shrub	0.90	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helichrysum indicum</i>	ASF	Herb	0.35	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Helichrysum moeserianum</i>	LDS	Herb	0.93	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helichrysum pandurifolium</i>	ASF, SSR	Low shrub	0.55	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Helichrysum sp. 1</i>	ASF	Dwarf shrub	0.15	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helichrysum teretifolium</i>	SSR	Dwarf shrub	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Helictotrichon capense</i>	SSR	Graminoid	0.55	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Heliophila cf. digitata</i>	LDS	Herb	0.74	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Hemimeris racemosa</i>	SSR	Herb	0.26	Short	Annual	Seeder	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Hermannia cf. hyssopifolia</i>	SSR	Low shrub	1.30	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Hermannia cf. multiflora</i>	ASF	Low shrub	0.65	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Hermannia rugosa</i>	SSR	Low shrub	0.35	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Hermannia trifurca</i>	LDS	Low shrub	0.70	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Hesperantha falcata</i>	SSR	Geophytic herb	0.18	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Hyparrhenia hirta</i>	SSR	Graminoid	0.80	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Hypodiscus rugosus</i>	ASF	Graminoid	0.50	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Hypodiscus willdenowia</i>	ASF	Graminoid	0.60	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Indigofera digitata</i>	SSR	Dwarf shrub	0.45	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Indigofera incana</i>	SSR	Dwarf shrub	0.45	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Ischyrolepis capense</i>	ASF, SSR	Graminoid	0.50	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Ischyrolepis cf. helenae</i>	ASF	Graminoid	0.70	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Ischyrolepis macer</i>	ASF	Graminoid	0.45	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Ischyrolepis monanthos</i>	ASF	Graminoid	0.55	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Ischyrolepis paludosa</i>	ASF	Graminoid	0.30	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Isolepis marginata</i>	ASF, LDS	Graminoid	0.07	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ixia dubia</i>	SSR	Geophytic herb	0.55	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Lachnaea capitata</i>	ASF	Low shrub	1.50	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Lachnaea grandiflora</i>	ASF	Low shrub	0.55	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Lachnaea uniflora</i>	ASF	Dwarf shrub	0.45	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Lampranthus cf. elegans</i>	ASF	Succulent shrub	0.32	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Lampranthus sp. 1</i>	SSR	Succulent shrub		Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Lampranthus sp. 2</i>	SSR	Succulent shrub		Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Lampranthus sp. 3</i>	LDS	Succulent shrub	0.71	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Lampranthus stenopetalus</i>	ASF	Succulent shrub	0.40	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Lebeckia multiflora</i>	LDS	Low shrub	1.39	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Lessertia excissa</i>	SSR	Herb	0.35	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Leucadendron brunoides</i> subsp. <i>flumenlupinum</i>	LDS	Low shrub	1.82	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Leucadendron cinereum</i>	ASF	Low shrub	1.2	Short	Perennial	Seeder	Dioecious	Spec	Mono	Poly	No	Endemic
<i>Leucadendron lanigerum</i> subsp. <i>lanigerum</i>	ASF	Low shrub	1.5	Long	Perennial	Resprouter	Dioecious	Spec	Mono	Mono	No	Endemic
<i>Leucospermum hypophyllocarpodendron</i> subsp. <i>canaliculatum</i>	ASF	Dwarf shrub	0.12	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Leucospermum parile</i>	ASF	Low shrub	1.60	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Leysera gnaphalodes</i>	SSR, LDS	Herb	0.40	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Lobostemon glaber</i>	SSR	Dwarf shrub	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Lycium afrum</i>	SSR	Low shrub	0.75	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Endemic
<i>Lycium cinereum</i>	LDS	Low shrub	0.12	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Macrostylis cassioides</i>	ASF	Low shrub	1.10	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Macrostylis villosa</i>	ASF	Dwarf shrub	0.30	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Melianthus elongatus</i>	LDS	Low shrub	1.40	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Melica racemosa</i>	SSR	Graminoid	0.45	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Metasia capitata</i>	ASF	Low shrub	0.70	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Metasia cf. densa</i>	ASF	Low shrub	2	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Metasia sp.</i>	ASF	Low shrub	0.72	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Microloma sagittatum</i>	LDS	Climber (herb)	1.30	Long	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Mohria caffrorum</i>	SSR	Geophytic herb	0.15	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	n/a	No	Native
