The Effects of Fragmentation of South Coast Renosterveld on Vegetation Patterns and Processes

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CHAPTER 3

CHAPTER 4

Summary

This thesis investigates the effects of fragmentation on vegetation patterns and processes of South Coast Renosterveld at three hierarchical levels. South Coast Renosterveld is a grassy shrubland derived from shales on the coastal forelands of the Western Cape Province, South Africa. The area forms part of the Cape Floristic Region. It occurs on fine-grained, moderately fertile soils. Thus, most South Coast Renosterveld has been replaced by agriculture. This vegetation type is particularly rich in geophytes, many of which have highly localised distributions. Almost no research has been carried out on the composition and structure of South Coast Renosterveld. However, fragmentation theory suggests that the fragmentation process iof South Coast Renosterveld would cause a loss of biodiversity. Although South Coast Renosterveld is one of the most threatened vegetation types in South Africa, only 0.8% of its area is formally conserved.

An analysis of landscape-scale patterns revealed that up to 82% of the natural extent of South Coast Renosterveld has been cultivated with cereals and pasture crops over the last century. The remaining areas of renosterveld are patches scattered throughout the agricultural lands. Towards the eastern boundary of its extent, large, well-connected tracts of South Coast Renosterveld still remain, thus providing potential for large reserves and corridor-networks. However, expected higher biodiversity levels towards the western boundary emphasise the need to formally conserve small fragments there. The extent of remaining renosterveld was best correlated with topographical variables. This indicates that renosterveld fragments are largely confined to steep slopes, where agricultural potential is low. It therefore appears that the remaining tracts of renosterveld could face little threat of future cultivation.

I investigated vegetation composition and guild structure on fragments of different sizes (small, medium and large). The effect of fragmentation on habitat diversity was not explored. Although fragmentation theory suggests a loss in biodiversity with increasing fragmentation, I generally did not find significant differences in vegetation composition or guild structure in different-sized fragments. There were, however, some exceptions. Firstly, TWINSPAN classification analysis showed that large fragments were more similar to each other than small or medium fragments were to each other in terms of vegetation composition. This suggests that large fragments appear more stable than small or medium fragments. This may be a reflection of fragmentation processes, such as extinctions, invasions and edge effects operating on small and medium fragments. Secondly, Detrended Correspondence Analysis (DCA) revealed that small and medium fragments tend to occur on more rocky soils than large fragments set aside as natural rangelands. This underlines the non-random nature of fragmentation in the area, where more fertile soils are most likely to be transformed first. Finally, medium fragments, although maintaining the highest number of native species, supported a significantly higher number and cover of alien species, possibly the result of edge effects. Many species are able to persist successfully in small populations on fragments; South Coast Renosterveld, therefore, appears to be a low-risk vegetation type. The results, therefore, emphasise the important role of small fragments as relatively intact islands of biodiversity in a fragmented landscape. Fragmentation may, however, have been too recent for any effects to have been translated into extinctions.

I compared for selected species reproductive success, measured by fruit set, seed set, germination success and number of individuals produced per plant, of two plant species on different-sized fragments. I chose two insect-pollinated geophyte species with

different reproductive strategies: *Omithogalum thyrsoides* (Hyacinthaceae), a selfer with a host of common pollinators and *Babiana ambigua* (Iridaceae), which is incapable of selfing and has few pollinator species. Reproductive success of *O. thyrsoides* was generally high, regardless of fragment size. Fragment size appeared to affect reproductive success of *B. ambigua*, although in conflict with fragmentation theory. On average, small fragments produced significantly more fruits per flower, seeds per fruit, and number of individuals per plant than large fragments. Germination success was, however, significantly higher on large fragments than small or medium fragments. Reasons for this pattem include low pollen quantity on large fragments and low pollen quality on small fragments. The comparison of species with different reproductive strategies showed that conservation priority should be given to species with specialised reproductive strategies.

This thesis contributed to our understanding of South Coast Renosterveld fragmention pattems and, to a lesser degree, processes. In particular, the results highlight the urgency for formulating and implementing conservation measures for South Coast Renosterveld. Although it is not viable to incorporate small fragments into formal reserves, these present a valuable source of biodiversity. The challenge is to identify services associated with these fragments (for example grazing value and soil erosion control) that will encourage farmers to maintain these patches. Farm managers need to be made aware of the importance of small fragments, and should be given guidelines on how to manage these fragments effectively.

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Chapter 2 on renosterveld landscape patterns would have never materialised without the kind assistance of ENVIRONMENTEK, CSIR. Greg Forsyth and David McKelly are thanked in particular for producing and manipulating the coverages, running the data through FRAGSTATS and producing the map on page 42.

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Chapter 1

General Introduction

1.1 Fragmentation - a review

With the alarming world-wide increase in the destruction of natural habitats (Meffe and Carroll 1994), fragmentation has become a major subject of research and debate in conservation biology. Much fragmentation research focuses on the application of island biogeography theory and its importance to nature reserve design (for example the SLOSS or "single large or several small" debate) (Simberloff and Abele 1976, Gilpin and Diamond 1980). Island biogeography theory, developed by MacArthur and Wilson (1967), proposes a relationship between species number, island size and isolation, and predicts a dynamic equilibrium between extinction and immigration on oceanic islands. It has subsequently been used to predict species numbers on habitat "islands". Brown and Kodric-Brown (1977) incorporated the 'rescue effect' into the theory, to emphasise the importance of the immigration of new, unrelated individuals in maintaining small populations and reducing the risk of genetic inbreeding. Both the theory and its application have been widely criticised for the simple yet unrealistic generalisations the theory makes (Gilbert 1980, Simberloff and Abele 1982, Haila *et al.* 1993, Boecklen and Gotelli 1984). More recently, fragmentation research has shifted towards understanding changes of patterns and processes created by fragmentation at different spatial and temporal scales (Robinson *et al.* 1992, Haila *et al.* 1993), and the implications of this information for developing policies for managing already fragmented areas (Saunders *et al.* 1991).

Anthropogenic fragmentation, generally caused by clearing for agriculture or forestry (Hobbs 1987), results in a number of fundamental changes, both to the patterns and the processes at all scales of an ecosystem (Figure 1.1). It produces a series of patches of natural ecosystems, surrounded by a matrix of semi-natural or agricultural ecosystems . This leads to the reduction in the total area of natural habitat, a change in patch shape and the isolation of disjunct patches to varying degrees. A decrease in area mainly affects population sizes and therefore increases local extinction rates, while the degree of isolation and nature of the modified matrix primarily affects dispersal, and thus immigration rates. Increased isolation and a highly modified matrix further amplifies the risk of local extinction. Mechanisms of extinction related to population size are termed primary extinctions (Terborgh and Winter 1980) and include demographic, genetic and environmental stochasticity (Gilpin and Soulé 1986, Mills and Smouse 1994). The risk of local extinction is greatly influenced by the organism's life-history attributes (Richardson *et al.* 1996, Trinder-Smith *et al.* 1996), and particularly by its ability to persist and colonise (Midgley 1996, Turner 1996).

Edge effects, caused by the sudden creation of a sharp boundary between the patch margin and the surrounding landscape, are influenced by patch shape (Lovejoy *et al.* 1986), and can lead to further system degradation, for example through an altered microclimate, such as changes in radiation- and water run-off levels (Saunders *et al.* 1991). Similarly, the incorporation of fragments into surrounding agricultural land management may cause a "spill-over" of agricultural practices to extend well past the edge of a fragment. This can lead to a modified disturbance regime of natural vegetation, including burning (Bond *et al.* 1988), grazing (see Hobbs 1987 for examples) and the use of pesticides (see Freemark and Boutin 1995 and references therein). These impacts, in turn, can result in secondary and even higher-order extinctions, for example through a breakdown in plant-animal interactions (Terborgh and Winter 1980, Buchmann and Nabhan 1996). Edge effects have been shown to restrict certain species to the core of a fragment (Bierregaard *et al.* 1992) and to promote deterministic processes such as the invasion of edge-tolerant, often weedy, species with good colonising abilities (Scougall *et al.* 1993). Ultimately, patch size, shape and position in the landscape, together with plant life history attributes dictates vegetation composition and distribution. Anthropogenic fragmentation is usually not a random process (Usher 1987), with habitats occurring on more fertile land generally transformed first. This implies that fragments of natural vegetation are restricted to certain habitats (e.g. poorer soils), which may further boost the effects of fragmentation on species diversity.

Species loss due to fragmentation has been successfully demonstrated for a large range of animals (Haila *et al.* 1993). However, the effect of fragmentation on plant species diversity has been documented with varying results: studies on forest fragmentation for example, have shown negative influences on species diversity (Lovejoy *et al.* 1986, Kadmon and Pullinam 1993, Iida and Nakashizuka 1995), an increase in species diversity (Quinn and Hastings 1987, Robinson and Quinn 1988) or no effect (Weaver and Kellman 1981). Lord and Norton (1990), Robinson *et al.* (1992) and Haila *et al.* (1993) warn, however, that generalisations about the effects of fragmentation should be made with caution, since the degree of fragmentation and its impact varies with scale, as different components of an ecosytem react in different ways to fragmentation. Hobbs *et al.* (1992, in Haila *et. al* 1993), for example, recorded lower extinction levels for plants than for animals in the Western Australian wheatbelt. They attributed this to longer lifespans for plants, showing that extinction scales for animals differ to that of plants. It follows therefore that experimental studies of fragmentation effects must be designed and assessed carefully at the relevant scale under investigation.

1.2 Fragmentation research in the Cape Floristic Region (CFR)

The Cape Floristic Region of South Africa, one of six plant kingdoms world-wide, is dominated by fynbos (Cowling and Holmes 1992), an exceptionally species-rich vegetation type with high levels of local endemism (Cowling *et al.* 1992). Large parts are being increasingly threatened by agriculture, urbanisation and forestry (Deacon 1992, Rebelo 1992). Several studies have assessed the extent to which natural vegetation has already been transformed in the Cape Floristic Region (for example Boucher 1981, Moll and Bossi 1984, Jarman 1986), but only few comprehensive studies explicitly link the effects of fragmentation to species diversity or attempt to understand underlying processes. Bond *et al.* (1988) showed a significant decrease in species diversity on isolated "islands" of fynbos in Knysna forest. They concluded that longer fire cycles in small fynbos patches surrounded by fire-proof forest result in the loss of species requiring more frequent fires. Cowling and Bond (1991) investigated the effects of fragmentation on isolated outcrops of limestone fynbos surrounded by acid sand fynbos, and identified species at risk of extinction, though their study did not deal specifically with anthropogenic fragmentation. The effect of small population sizes on gene flow in fynbos and its importance in conservation planning has been recognised by Hall (1987), but experimental work is lacking. Other, largely preliminary studies have assessed the effects of land development along the South and West

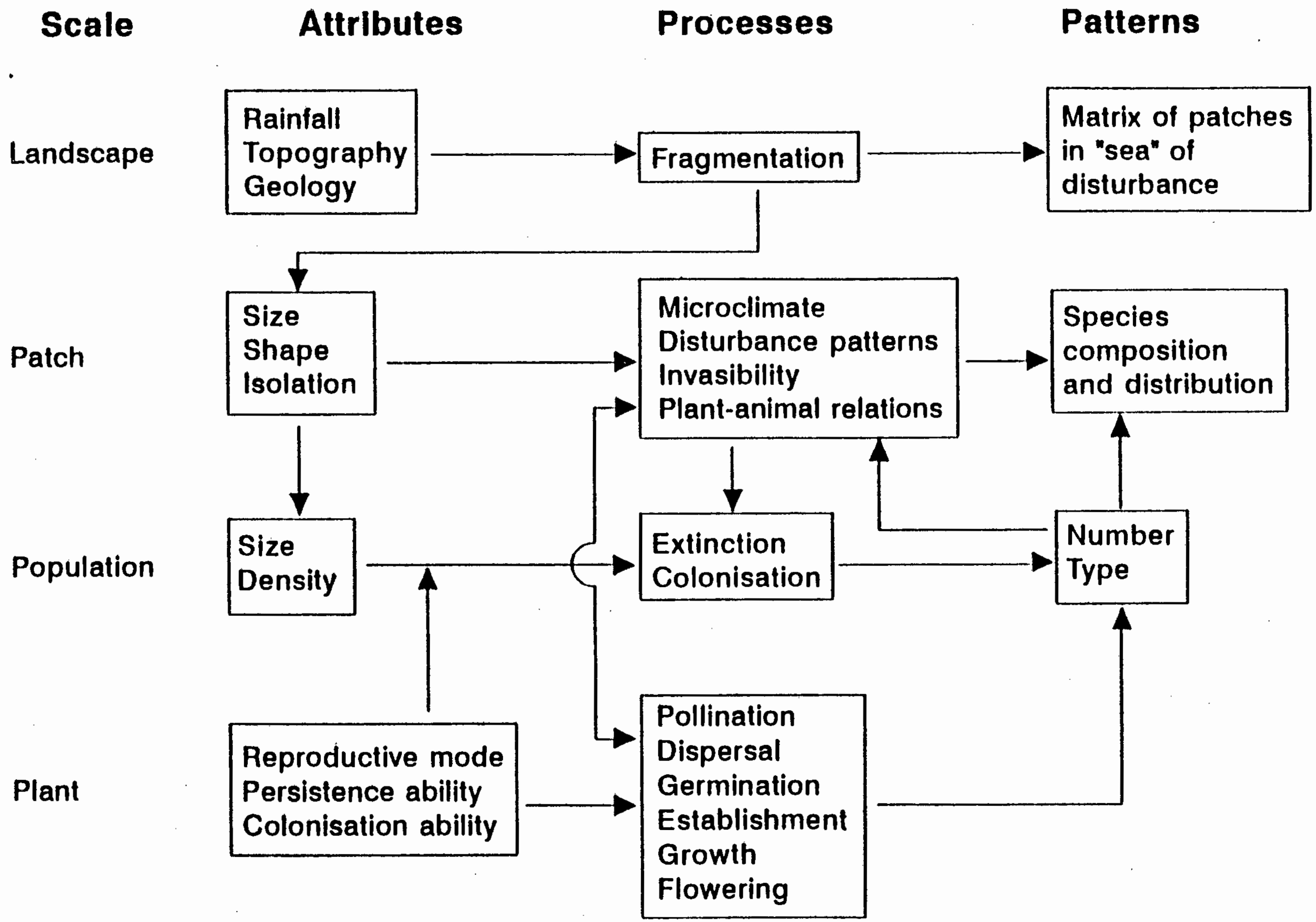

Figure 1.1: Conceptual model of fragmentation effects on vegetation at four interacting scales

Coast on the conservation status of the area (for example Tansley 1982, Jeffrey and Moll 1987, Moll *et al.* 1989, Jeffrey and Hilton-Taylor 1990, Killian 1995, Heydenrych and Littlewort 1996). It is thus evident that little in-depth work has been done on the effects of anthropogenic fragmentation in the species-rich Cape Floristic Region. This study, therefore, allows the opportunity for not only testing general theories relating to fragmentation, but also for identifying patterns and processes affected by fragmentation which may help in managing the remaining tracts of South Coast Renosterveld.

1.3 South Coast Renosterveld

South Coast Renosterveld is one of three forms of Coastal Renosterveld (Cowling and Holmes 1992). Recently, however, South Coast Renosterveld and South-west Coast Renosterveld have been redefined as one vegetation type (Low and Rebelo 1996). It is a non-fynbos vegetation type found within the fynbos biome (Cowling and Holmes 1992) and is mostly confined to the semi-arid and sub-humid coastal forelands of the southern Cape coast, with disjunct areas found along the south-eastern Cape coast (Figure 1.2). It is a small-leaved, grassy shrubland, largely restricted to fine-grained, clay-rich (Bokkeveld shale-derived) and moderately fertile soils, while neighbouring fynbos occurs on less fertile, acid sands. Rainfall varies from 300 to 600 mm per year, with most rain falling during the winter months (May to August) in the western parts, becoming more bimodal (spring-autumn) towards the east. Where rainfall drops below 300 mm, renosterveld is replaced by karoo vegetation; where rainfall exceeds 600 mm, it is replaced by asteraceous fynbos (Rebelo 1995). Where topographic features, such as river valleys, limit the spread of fires, renosterveld is replaced by thicket. It is not clear whether renosterveld is edaphically determined and it has been implied that in some cases fynbos has been replaced by renosterveld on the south-western (Cowling *et al.* 1988) and western coast (Boucher 1983), mainly as a result of repeated short-interval fires and overgrazing. Cowling *et al.* (1986) argued that present-day South Coast Renosterveld has been derived from grassland, dominated by *Themeda triandra*, a C_4 species, but owing to poor veld management and overstocking (Botha 1924, du Toit and du Toit 1938), has become increasingly shrubby. Isotope evidence from soil carbon (Stock *et al.* 1993) shows that renosterveld could have been a grassland before European settlement, but was dominated by C_3 species such as *Merxmuellera disticha*, *Erharta spp.* and *Pentaschistis spp.* rather than C_4 species.

South Coast Renosterveld is a biogeographically complex vegetation type, drawing elements from the Cape, the Karoo-Namib and the Afromontane floras (Taylor 1978). Regional species diversity levels are comparable to those of fynbos (Taylor 1978), with 1320 species listed by Acocks (unpublished data, in Taylor 1978); local richness is often higher in renosterveld than fynbos (Cowling *et al.* 1989). However, levels of endemism in South Coast Renosterveld are generally lower than in fynbos (Cowling 1984, Cowling *et al.* 1992). Members of the Asteraceae are common, particularly *Elytropappus rhinocerotis*, the renosterbos, after which this vegetation type was named. This is an indigenous but invasive species. Other ericoid-leaved shrubs include *Metalasia spp.*, *Helichrysum spp.* and *Eriocephalus spp.*. Grasses are abundant and include widespread taxa (for example *T. triandra*), but Cape taxa such as *Pentaschistis* and *Ehrharta* are common (Cowling *et al.* 1986). Although geophytes are less abundant in South Coast Renosterveld than West Coast Renosterveld (Acocks 1979), they form an important component of this vegetation type, with

Iridaceae and Oxalidaceae particularly well-represented. Ericaceae, Proteaceae, and Restionaceae, which are usually present in fynbos, are generally lacking in South Coast Renosterveld (Cowling and Holmes 1992, Rebelo 1995).

South Coast Renosterveld originally sustained large herds of eland, hartebeest, zebra and livestock belonging to Khoi herders before Euopean settlement (Rebelo 1995). For centuries, Khoi pastoralists migrated with sheep and later cattle along the Cape forelands, both in renosterveld and fynbos (Deacon 1992). It is estimated that up to one million sheep and 500 000 cattle were being herded in the southwestern Cape in the mid-17th century (Deacon 1992). Details of the fire and grazing practices of Khoi pastoralists and their effects on the vegetation and fauna are sketchy. It is known, however, that they used fire as a tool to encourage grass growth, but did not graze livestock on recently burned areas (Deacon 1992). Shortly after European settlement in the Cape in 1652, all large game within 200 km of Cape Town had been hunted to extinction (Deacon 1992). Although some animal species have been reintroduced, some species, such as the Bluebuck and Quagga are now globally extinct (Rebelo 1995).

1.4 Rationale

The relatively fertile substratum on which Coastal Renosterveld occurs makes it more prone to clearing for agriculture than neighbouring fynbos areas. Since the First World War, mechanisation made large-scale agriculture feasible in the southern Cape (Rebelo 1995). Since cereal cultivation began earlier in West Coast Renosterveld, fragments of natural vegetation in South Coast Renosterveld are generally younger

(Hoffman 1997). Between 32% and 85% of the natural extent of South Coast Renosterveld is estimated to have already been converted for agriculture to date (Moll and Bossi 1984, Rebelo 1995, Low and Rebelo 1996). Rates of transformation differ greatly between the two vegetation types. West Coast Renosterveld was transformed more gradually, with an estimated 80 000 ha cultivated between 1918 and 1990. In South Coast Renosterveld, 160 000 ha were transformed over the same period (Hoffman 1997). West Coast Renosterveld occurs on a level to gently undulating landscape and patches of natural vegetation are almost completely restricted to hilltops. Consequently, only 3-4% of its original extent remain (McDowell 1988, Rebelo 1995). South Coast Renosterveld is found on more incised, steeply rolling country, and patches are largely confined along steep incisions or in areas too rocky or dry for cultivation.

In addition, areas of South Coast Renosterveld which have traditionally been used as natural pastures, have been replaced by artificial pastures due to the vegetation's low carrying capacity, especially after prolonged overgrazing (Cowling *et al.* 1986). The remaining highly fragmented areas of South Coast Renosterveld should therefore be given top conservation priority, but only an estimated 0.8% of its original extent is conserved to date (Rebelo 1992). Reasons include the high cost of purchasing land with high agricultural potential (Cowling 1986, Rebelo 1992), relatively low levels of endemism (Rebelo 1992), and lack of attractiveness due to its fragmented nature and position in the landscape. The latter is identified as a major problem for the conservation of West Coast Renosterveld (McDowell 1988).

Although South Coast Renosterveld communities have been described in some detail in the eastern Cape (Cowling 1984), there are only a few generalised accounts of community structure for the southern Cape (see Muir 1929, Levyns1935, Rebelo 1995, Low and Rebelo 1996). This study was, therefore, initiated to increase the knowledge of South Coast Renosterveld community structure and the effects that fragmentation has had on this vegetation type. It forms part of a multi-disciplinary study with Western Cape Nature Conservation and the National Botanical Institute, with the broad aim of using this information to identify conservation priorities and improving management strategies in an already fragmented system.

1.5 Study sites

Most of the project (Chapters 3, 4 and 5) was carried out on Fairfield Farm, about 15 km northwest of Napier in the Overberg region of the southern Cape (24°50'S 19°46'E) (Figure 1.2). It receives a mean annual rainfall of 390 mm, with June to August being the wettest and December and January the driest months of the year. Mean monthly temperatures range from 11.5°C in July to 22°C in January (see Figure 1.3 for details). Roughly 50% of the 9000ha farm occurs on moderately fertile, clayey soils, once occupied by renosterveld. The major crop is wheat (see Table 1.1); livestock include sheep, cattle and some game. The landscape is gently undulating with steep, winding incisions, along which large stretches of renosterveld can still be found.