<i>Monoculus monstruosus</i>	SSR	Herb	0.40	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Montinia caryophyllacea</i>	SSR	Low shrub	1.20	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Moraea bellendenii</i>	SSR	Geophytic herb	1.00	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Moraea fugax</i>	ASF	Geophytic herb	0.50	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Moraea gawleri</i>	SSR	Geophytic herb		Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Moraea miniata</i>	SSR	Geophytic herb	0.40	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Muraltia brevicornu</i>	ASF	Low shrub	1.80	Short	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Muraltia cf. pungens</i>	SSR	Dwarf shrub	0.45	Short	Perennial	Seeder	Non-dioecious	Spec	Poly	Mono	Yes	Endemic
<i>Muraltia dumosa</i>	ASF	Dwarf shrub	0.35	Short	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Muraltia filiformis</i>	ASF	Dwarf shrub	0.35	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Muraltia sp.</i>	LDS	Low shrub	1.00	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Nemesia affinis</i>	ASF	Herb	0.15	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Nemesia barbata</i>	SSR	Herb	0.30	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Nemesia cf. bicornis</i>	LDS	Herb		Short	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Nestlera biennis</i>	LDS	Herb	0.50	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Nidorella foetida</i>	SSR	Herb	0.50	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Nylandtia spinosa</i>	LDS	Low shrub	0.75	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	Yes	Native
<i>Olea europaea</i> subsp. <i>africana</i>	SSR	Tall shrub	2.00	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Oncosiphon grandiflorum</i>	LDS	Herb	0.32	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Ornithogalum cf. conicum</i>	LDS	Geophytic herb	0.78	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ornithogalum suaveolens</i>	ASF	Geophytic herb	0.20	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Ornithogalum thyrsooides</i>	SSR	Geophytic herb	0.25	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Osteospermum spinosum</i>	SSR	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	Yes	Endemic
<i>Otholobium hirtum</i>	SSR	Low shrub	1.60	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Othonna ciliata</i>	SSR	Dwarf shrub	0.30	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Othonna cylindrica</i>	LDS	Succulent shrub	0.85	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Oxalis cf. bifida</i>	SSR	Geophytic herb	0.15	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Oxalis glabra</i>	SSR	Geophytic herb	0.13	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Oxalis lanata</i>	SSR	Geophytic herb	0.15	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Oxalis livida</i>	SSR	Geophytic herb	0.12	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Oxalis obtusa</i>	SSR	Geophytic herb	0.05	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Oxalis pes-caprae</i>	SSR	Geophytic herb	0.20	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Oxalis purpurea</i>	SSR	Geophytic herb	0.05	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Oxalis sp.</i>	SSR	Geophytic herb		Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	indet
<i>Oxalis tenuifolia</i>	SSR	Geophytic herb	0.25	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Oxalis tomentosa</i>	SSR	Geophytic herb	0.01	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Passerina cf. vulgaris</i>	ASF, SSR	Low shrub	1.30	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Passerina sp.</i>	LDS	Low shrub	1.20	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Pelargonium anethifolium</i>	SSR	Geophytic herb	0.35	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Pelargonium hirtum</i>	LDS	Dwarf shrub	0.30	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Pelargonium myrrhifolium</i>	SSR	Herb	0.30	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Pelargonium oenothera</i>	ASF	Dwarf shrub	0.20	Long	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Pelargonium proliferum</i>	ASF	Geophytic herb	0.40	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Pelargonium senecioides</i>	ASF, LDS	Herb	0.60	Long	Annual	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Pelargonium triste</i>	ASF	Geophytic herb	0.40	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Pentaschistis barbata</i>	ASF, LDS	Graminoid	0.60	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Pentaschistis curvifolia</i>	ASF	Graminoid	0.60	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Pentaschistis patula</i>	ASF	Graminoid	0.30	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Petalacte coronata</i>	ASF	Dwarf shrub	