The farm is divided into a series of fenced camps. Large tracts of renosterveld are used as natural grazing camps and are managed by burning to encourage the growth of palatable grasses. Other camps consist of cereal fields or artificial pastures with scattered patches of renosterveld. These patches are grazed seasonally, especially between harvest and sowing of the next crop. Cereal fields are ploughed in autumn, just before the first rains. Between July and early September, fields are sprayed twice with pesticides. Crops are harvested during late spring, and the remaining stubble is burned in late summer. Small and medium-sized fragments are managed inclusive of cultivated fields, and are therefore directly exposed to spraying with herbicides and insecticides and seasonal burning. However, fragments do not burn every year.

The majority of the study (see Chapters 3 and 4) is based on "natural snapshot experiments" (*sensu* Diamond 1986) - the comparison of systems thought to have attained a state of equilibrium with respect to the variable of interest. While this approach is completely realistic, without need for extrapolation, variables other than the one being investigated cannot be controlled. Thus, true replication of sites (*sensu* Hurlbert 1984) is not possible. In addition, a "snapshot" approach only allows the comparison of systems at one point in time, and does not permit the monitoring of system change with time. This should be kept in mind when interpreting results.

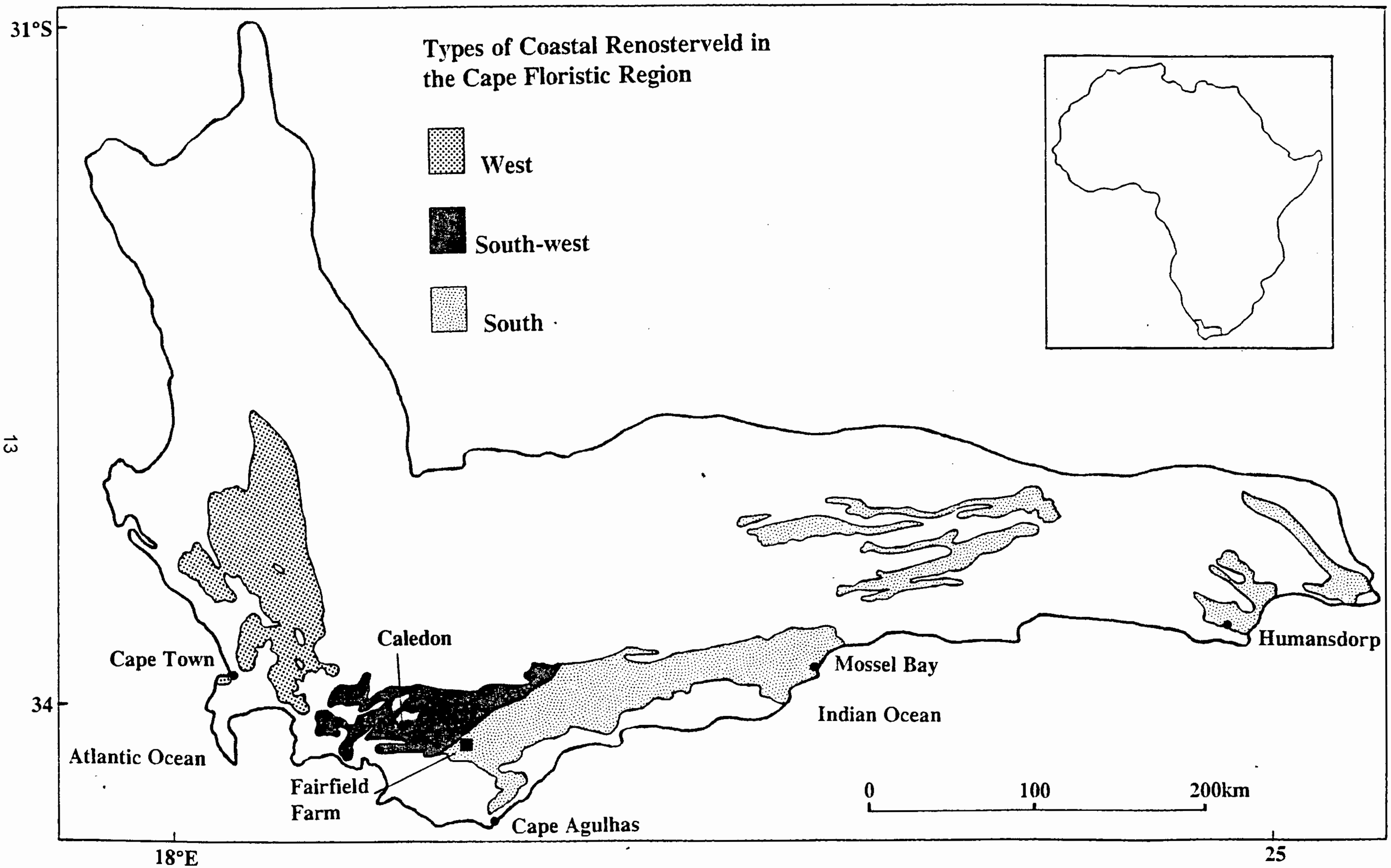

Figure 1.2: The distribution and original extent of the three major types of Coastal Renosterveld in the Cape Floristic Region (adapted from Rebelo 1995). Note that South-west and South Coast Renosterveld are now regarded as one vegetation type (Low and Rebelo 1996)

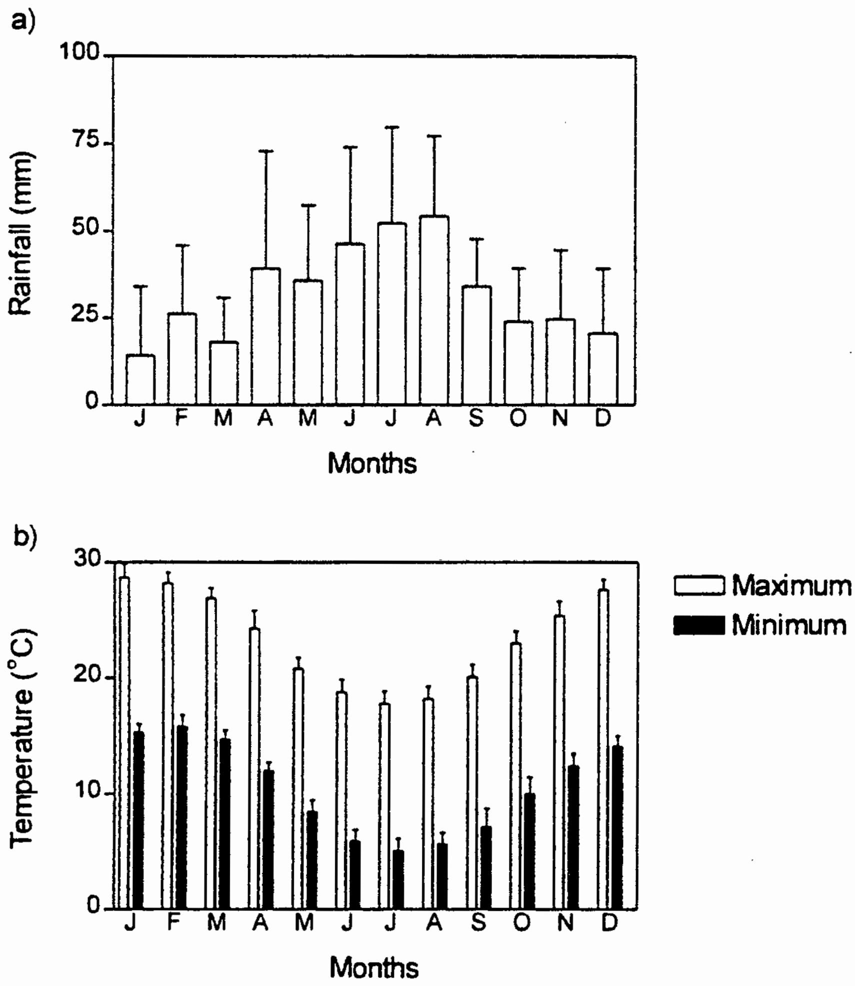

Figure 1.3: Climate data for the study site. Data are from the Napier police station (rainfall) and Riviersonderend weather station (temperature) (South African Weather Bureau) a) mean (+SD) monthly rainfall (1968-1983); b) mean (+SD) monthly minimum and maximum temperatures (1965-1987).

For the purposes of this study, we identified three fragment size-classes: small = <2ha, medium = 2.5-12ha, large = >30ha. This design therefore lacks a true "control" since large tracts are also fragments. We selected eight replicates of each fragment size-class (see Table 1.2 for exact sizes), choosing only one site per camp to ensure adequate "replication". Three sites were chosen from adjacent farms with the same management strategies. Sites were selected with similar aspects (E-SE), on moderate slopes, and on shallow duplex soils with mature vegetation. One small fragment burned during the course of the experiment and could not be replaced by another suitable fragment. The experimental design focuses on the effects of fragmentation on vegetation patterns at the local or point scale. It therefore explicitly factors out habitat diversity.

Fairfield has been owned by the same family since 1853 and the pattern of landuse has changed little since 1945 (P.K. van der Byl pers. comm.). Aerial photographs show that by 1938, five out of the 15 small and medium-sized fragments used in the study were already fragmented to their current size, with 10 fragments either unfragmented or larger than today. By 1961, nine fragments had been fragmented to their present extent; six fragments have undergone further fragmentation since 1961 (Table 1.3). Hence, the experiment has been "initiated" at different times.

Table 1.1: Landuse on Fairfield Farm and two adjacent farms (adapted from Donaldson *et al.* in prep.)

Total area surveyed	4900 ha
Cereals and pastures	79.9%
Natural vegetation	16.4%
Other	3.7%
No. of patches of natural vegetation	57

Table 1.2: Dimensions of fragments of renosterveld on Fairfield farm used in the study of vegetation patterns and processes. The dimensions of small and medium fragments have changed substantially over the last 60 years (see Table 1.3).

Fragment size class	Fragment number	Area (ha)	Perimeter (m)	Perimeter : Area ratio (m/ha)
Small	1	0.57	663.05	1163.24
	2	0.81	506.13	624.85
	3	0.41	358.08	873.37
	4	1.97	757.65	384.59
	5	0.21	229.50	1092.87
	6	0.22	214.11	973.25
	7	0.06	107.77	1796.12
	Mean:	0.61	405.18	986.90
Medium	8	12.19	2172.84	178.25
	9	3.43	1027.96	299.70
	10	2.66	787.99	296.24
	11	6.12	2180.92	356.36
	12	9.00	4198.319	466.48
	13	3.62	1587.74	438.60
	14	10.00	1972.38	197.24
	15	2.59	765.71	295.64
	Mean:	6.20	1836.73	316.06
Large	16	46.49	3191.42	68.65
	17	29.89	3200.48	107.07
	18	30.00	2318.06	77.27
	19	153.35	5396.09	35.19
	20	84.67	7310.02	86.34
	21	58.29	4697.72	80.59
	22	118.84	9472.98	79.71
	23	42.37	5868.62	138.51
	Mean:	70.49	5181.92	84.17

Table 1.3: Change in sizes of small and medium-sized fragments between 1938 and 1994

Fragment number	1938	1961	1994
1	large	medium	small
2	medium	medium	small
3	medium	medium	small
4	large	medium	small
5	small	small	small
6	small	small	small
7	large	large	small
8	large	medium	medium
9	medium	medium	medium
10	large	medium	medium
11	large	medium	medium
12	large	medium	medium
13	medium	medium	medium
14	medium	medium	medium
15	large	large	medium

1.6 Specific Aims

This thesis is divided into three substantive parts, each with its own but interlinked set of aims. The different parts address different hierarchical levels in terms of both spatial and temporal patterns and processes. Part 1 deals with landscape level phenomena, part 2 with community level phenomena and part 3 with population level phenomena.

1.6.1 Fragmentation patterns at the landscape scale

The study of landscape ecology has provided a strong basis for understanding landscape structure and function (Forman and Godron 1986, Turner 1989). Much emphasis has been placed on developing procedures for quantifying landscape structure, and the advances of GIS technology have made a variety of analytical tools accessible for analysing and managing landscapes (McGarigal and Marks 1994). Only scant information exists regarding the extent to which South Coast Renosterveld as a whole has been fragmented by agriculture (see Moll and Bossi 1984). The primary objective is therefore to assess the overall extent of South Coast Renosterveld fragmentation and to quantify fragmentation patterns in terms of landscape attributes using GIS technology. Since patterns of fragmentation can be directly linked to agricultural potential, fragments are expected to be generally associated with steep slopes, in areas where rainfall seasonality is not suitable for the production of winter cereals. Since topography and rainfall seasonality patterns change from the western to the eastern boundary of South Coast Renosterveld, fragmentation patterns are therefore hypothesised to change along that gradient. An assessment of fragmentation patterns and in particular patch size and connectivity can yield important insights for identifying suitable conservation areas.

1.6.2 Vegetation composition and guild structure of South Coast Renosterveld fragments

Anthropogenic fragmentation has been shown to be detrimental to many species and may contribute substantially to the loss of regional biodiversity (Saunders *et al.* 1991). The aims of this study were therefore to compare floristic composition, diversity and guild structures across fragments of different sizes, and to assess to what extent species composition on small fragments are impoverished subsets of those found on large, continuous tracts of natural vegetation. The results allow the identification of species or functional groups which are likely to become locally extinct first. This information will help recognise underlying processes affected by fragmentation and may provide management guidelines for conserving threatened plant groups. The identification of a relationship between patch area, shape and isolation and species diversity patterns will help in determining the potential value of patches of different size in preserving biodiversity.

1.6.3 Plant reproductive success

Plant reproductive success can be influenced by fragmentation in various ways: changes in plant-pollinator interactions and reduced population sizes affect plant reproductive success in various ways. The degree to which fragmentation will affect reproductive success ultimately depends on the reproductive strategy of the plant (Bond 1994). This study therefore examines the influence of fragmentation on reproductive success measured through fruit and seed production and germination success in two plant species with different reproductive strategies. This information provides the basis for identifying processes affecting plant demography and how this understanding should influence decisions on conservation priorities.

1.7 Thesis Structure

This thesis is divided into six chapters including this introductory chapter. The following chapters form the main body of the thesis, where findings are presented and discussed. Chapters were written in a format that can easily be adapted for scientific publication, which means that some details are repeated in more than one chapter. Owing to the more extensive literature review required by a thesis, chapters tend to be longer than required for publication. A scale-based approach in dividing the study into chapters was used. Chapter 2 describes landscape patterns of South Coast Renosterveld. Chapter 3 compares floristic composition across fragments and discusses whether any patterns can be explained in terms of fragmentation effects or other environmental variables. Chapter 4 investigates species diversity and guild structure patterns with different fragment sizes. Chapter 5 discusses the consequences of fragmentation on reproductive attributes of two geophyte species. Chapter 6 is a concluding discussion, where significant findings and limitations of this study are reviewed. Appendix 1 comprises a species list recorded at the study site.

Plate 1.1: Aerial view of the mosaic of agricultural lands and South Coast Renosterveld fragments.

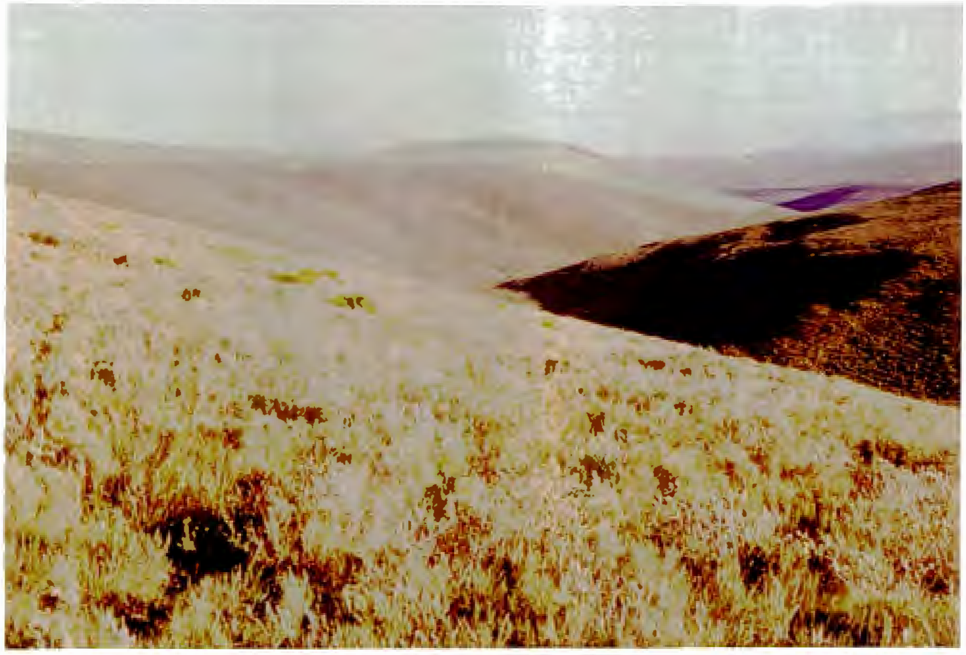

Plate 1.2: Large fragments tend to be confined to steep, winding incisions (top). This fragment is used as a natural grazing camp. Small fragments are managed inclusive of surrounding wheatfield (bottom) and are therefore exposed to intense seasonal grazing, frequent burning and crop-spraying.

1.8 References

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Chapter 2

Landscape patterns and their correlates

2.1 Abstract

South Coast Renosterveld has been transformed extensively by agriculture. The extent and pattern of this transformation has not been studied, thereby limiting the development of conservation strategies for this vegetation type. I described renosterveld fragmentation patterns and spatial arrangement along a west-east gradient using LANDSAT imagery and a Geographical Information System-based spatial pattern analysis programme. I correlated fragmentation patterns with rainfall and topography measures as indices of agricultural potential. Over 80% of South Coast Renosterveld has been cultivated. This confirms its critical conservation status. Fragmentation levels decreased significantly along a west-east gradient with 4% of natural vegetation remaining in the west, and 33% in the east. This indicates the potential for large reserves in the east, as well as corridor reserves along major river valleys. However, the expected greater species richness in the west suggests that small western reserves will also be needed. Topographical variables were the strongest correlates of the extent of untransformed renosterveld; renosterveld fragments were largely confined to slopes too steep for ploughing. They, therefore, face little risk of future cultivation. My results will allow the formulation of strategies for renosterveld conservation, and the integration of agricultural and conservation goals.

2.2 Introduction

Human activity is causing the global destruction and modification of vast areas of natural vegetation. The resultant landscape mosaic is a combination of natural and human-managed fragments that differ in type, abundance, size, shape and arrangement (Forman and Godron 1981, Krummel *et al.* 1987, Turner and Ruscher 1988, Turner 1989). In agricultural landscapes, most of the native vegetation has been removed, and the size and degree of isolation of the remaining fragments create a high risk of species extinction and genetic isolation (Ledig 1986, Wilcove *et al.* 1986, Meffe and Carroll 1994). Landscape ecology developed in response to the need to increase the scale of investigation from single species or communities to complex landscape mosaics (O'Neill *et al.* 1988). Landscapes are ecological units which are defined by structure (composition and configuration), function (e.g. nutrient fluxes, metapopulation dynamics, disturbance regimes) and change in structure and function with time (Forman and Godron 1981, Turner 1989, Hobbs 1995).

Numerous methods and indices for quantifying patterns at the patch, patch type and landscape scale have been developed (O'Neill *et al.* 1988, Turner 1990, Turner and Gardner 1991, Cullinan and Thomas 1992, Baskent and Jordan 1995, Medley *et al.* 1995). Used together with remote-sensing and image-processing techniques and Geographical Information System (GIS) technology, these landscape indices allow the identification, measurement and monitoring of regional ecological patterns and the spatial relationship between natural and man-made systems. A number of theoretical and empirical studies have used the principles and methods of landscape ecology to examine landscape structure, function and change and how they influence smaller-scale structure and function:

For example, Franklin and Forman (1987) showed empirically that fragments size, and the amount of edge and distance between habitat patches following forest clear-cutting, have direct effects on the native flora and fauna. Studies by Fahrig and Merriam (1985) and Fahrig and Paloheimo (1988) examined the relative importance of spatial relationships among habitat patches for different organisms. They concluded that the importance of spatial relationships among patches varies with the dispersal strategy of the organism. Harrison *et al.* (1988) illustrated that the distribution of the bay checkspot butterfly is sensitive to patch spatial arrangement. High patch size variance was proposed to increase the probability of the species' survival.

Aspects of the relationship between landscape structure and function have been explored by Baker (1993) who used simulation experiments to show that fire suppression has altered several aspects of landscape structure in the Boundary Waters Canoe Area, Minnesota. He concluded that spatially-explicit prescribed burning programmes were needed to restore these altered landscapes. Medley *et al.* (1995) attributed changes in fragmentation patterns and their effect on decreasing water quality to changes in agricultural practices since World War II. Removal of natural vegetation has been shown to increase soil salinity and erosion in the wheatbelt of Southwestern Australia (Saunders *et al.* 1993). Fragmentation is generally not a haphazard process (Usher 1987), and landscape structure may mirror environmental factors such as topography and soil type (Turner 1989). Sharpe *et al.* (1987) correlated size and isolation of forest patches in Wisconsin with environmental data and found patterns of presettlement forest closely related to topography and natural disturbance. Any subsequent deforestation was selective.

Theoretical studies on changes in landscape pattern have generally found that the rate of change is far more important than the spatial pattern itself (Harrison and Fahrig 1995). A large number of recent studies have quantitatively analysed changes in landscape pattern through time (Turner and Rusher 1988, Dunn *et al.* 1990, Fojt and Harding 1995, Hulshoff 1995, Vogelmann 1995, Reed *et al.* 1996). This information is used to evaluate the changing character of interior to edge habitat (Ripple *et al.* 1991) or is coupled with simulation modelling to predict future landscape pattern changes (Turner 1987) and how they will affect landscape function (Hall *et al.* 1995).