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Phyllica cephalantha</i>	ASF	Low shrub	0.95	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Phyllica imberbis</i>	ASF	Dwarf shrub	0.50	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Phyllopodium cephalophorum</i>	LDS	Herb	0.24	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Polygala garcinii</i>	ASF	Dwarf shrub	0.50	Short	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Printzia polifolia</i>	SSR	Low shrub	1.40	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Protea acaulos</i>	ASF	Dwarf shrub	0.15	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Protea burchellii</i>	ASF	Low shrub	1.50	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Protea scolymocephala</i>	ASF	Low shrub	1.30	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Pseudognaphalium undulatum</i>	ASF	Herb	0.50	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Pseudopentameris caespitosa</i>	ASF	Graminoid	0.95	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Pseudoselago spuria</i>	ASF	Dwarf shrub	0.65	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Pterona divaricata</i>	LDS	Low shrub	1.33	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Pterona onobromoides</i>	LDS	Low shrub	0.78	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Pterona ovalifolia</i>	LDS	Low shrub	0.65	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Pterygodium catholicum</i>	SSR	Geophytic herb	0.20	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Putterlickia pyracantha</i>	SSR, LDS	Low shrub	1.50	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	Yes	Native
<i>Rafnia angulata</i>	ASF	Dwarf shrub	0.50	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Rafnia lancea</i>	ASF	Dwarf shrub	0.33	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Restio bifurcus</i>	ASF	Graminoid	1.40	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Restio praeacutus</i>	ASF	Graminoid	0.75	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Restio quinquefarius</i>	ASF	Graminoid	0.60	Short	Perennial	Seeder	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Restio triticeus</i>	ASF	Graminoid	1.00	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Rhus cf. angustifolia</i>	SSR	Tall shrub	2.50	Long	Perennial	Seeder	Dioecious	Gen	Poly	Mono	No	Native
<i>Rhus dissecta</i>	LDS	Low shrub	1.30	Long	Perennial	Seeder	Dioecious	Gen	Mono	Mono	Yes	Endemic
<i>Rhus glauca</i>	LDS	Low shrub	1.48	Long	Perennial	Seeder	Dioecious	Gen	Poly	Mono	No	Native
<i>Rhus laevigata var. laevigata</i>	LDS	Tall shrub	2.35	Long	Perennial	Seeder	Dioecious	Gen	Poly	Mono	No	Native
<i>Rhus laevigata var. villosa</i>	SSR	Tall shrub	2.3	Long	Perennial	Seeder	Dioecious	Gen	Poly	Mono	No	Native
<i>Roella ciliata</i>	ASF	Dwarf shrub	0.40	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Rumex lativalvis</i>	SSR	Geophytic herb	0.25	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Ruschia cf. subpaniculata</i>	LDS	Succulent shrub	0.30	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Ruschia sp. 1</i>	LDS	Succulent shrub	1.33	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Ruschia sp. 2</i>	LDS	Succulent shrub	1.33	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Salvia africana-caerulea</i>	ASF, SSR	Low shrub	1.20	Short	Perennial	Seeder	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Salvia africana-lutea</i>	SSR	Low shrub	1.00	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Salvia lanceolata</i>	LDS	Low shrub	1.52	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Scabiosa columbaria</i>	SSR	Herb	0.50	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Sebaea exacoides</i>	SSR	Herb	0.15	Short	Annual	Seeder	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Selago cf. fruticosa</i>	SSR	Dwarf shrub	0.40	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Selago corymbosa</i>	SSR	Low shrub	0.60	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Senecio aloides</i>	LDS	Succulent shrub	0.74	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Senecio burchellii</i>	ASF	Herb	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Senecio elegans</i>	ASF	Herb	0.50	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Senecio halimifolius</i>	SSR, LDS	Low shrub	1.60	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Senecio hastatus</i>	SSR	Herb	0.50	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Senecio pubigerus</i>	SSR	Low shrub	0.75	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Senecio rosmarinifolius</i>	SSR	Low shrub	0.60	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Senecio scapiflorus</i>	SSR	Herb	0.30	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Senecio sp.</i>	SSR	Herb		Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Serruria brownii</i>	ASF	Dwarf shrub	0.50	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Serruria fasciflora</i>	ASF	Low shrub	0.75	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Serruria fucifolia</i>	LDS	Low shrub	1.18	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Serruria linearis</i>	ASF	Low shrub	0.60	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Silene sp.