The results of landscape analyses are widely used to monitor natural resources and to aid conservation and development planning (Noss 1983, Knight and Wallace 1989, Turner 1989, Hobbs *et al.* 1993, Reed *et al.* 1996). Conservation programmes are either designed for individual (endangered) species or for preserving biodiversity. Individual species programmes focus on integrating the species' resource requirements with landscape patterns (Arnold 1995). A classic case is the northern spotted owl (Lamberson *et al.* 1992, McKelvey *et al.* 1993) which requires habitat patches of a minimum size as well as a specific arrangement to conserve metapopulations of the species over its whole range. Management of species diversity focuses on the retention of as many areas as possible of each community type (landscape heterogeneity) and the role of corridors in linking fragments (Arnold 1995).

South Coast Renosterveld occurs on clay-rich, fertile soils, which make this area highly suitable for cereal cultivation (see Chapter 1 for a detailed account). During the last century, it has undergone large-scale loss of natural vegetation (Cowling *et al.* 1986). Only rough estimates of the amount of loss of natural vegetation are available (Moll and Bossi 1984, Low and Rebelo 1996) and no account of the number, size and spatial arrangement of renosterveld fragments exists. Despite its critical conservation status, only 0.8% of South Coast Renosterveld is formally conserved (Rebelo 1992). An overview of renosterveld patterns and spatial arrangement, together with a knowledge of smaller scale patterns and processes (see following chapters) may provide useful information for developing strategies for renosterveld conservation. The identification of environmental correlates of the extent of natural vegetation will allow predictions of future threats to the remaining natural vegetation.

Reliable winter rainfall is a prerequisite for cereal cultivation in the warm temperate Western Cape. Rainfall patterns across the distribution of South Coast Renosterveld change along a west-east gradient: winter rainfall (west) changes to a bimodal spring-autumn regime (east) (Deacon *et al.* 1992). In addition, slope strongly influences agricultural practices. The following guidelines are set by the Agricultural Resources Act: land can be worked on slopes <1.8°; on slopes between 1.8° and 8.1°, land can be worked but measures to prevent erosion, such as the construction of contours, must be taken; land with slopes >8.1° cannot be worked. Slope also changes along a west-east gradient, with gently rolling, almost flat country in the west being gradually replaced by a steeper topography in the east.

In this study I examine South Coast Renosterveld landscape structure. My objectives were to: (1) provide a broad regional overview of the patterns of fragmentation of South Coast Renosterveld, and of the spatial relationship between natural and modified patches; (2) describe how these patterns change along a west-east gradient; and (3) identify correlates of landscape patterns in terms of agricultural potential, as indexed by measures of rainfall and topography.

2.3 Methods

2.3.1 Landscape composition and configuration

1992-1994 LANDSAT Thematic Mapper satellite imagery was used to develop a landcover map. This landcover map forms part of a standardised landcover database for the entire country, at a 1:250000 scale. This national project was initiated by the Council for Scientific and Industrial Research (CSIR) and the Institute of Soil, Climate and Water (Agricultural Research Council). Landcover data were classified based on known and identifiable landcover types (Thompson 1996). The extent of my study area was limited to those areas underlain by Bokkeveld shale and further bounded by the foothills of the Riviersonderend and Langeberg mountain chains in the north and the town of Mossel Bay to the east (Figure 2.1). This area includes the largest contiguous block of South Coast Renosterveld in the Cape Region (Low and Rebelo 1996).

I categorised landcover into three classes: renosterveld; cultivated land, including perennial crops (e.g. orchards, vineyards) and annual crops (cereals, artificial pastures); other, including waterbodies, fragments of non-renosterveld vegetation, residential and industrial sites and quarries. Annual crops make up the bulk of cultivated land in the study area. I included only fragments > 6ha (all classes). The landcover map was manipulated on a SUN workstation using ARC/INFO ver. 7.0.4.

Edge width was set at 30m. I assessed and improved mapping accuracy by ground referencing accessible sites. I divided the study area subjectively into three sectors (west, central, east) to allow the quantification of landscape pattern change along a west-east gradient. The boundaries were drawn to ensure minimal splitting of fragments into different sectors.

I analysed the full landcover dataset as well as the three subsets with the vector version of FRAGSTATS version 2.0 (McGarigal and Marks 1994). This is a spatial pattern analysis programme which computes a number of statistics describing landscape composition and configuration. I used the raster version of FRAGSTATS to calculate nearest-neighbour distance. Table 2.1 gives detailed definitions for measures core area, shape index, nearest-neighbour distance and interspersion and juxtaposition index.

Table 2.1: Definitions of some landscape measures. Adapted from McGarigal and Marks 1994).

Measure	Definition/Calculation	Unit	Range
Core area	Area within fragment further than the specified edge distance from the patch perimeter, here 30m	ha	≥0
Shape index	$p_i/(2\sqrt{\pi a_i})$ where p_i = perimeter of fragment i, a_i = area of fragment i. Shape = 1, if fragment is circular	n/a	≥1
Nearest-neighbour distance	Distance to nearest neighbouring fragment of the same landcover class, based on edge-to-edge distance	m	>0
Interspersion and juxtaposition index	$-\sum[\{(e_{ik} / \sum e_{ik}) \ln (e_{ik} / \sum e_{ik})\} / \{\ln (m-1)\}]$ where e = total length of edge in the landscape between landcover classes i and k; m = number of landcover classes. Index approaches 0 if landcover classes are poorly interspersed, 100 if maximally interspersed (i.e. equally adjacent to each other)	%	$0<x\leq100$

I tested for significant differences in mean values for each sector (west, central, east) of fragment area, perimeter, shape and nearest neighbour distance of renosterveld, as well as mean fragment area of cultivated land using Kruskal-Wallis one-way analysis of variance by ranks. This non-parametric analysis was chosen because data were non-normally distributed. In addition, chi-square analysis was used to test the null hypothesis that renosterveld fragment size classes were distributed in the same frequency in the different sectors. Classes were as follows: <10ha, 10-50ha, 51-200ha, >200ha.

2.3.2 Correlates of landscape patterns

I obtained annual and monthly rainfall figures for 17 weather stations located in the study area from a national rainfall database (Anonymous 1996a). The weather stations were located on the landcover map and a cell (10X10km) was centred on each station. I assumed climate data to remain uniform within the $100km^2$ cell. In six cases, cells fell partially outside the study area; these were shifted to be completely included (Figure 2.1). The landcover map was used to calculate percent renosterveld within each cell. This experimental design was limited by the non-random distribution of weather stations.

I used a national digital elevation model (Anonymous 1996b) to measure slope within each $100km^2$ cell. Resolution was 400 x 400m, with steep areas interpolated to 200 x 200m. This coverage was overlaid on the landcover map. Slope was sampled from 50 randomly located points within each $100km^2$ cell. I chose the following explanatory variables in attempts to describe the distribution of renosterveld in the study area:

- total annual rainfall (mm)

- rainfall seasonality: (rainfall between May and September / total annual rainfall*100) (%)
- coefficient of variation of the rainfall in the three wettest months: (standard deviation / mean rainfall of the three wettest months over n years) (%)
- mean slope angle (°)
- coefficient of variation of slope angle: (standard deviation / mean slope angle) (%)

All variables were tested for normality. Percent renosterveld and rainfall seasonality were arcsin-transformed. Spearman rank correlation analysis was performed to test for collinearity among explanatory variables and for the strength and form of relationships between % renosterveld and the explanatory variables. Multiple regression was used to model renosterveld cover.

2.4 Results

2.4.1 Landscape composition and configuration

The study area covered 816796 ha (Figure 2.1); of this 117967 ha (14.4%) was natural vegetation, 672194 ha (82.3%) was cultivated, 26954 ha (3.3%) was classified as "other" and will not be discussed further (Table 2.2). Thus, the area is overwhelmingly dominated by agricultural and natural vegetation as opposed to residential/industrial landcover types. Renosterveld was highly fragmented with 394 fragments scattered throughout the landscape (Table 2.2). On average, renosterveld fragments were 4% the size of cultivated fragments (Table 2.2). Variance of fragment size was similar for both landcover classes.

Both renosterveld and cultivated land showed changes in landscape measures along a west-east gradient (Table 2.2). Renosterveld was most fragmented in the west with a large number of small fragments embedded in a sea of cultivated land. Renosterveld made up 4.4% of the western sector. By contrast, 33.4% of the eastern sector was composed of renosterveld, with a mean fragment size nearly 20 times greater than in the west and more than twice the mean fragment size in the central sector. The extent of cultivated land decreased from nearly 89.7% in the west to 62.8% in the east, where cultivated land was most fragmented. Mean size of cultivated fragments decreased from west to east by nearly 97%. Despite these drastic changes in mean fragment sizes along a west-east gradient , median fragment size remained fairly even for both renosterveld and cultivated land. This reflects the skew (non-normal) distribution of fragment sizes. Most renosterveld and cultivated fragments were comparatively small, and the presence of a few very large fragments resulted in large mean fragment size values. The variance of renosterveld and cultivated fragment size increased from west to east. Kruskal-Wallis analysis of variance for both landcover classes showed that renosterveld fragment size differed significantly between sectors ($H = 41.68$, $p<0.001$). Mean fragment size of cultivated land did not differ significantly between sectors ($H = 1.74$, $p = 0.419$).

Table 2.3 lists a number of additional composition and configuration measures for renosterveld. Core area, or the area of renosterveld not affected by edge effects, a function of fragment shape and edge width, made up 13.28% of the total landscape, again showing an increase from west to east. The amount of edge (as indexed by total edge and edge density) also increased from west to east. This is the direct result of an increase in total renosterveld area as well an indication of an increase in shape complexity along a west-east gradient. The increase in mean fragment shape from west to east indicates that fragments changed from rounded, compact shapes to more irregular, elongated shapes. Median shapes followed a similar pattern.

Associated with an increase in size and shape complexity was a decrease in mean isolation towards the east as measured by nearest-neighbourhood distance. However, inter-fragment distances tended to vary more towards the east. Median nearest-neighbour distances however suggested that isolation was generally lower than the means suggest, except in the eastern sector. A high interspersion and juxtaposition index showed that renosterveld fragments were well interspersed within the central sector, whereas in the western and eastern sectors, fragments were poorly interspersed and tended to be clumped. Kruskal-Wallis one-way analysis of variance of mean fragment perimeter, mean shape, and mean nearest-neighbour distance showed significant changes along a west-east gradient in terms of edge per fragment ($H = 43.518$, $p<0.001$), shape complexity ($H = 28.105$, $p<0.001$) and isolation ($H = 22.576$, $p<0.001$).

The results of the Chi-square analysis (Figure 2.2) show that the frequency of fragment size classes varied significantly along the gradient. Small fragments (<10 ha) were overrepresented in the west. Large fragments (>200 ha) were overrepresented in the east.

2.4.2 Correlates of landscape patterns

Spearman rank correlation analysis revealed a weak but significant negative relationship between rainfall seasonality and rainfall variation (CV) of the three wettest months ($r_s = -0.65$, $p<0.01$), as well as rainfall seasonality and mean slope ($r_s = -0.60$, $p<0.05$) (Table 2.4). This indicates some collinearity between these explanatory variables. No other significant collinearities were found. The strongest relationship between renosterveld extent and each of the rainfall and topographic variables is shown Figure 2.3. The correlations indicate a decrease in renosterveld extent with a shift in rainfall seasonality from a bimodal spring-autumn to a winter rainfall pattern (Figure 2.3.a). There was a strong positive relationship between slope increase and renosterveld extent (Figure 2.3.b). Total annual rainfall and variation in rainfall of the three wettest months was least correlated with renosterveld extent. All bivariate relationships were linear. The multiple regression equation using the explanatory variables most strongly correlated with renosterveld extent, rainfall seasonality and mean slope, was:

REN = - 16.312 - 0.520 SEA - 16.598 MES

R^2 (adj) = 0.82, n = 17, F-ratio = 38.283, p<0.001

where REN = percent renosterveld (arcsin-transformed), SEA = rainfall seasonality (arcsin-transformed), MES = mean slope.

The equation for the final model of stepwise multiple regression using all five rainfall and slope variables was:

REN = - 84.082 + 17.288 MES + 70.531 CVS

R^2(adj) = 0.9, n = 17, F-ratio = 71.375, p<0.001

where REN = percent renosterveld, MES = mean slope, CVS = variation in slope.

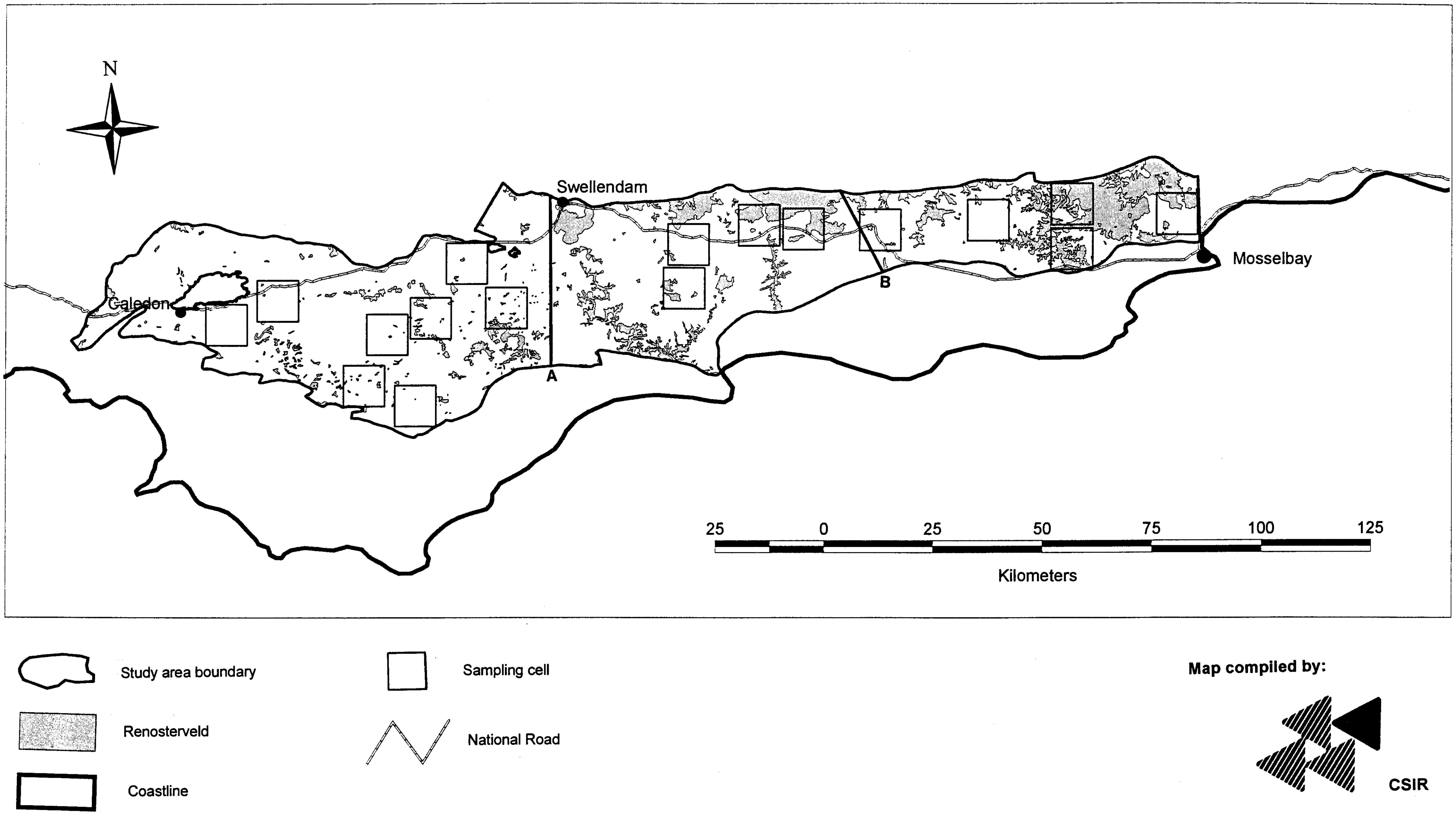


Figure 2.1: Extent of the study area showing renosterveld fragments and position of the 17 sampling cells. A=boundary between western and central sectors; B=boundary between central and eastern sectors. See text for details.

Table 2.2: Summary of landcover class composition in each of three study area sectors and for the total study area. Landcover classes: renosterveld (Natural) and cultivated land (Cultivated). Figures for landcover class "other" are not shown.

Metric (units)	Sector						Total	
	West		Central		East			
Total extent (ha)	395 587.4		258 336.3		162 872.7		816 796.3	
	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated
Number of fragments	271	6	81	13	42	59	394	76
Fragment density (no/100ha)	0.07	0	0.03	0.01	0.03	0.04	0.05	0.01
Total area (ha)	17 420.7	354 674.1	46 196.3	210 866.4	54 349.5	106 652.9	117 966.6	672 193.5
Percentage of landscape (%)	4.4	89.7	17.9	81.6	33.4	62.8	14.4	82.3
Mean fragment size (ha)	64.9	59 112.4	570.3	16 220.5	1 294.0	1 807.7	300.2	8 844.7
Median fragment size (ha)	24.6	41.1	69.9	76.6	86.9	106.2	30.7	88.2
CV[1] of fragment size (%)	249.1	223.4	339.3	340.7	441.7	578.8	702.7	735.4

[1]CV = coefficient of variation

Table 2.3: Summary of statistics describing renosterveld fragment composition and configuration in each of the three study area sectors and for total study area. Refer to Table 2.1 for the definitions of some metrics.

Metric (units)	Sector			Total
	West	Central	East	
Total core area (ha)	14 523.4	42 921.8	54 096.1	108 450
Core area percentage of landscape (%)	3.67	16.61	33.2	13.28
Total edge (km)	100.3	110.8	112.9	323.6
Edge density (m/ha)	2.54	4.29	6.93	3.96
Mean shape index	1.44	1.85	1.97	1.58
Median shape index	1.34	1.57	1.60	1.40
Mean nearest-neighbour distance (m)	903.2	764.8	704.4	839.2
Median nearest-neighbour distance (m)	600.0	400.0	712.3	447.2
CV[1] of nearest-neighbour distance (%)	91.52	105.87	162.19	98.87
Interspersion and juxtaposition index (%)	4.51	18.78	8.11	10.81

[1]CV = coefficient of variation

Table 2.4: Spearman rank correlation analysis of explanatory and response variables.

	Total Rainfall	Seasonality	CV[1] 3 wettest months	Mean slope	CV slope
Seasonality	r_s=-0.1667 NS				
CV 3 wettest months	r_s=-0.3113 NS	r_s=-0.6520 **			
Mean slope	r_s=1.667 NS	r_s=-0.6029 *	r_s=0.2770 NS		
CV slope	r_s=0.1373 NS	r_s=-0.4485 NS	r_s=0.2059 NS	r_s=0.2525 NS	
% renosterveld	r_s=-0.0833 NS	r_s=-0.6642 **	r_s=0.4216 NS	r_s=0.7034 **	r_s=0.5931 *

[1]CV = Coefficient of variation

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

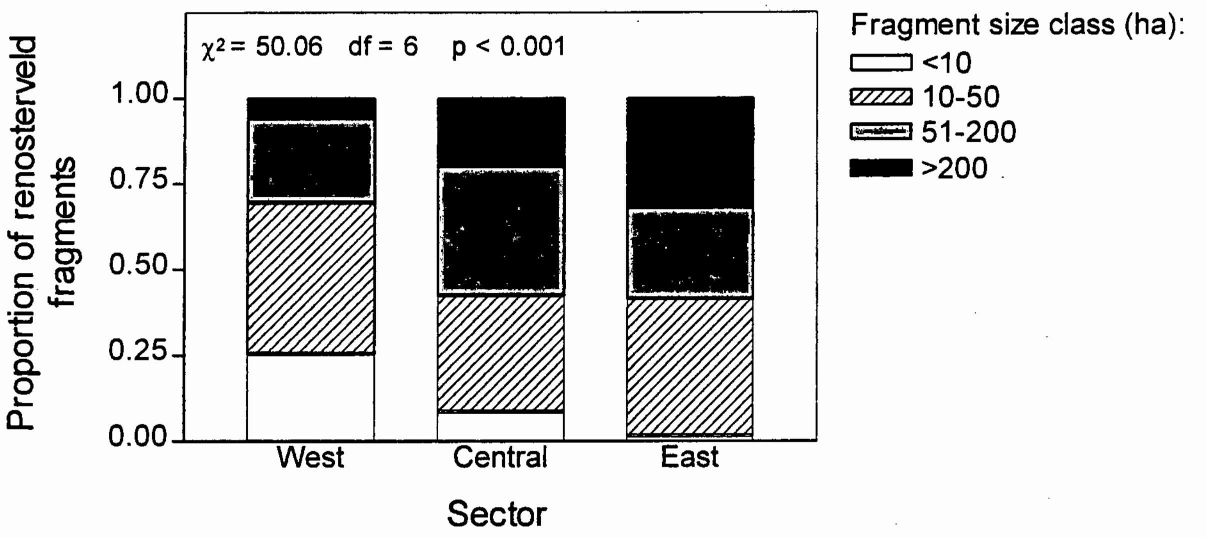
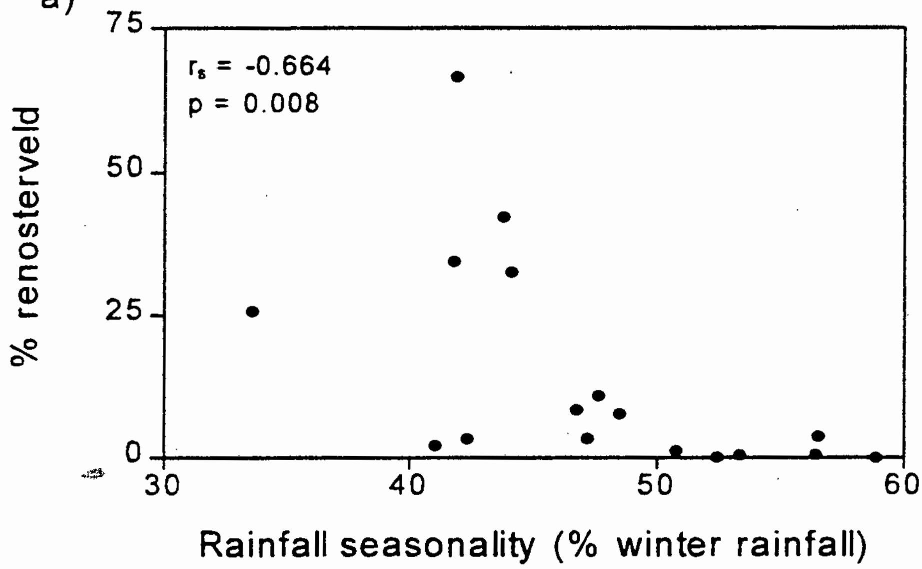