</i>	LDS	Herb	1.12	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Sisymbrium capense</i>	ASF	Herb	0.70	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Solanum guineense</i>	SSR	Low shrub	1.50	Long	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Spiloxene capensis</i>	SSR	Geophytic herb	0.30	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Spiloxene flaccida</i>	SSR	Geophytic herb	0.16	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Staavia radiata</i>	ASF	Low shrub	0.80	Short	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Staberoha distachyos</i>	ASF	Graminoid	0.70	Long	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Stachys aethiopica</i>	SSR	Herb	0.30	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Stilbe ericoides</i>	ASF	Low shrub	0.65	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Poly	No	Endemic
<i>Stipagrostis zeyheri</i>	ASF	Graminoid	0.70	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Stoebe gomphrenoides</i>	ASF	Dwarf shrub	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Stoebe leucocephala</i>	ASF	Dwarf shrub	0.45	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Stoebe nervigera</i>	LDS	Low shrub	0.74	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Stoebe plumosa</i>	ASF	Low shrub	0.55	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Struthiola ciliata</i>	ASF	Low shrub	1.2	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Sutera sp.</i>	SSR	Dwarf shrub	0.50	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Tetragonia decumbens</i>	LDS	Succulent shrub	1.38	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Tetragonia spicata</i>	SSR	Succulent shrub	1.00	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Thamnochortus erectus</i>	LDS	Graminoid	0.80	Long	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Thamnochortus fruticosus</i>	ASF	Graminoid	0.50	Long	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Thamnochortus obtusus</i>	ASF	Graminoid	0.65	Long	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Native
<i>Thamnochortus punctatus</i>	ASF	Graminoid	1.00	Long	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Themeda triandra</i>	SSR	Graminoid	0.60	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Thesium cf. strictum</i>	ASF	Low shrub	0.80	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Torillis arvensis</i>	SSR	Climber (herb)		Long	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Trachyandra chlamydophylla</i>	SSR	Geophytic herb	0.60	Short	Perennial	Resprouter	Non-dioecious	Spec	Poly	Mono	No	Endemic
<i>Trachyandra divaricata</i>	LDS	Geophytic herb	0.69	Long	Perennial	Resprouter	Non-dioecious	Spec	Poly	Mono	No	Native
<i>Trachyandra muricata</i>	SSR	Geophytic herb	0.45	Long	Perennial	Resprouter	Non-dioecious	Spec	Poly	Mono	No	Native
<i>Tribolium echinatum</i>	LDS	Graminoid	0.15	Long	Annual	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Tribolium hispidum</i>	SSR	Graminoid	0.30	Long	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Tribolium uniolae</i>	ASF, SSR	Graminoid	0.30	Long	Perennial	Resprouter	Non-dioecious	Gen	Mono	Mono	No	Endemic
<i>Trichocephalus stipularis</i>	ASF	Low shrub	0.80	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Tylecodon wallichii</i>	LDS	Succulent shrub	0.65	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Ursina anthemoides</i>	All	Herb	0.40	Long	Annual	Seeder	Non-dioecious	Gen	Mono	Poly	No	Native
<i>Wachendorfia multiflora</i>	SSR	Geophytic herb	0.25	Short	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Native
<i>Wahlenbergia adpressa</i>	LDS	Dwarf shrub	0.42	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Poly	No	Endemic
<i>Wahlenbergia androsacea</i>	ASF	Herb	0.40	Short	Annual	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native

Species	Veg	Growth Form	Ht (m)	DD	Life span	Regeneration	Breeding	Poll	DV	PV	Spine	Status in CFR
<i>Wahlenbergia tenella</i>	ASF	Dwarf shrub	0.35	Short	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Watsonia coccinea</i>	ASF	Geophytic herb	0.90	Long	Perennial	Resprouter	Non-dioecious	Spec	Mono	Mono	No	Endemic
<i>Wiborgia cf. fusca</i>	LDS	Low shrub	1.60	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Poly	No	Native
<i>Willdenowia arescens</i>	ASF	Graminoid	1.20	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Willdenowia incurvata</i>	ASF, LDS	Graminoid	1.20	Long	Perennial	Resprouter	Dioecious	Gen	Poly	Mono	No	Endemic
<i>Willdenowia sulcata</i>	ASF	Graminoid	0.95	Short	Perennial	Resprouter	Dioecious	Gen	Mono	Mono	No	Endemic
<i>Xiphotheca reflexa</i>	ASF	Dwarf shrub	0.50	Short	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Endemic
<i>Zantedeschia aethiopica</i>	SSR	Geophytic herb	0.80	Long	Perennial	Resprouter	Non-dioecious	Gen	Poly	Mono	No	Native
<i>Zygophyllum morgsana</i>	LDS	Low shrub	1.10	Long	Perennial	Seeder	Non-dioecious	Gen	Mono	Mono	No	Native
<i>Zygophyllum sessilifolium</i>	ASF, SSR	Dwarf shrub	0.35	Short	Perennial	Seeder	Non-dioecious	Gen	Poly	Mono	No	Endemic