Figure 2.2: Proportion of South Coast Renosterveld fragments in each of four size classes for three study area sectors. Results of Chi-square analysis, degrees of freedom and significance are shown. Chi-square analysis was carried out on frequency (untransformed) data.

a)



b)

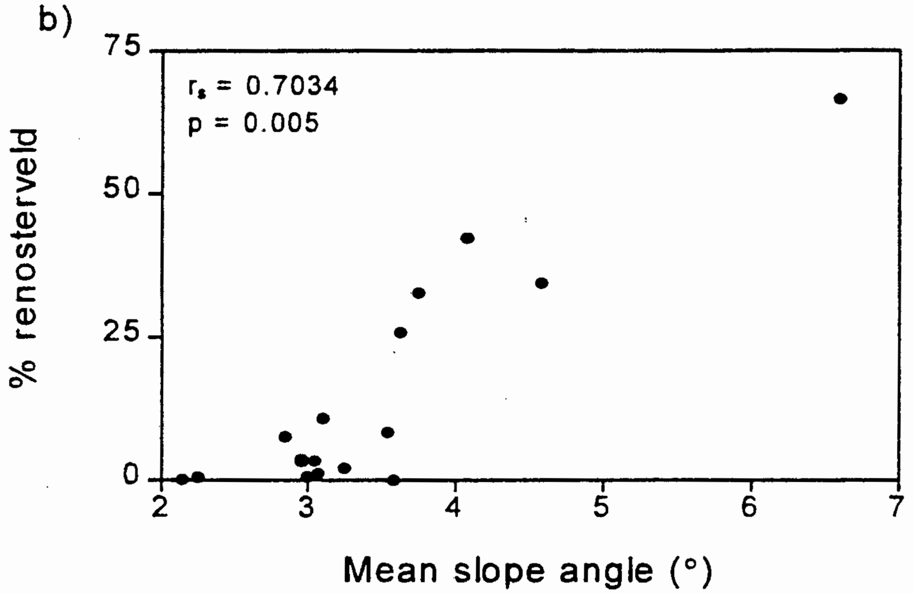


Figure 2.3: Scatter diagram of renosterveld extent per square plotted against a) rainfall seasonality, b) mean slope angle. Percentage data was arcsin-transformed. Correlation coefficients obtained from Spearman's rank correlation analysis and significance levels are reported. Data were tested for normality

2.5 Discussion

2.5.1 Landscape composition and configuration

Two main patterns emerge from this study. Firstly, over 80% of South Coast Renosterveld has been replaced by cultivation. This value is particularly alarming, because cultivated land can be classified as a "hostile" landcover type, which forms sharp boundaries with fragments of natural vegetation (Wiens 1995). Cultivated land is ploughed, planted, sprayed and burned annually, and therefore offers virtually no chance for the colonisation and establishment of biota from renosterveld fragments. Vast areas of hostile matrix, moreover, form barriers between fragments of natural vegetation, minimising successful dispersal and increasing the risk of species extinction (Meffe and Carroll 1994).

Secondly, the study showed a significant decrease in fragmentation levels of South Coast Renosterveld along a west-east gradient. Decreases in number of renosterveld fragments and nearest neighbour distance were accompanied by increases in total fragment area, mean fragment size, shape complexity as well as fragment size variability. These results agree well with the trends described by Godron and Forman (1983) and Krummel *et al.* (1987), which predicted that in an increasingly managed landscape, the overall number of fragments would increase, fragments would become smaller, and the shape of fragments would become more regular and circular, a common consequence of human activities, which often simplify patch boundary complexity. The level of fragmentation of South Coast Renosterveld in the western sector is comparable to that of West Coast Renosterveld, where only 3% natural vegetation remains (McDowell 1988, Heydenrych and Littlewort 1995). Both areas have similar levels of agricultural potential, expressed as reliable winter rainfall and are found on flat to gently rolling topography. Together, they represent the most fragmented and transformed vegetation types in the species-rich Cape Floristic Region.

2.5.2 Correlates of landscape patterns

Although rainfall seasonality and mean slope were most closely correlated with the extent of renosterveld, the results of the stepwise multiple regression model suggest that the extent of renosterveld is best explained by a combination of mean slope and slope variation. These variables were not collinear. Therefore, although rainfall seasonality undoubtedly influences suitability for sustainable wheat cultivation and therefore indirectly renosterveld extent, topographical variables are the best correlates of the extent of remaining natural vegetation. This agrees with the notion that landscape patterns produced by fragmentation are not random (Usher 1987, Sharpe *et al.* 1987). In fact, the more dissected landscapes of the east, coupled with less reliable winter rainfall and higher summer rainfall produce a higher grass cover (Cowling 1984). As a result, renosterveld is increasingly used as a natural pasture in these areas (Cowling *et al.* 1986, Low and Rebelo 1996).

2.5.3 Conservation management implications

My results, in conjunction with theories of fragmentation (MacArthur and Wilson 1967) confirm that the formulation of a conservation programme for South Coast Renosterveld is urgently needed. Since South Coast Renosterveld is species-rich, particularly in geophytes with low dispersal ability (see Chapter 4), the future management of the area should focus on conserving biodiversity. The comparatively high percentage of natural vegetation remaining in the eastern parts of its distribution, together with a fairly high degree of connectivity and low threat of future cultivation implies that it is still possible to proclaim fairly large reserves in the east. In addition, there is a potential for creating large corridor reserves along major (steep) river valleys, for example the Breede and Gouritz rivers, thus linking the mountains with the sea. However a two-fold reduction in regional species richness has been shown in east versus west Cape Floristic Region landscapes (Cowling *et al.* 1992). This therefore raises the debate on the conservation strategy of "single large or several small (SLOSS)" reserves (Gilpin and Diamond 1980, Simberloff and Gotelli 1984, Wilcox and Murphy 1985). Conservation planning faces the following dilemma: should areas of unfragmented natural vegetation in the eastern part of South Coast Renosterveld be conserved, where vegetation patterns and processes are still in fairly pristine condition in terms of extent and core area but only represent a depauperate component of South Coast Renosterveld? Alternatively, should a network of more species-rich but smaller fragments of unknown long-term viability be conserved in the western sector? The final answer to this debate may rest with the formulation of specific conservation objectives, the availability and cost of land to set aside as reserves, and the question of how persistent species are in small fragments (see following chapters). Although perhaps no panacea, a formal reserve selection analysis using a number of factors/indices/criteria may be the appropriate way for designing a reserve system for renosterveld (for example see Rebelo and Siegfried 1992).

My study serves as a broad, largely descriptive overview of landscape patterns and their environmental correlates. Any patterns detected are a function of the scale, grain and extent of the study (Forman and Godron 1986, Turner 1989, Turner *et al.* 1989, Wiens 1989, McGarigal and Marks 1994). My data were sampled at a relatively coarse grain and fragments < 6 ha were not included in this study. This study therefore underestimates the true extent of South Coast Renosterveld as well as the connectivity between fragments. This can have important implications for applying the results to conservation planning, since even small fragments can play a vital role in maintaining the structure and functioning of natural systems. Small fragments can perform a corridor function (for example road verges) to sustain metapopulations which need links between fragments for recolonisation to compensate for local extinction (Hanski 1991, Hanski and Thomas 1994, Husband and Barrett 1996 and references therein) or act as dispersal "stepping stones" (MacArthur and Wilson 1967) between larger fragments. The issue of biodiversity loss in small renosterveld fragments and their potential conservation value is examined in the following chapters. In addition, this study only considers present-day landscape patterns, and does not investigate pattern changes with time. The knowledge of the rate of transformation of South Coast Renosterveld would provide important explanations for observed patterns and processes at the community, species and population scale.

2.6 Conclusion

Despite some serious limitations caused by the resolution of the study, clear trends in landscape composition and configuration emerge. Together with insights into the consequences of fragmentation on species composition, richness, abundance and population viability (see Chapters 3, 4, 5), we will gain an understanding of the structure and functioning of the system. This understanding will enable managers and conservation bodies to set up specific conservation objectives and strategies, which integrate agriculture and conservation.

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Chapter 3

Vegetation composition of South Coast Renosterveld fragments

3.1 Abstract

Fragmentation leads to changes in species composition through extinction and invasion processes. I investigated the effect of fragmentation and environmental gradients on vegetation composition at the local scale on three fragment size classes (small, medium and large). TWINSPAN classification of fragments showed that large fragments were most similar to each other in terms of vegetation composition, with small and medium fragments more variable. This could be the result of extinction and/or edge effect mechanisms operating on small and medium fragments. Indirect gradient analysis techniques (PCA, DCA) indicated that different-sized fragments were generally well interspersed, but small fragments had more outlier sites. The sites used in this study do not show any bias in terms of underlying environmental gradients. However, large fragments were associated with deeper soils. Small and medium fragments tended to be found on rocky soils and had higher levels of disturbance, as indexed by grazing and trampling. There was only a weak pattern of nestedness among fragments. The results suggest that fragment size is not strongly correlated with vegetation composition. However, any fragmentation effects may have been concealed by naturally high species turnover in this system as well as patchiness resulting from historical disturbance regimes.

3.2 Introduction

The process of fragmentation of natural ecosystems through area, isolation and edge effects ultimately changes the species composition of natural vegetation (MacArthur and Wilson 1967, Quinn and Hastings 1987, Saunders *et al.* 1991, Norton *et al.* 1995). This occurs because (1) weedy plants invade (Meffe and Carroll 1984, Saunders *et al.* 1991), and (2) some species cannot maintain large enough populations and thus go extinct (MacArthur and Wilson 1967, Pimm *et al.* 1988). Species with small populations, poor dispersal abilities, low reproductive capacity, special resource requirements or an inability to compete with invasive species are particularly at risk of local extinction (Meffe and Carroll 1984, Hobbs and Huenneke 1992, McIntyre and Lavorel 1994). Whereas weed invasions can occur over relatively short periods after fragmentation, extinctions only become evident after much longer periods.

Fragment-induced changes in vegetation composition have been documented by a number of empirical studies: Turner and Corlett (1996), for example, found that a small remnant of tropical rainforest in Singapore had lost 50% of its native plant species over the last century. Steep microclimate gradients on fragment edges have been associated with shifts in species composition in Mexican rainforests; shade-loving and drought-sensitive epiphytes have been replaced by sun-loving and drought-resistant species (Hietz-Seifert *et al.* 1996). In tropical forests of East Amazonia, selective logging has led to a drier microclimate and an increase in woody debris fuel mass. This has resulted in fire becoming the dominant disturbance event in a system which, under unfragmented conditions, has a very low probability of burning. Fire-simulation studies using bark tissue data showed that even low intensity fires will kill most standing vegetation in logged forest mosaics (Uhl and Kauffman 1990). Other studies have shown that forest fragmentation encourages the invasion of exotic plants (Pyle 1995), and Pettit *et al.* (1995) reported the loss of native plant species and the invasion of exotic species as a result of grazing disturbance on fragmented vegetation.

The original extent of South Coast Renosterveld has been greatly reduced by agricultural practises, resulting in a number of islands of natural vegetation surrounded by vastly transformed areas of cereal fields and artificial pastures (see Chapters 1 and 2). This chapter aims to detect whether broad shifts in plant community composition at a local scale have been caused by fragmentation. I chose the local scale because several studies have concluded that the majority of fragmentation effects on species richness are the result of larger fragments containing more habitats than small ones (Lescourret and Genard 1993, Hinsley *et al.* 1995). My study, therefore, focuses on the local or point scale in an attempt to factor out habitat diversity from the experimental design; therefore, I investigated only the effect of fragment area on vegetation patterns.

The bulk of this study (Chapters 3 and 4) is based on natural experiments (*sensu* Diamond 1986) rather than field or laboratory experiments (see Chapter 1 for details on site selection). This approach has the advantage that it is completely realistic and does not require extrapolation. The disadvantage is that the experimental design inevitably includes a number of variables. I attempted to minimise the potential impact of environment-related variables on vegetation composition by choosing fragments of similar habitats but different sizes for the study (see Chapter 1). I did, however, record a number of variables in order to test whether variations in vegetation composition are a function of environment or fragmentation effects. Univariate statistics and ordination procedures are useful tools for testing this.

I believe the role of isolation in influencing vegetation composition to be far less important than patch size or shape in this system. Although proximity of remnants is likely to increase the immigration rate of some species (Kirkpatrick and Gilfedder 1995), the majority of fragments in the study are isolated by large distances (mostly >300m). It has been shown that even though many pollinator species are physically capable of crossing large distances, they often do not cross even short stretches of agricultural lands to move between patches of natural vegetation (Thomas 1983, Waddington 1983, Warren 1987a, 1987b). The probability of inter-patch wind pollination and dispersal seems equally low. This chapter therefore concentrates on the effect of fragment area on the floristics of South Coast Renosterveld.

I will address three key questions:

1. Does vegetation composition vary with fragment size class?

If fragmentation causes predictable species extinctions and invasions, I would expect vegetation composition to be strongly associated with fragment size. Multivariate classification techniques (e.g. TWINSPAN) provide a quantitative method for detecting vegetation associations. This enables me to test whether fragments of similar sizes have similar vegetation composition.

2. Can vegetation composition be explained in terms of fragmentation variables (size, isolation, shape) and what is the importance of other environmental variables in explaining vegetation composition patterns?

Since this is a natural experiment, I needed to explore the relative importance of both fragmentation variables and other environmental variables. Ordination procedures (CANOCO, ter Braak 1990) allow the identification of any compositional gradients in the vegetation data and the extent to which they are associated with these variables.

3. Is the vegetation composition found on small and medium fragments an impoverished subset of that found on large fragments?

Species assemblages are nested when species-poor sites are subsets of more species-rich sites. Nestedness is hypothesised to be mainly caused by selective extinction (Wright and Reeves 1992, Patterson and Atmar 1986). Cook and Quinn (1995) compared groups of non-endemic species, differing in dispersal ability and showed that repeated colonisation can also enhance nestedness, with poor dispersers only present in rich sites and strong dispersers present on most sites (i.e. a function of colonisation and rescue effect). Nestedness in species assemblages, therefore, reflects predictable species loss and gain patterns. The concept of nestedness is, however, based directly on island biogeography theory and therefore assumes that larger sites have richer assemblages of species. If nestedness is strong, the species on depauperate sites will be common everywhere, whereas richer sites will maintain more uncommon species. This concept has been extensively applied to collections of oceanic, land-bridge and habitat islands (Wright and Reeves 1992, Cook 1995, Cook and Quinn 1995). Most data sets show significant nestedness, although the degree of nestedness varies widely.

3.3 Methods

3.3.1 Data collection

Eight sites per fragment size class (small, medium, large) were chosen (see Chapter 1 for the selection criteria and description of individual fragments). Three permanent plots, each measuring 10x5m, were located near the centre of each fragment. This plot size is within the area range suggested by other studies in similar vegetation types (e.g. Taylor 1969, Bond 1981). Plots were situated 5-10m apart. I sampled each plot at regular intervals between April 1994 and November 1995 to obtain lists of both the annual and perennial components of the vegetation. Species in each plot were identified and assigned to one of the following percentage cover classes: <1% = 1, 1-2% = 2, 3-5% = 3, 6-10% = 4, 11-20% = 5, 21-50% = 6, >51% = 7. Data for the three plots were pooled for each fragment. Eight wheatfields were sampled only once during the fallow period (December 1994), using the same approach. Nomenclature follows Arnold and de Wet (1993). Appendix 1 lists all species recorded during the study period.

For each plot (except the wheatfields), a number of fragmentation and other environmental variables were measured (Table 3.1). Soil data were collected in the following way: in each plot, three soil samples were taken to a depth of 10cm following the clearing of surface litter. The samples were bulked for each plot, dried at 60°C and sieved through a 2mm mesh. All soil texture and nutrient analyses, except pH, were performed by the Department of Agriculture, Elsenberg.

Table 3.1 Fragment and environmental variables recorded on all sites.

Variable	Abbreviation	Classes of variables, methods
Area (ha)	Area	from orthophotos
Perimeter (m)	Perimet	from orthophotos
Area : Perimeter ratio	Areape	
Distance to closest fragment (m)	Isol-n	from orthophotos
Distance to closest large fragment (m)	Isol-l	from orthophotos
Radslope ($cal/cm^2/day$)	Radslo	Potential solar radiation on a sloping surface, corrected for slope, aspect and latitude (Swift, 1976)
Disturbance (4 classes)	Disturb	Subjective estimate
% Bare ground (4 classes)	Bare	Subjective estimate
Topsoil depth (cm)	Topsoil	Estimated from augering in each plot
Rockiness (4 categories)	Rocki	Subjective estimate
Soil pH	pH	1 N KCL 1:2.5 solution
Total nitrogen (%)	Nitro	Citric acid method
Available phosphorus (mg/kg)	Phospho	Citric acid method
% Clay	%Clay	Texture analysis
% Silt	%Silt	Texture analysis
% Sand	%Sand	Texture analysis

3.3.2 Data analysis

Fragments and wheatfield sites were classified using TWINSPAN (Hill 1979), which produces a hierarchical classification of sites by the repeated splitting of groups of sites, which have been ordinated by reciprocal averaging (Kent and Coker 1992). The analysis was run using the full species by site dataset. Removing the wheatfield data did not change the classification pattern.

In order to analyse the importance of any other variables in the experimental design on vegetation patterns, one-way analysis of variance was used to detect significant differences of measured environmental variables within each fragment size class. Data were tested for normality. Significant differences among means were identified using Tukey multiple range tests.

Principal component analysis (PCA), an indirect gradient analysis, was used to explore the relationships between fragments and environmental variables. PCA is generally not recommended as an ordination procedure for species data, largely because it assumes that species respond in a linear rather than unimodal way to underlying environmental gradients. Nevertheless it is useful in describing patterns in environmental data (Kent and Coker 1992). Conspicuous grouping of fragments in the ordination diagram, particularly fragments of the same size class, would indicate bias in site selection. All sites except wheatfields were included in the ordination; fragmentation variables, including level of disturbance, were not included.

Species cover data of the reduced data set (without wheatfield sites) and environmental variable data were ordinated using Detrended Correspondence Analysis (DCA). DCA is an indirect gradient analysis technique, where the ordination axes are derived from the vegetation data, i.e. independently from the environmental data (Kent and Coker 1992). CA, an alternative indirect gradient analysis technique was not used, because it produced an 'arch effect' (ter Braak and Prentice 1988) in the data. Detrending with DCA removed this arch effect. Initial outliers (fragments 1, 13 and 14; refer to Table 1.2, Chapter 1) were removed from the ordination. This spread out the remaining fragments and displayed the similarities among them more clearly (Kent and Coker 1992). All environmental variables were used in the analysis. This allowed me to compare the relative importance of fragmentation variables (area, perimeter, area to perimeter ratio, isolation to closest fragment, isolation to closest large fragment) with other environmental variables (potential solar radiation, % bare ground, level of disturbance, pH, available phosphorus, total nitrogen, topsoil depth, rockiness, % clay, % silt, % sand). Note that this differs from conventional ordination studies which aim to identify a minimum set of environmental variables which can explain the variation in the species data set.

Nestedness was calculated (Nestcalc Ver. 1.0; Wright *et al.* 1990) using a presence-absence matrix, ordering fragments both by species richness and fragment area. A scaled metric, C (Wright and Reeves 1992) equals 1 where fragments are perfectly nested. C equals 0 in non-nested systems, i.e. where species are equally likely to occur on all fragments.

3.4 Results

3.4.1 Vegetation classification

The TWINSPAN classification of 31 sites produced 11 groups from five divisions (Figure 3.1). The first division split the wheatfields (1a) from all other sites (1b). *Brassica disticha* and *Silene gallica*, both alien weeds were identified by TWINSPAN as indicator species for the wheatfield sites. The second division separated five sites (2a), containing three small and two medium-sized fragments from the remaining sites (2b). These sites were characterised by the lack of *Ficinia filiformis* and *Restio multiflorus*, both common graminoids in the study area. From this group, one small fragment separated out at the next division (3a), on the basis of *Anthospermum aethiopicum*, a shrub only found on this site. The remaining sites were divided into two major groups, with one group comprising three small, five medium and two large fragments, characterised by a lack of *Elytropappus rhinocerotis* and lower cover values of *Restio multiflorus* (3b). This group subdivided twice more; the indicator species were *Helichrysum teretifolium* and *Senecio burchellii* respectively, two asteraceous shrubs. The second major group (3c) contains one small, one medium and six large fragments. This group subdivided into a group of five large fragments (4a) and a group of a small, medium and large fragments (4b). *Gnidia setosa*, a small-leaved shrub, was an indicator species for the latter group. One site was separated from the group of five large fragments (5a). This site was characterised by *Athanasia trifurcata*, an asteraceous shrub.

3.4.2 Analysis of variance

The ANOVA and Tukey multiple range tests showed that mean area, perimeter length and shape, (indexed by the area to perimeter ratio), were significantly higher in large fragments than in small and medium fragments. Levels of disturbance (measured with subjective grazing and trampling indices) were significantly lower on large fragments than on small or medium fragments. Significant differences were also detected for pH, with large fragments having more acidic soils than small fragments. No other significant differences between environmental variables were found (Table 3.2). There was, however, a weak trend towards higher fertility (total nitrogen and available phosphorus) on small and medium fragments

3.4.3 PCA

The eigenvalues for the first two axes were 0.436 and 0.177 respectively, accounting for 61.3% of the variation in the environmental data (Table 3.3). The biplot of 23 fragments and 10 environmental variables (Figure 3.2) shows that sites of different sizes were interspersed, with large fragments appearing more clustered along axis 1 than either small or medium fragments. Axis 1 was associated with soil texture, being strongly positively correlated with rockiness, and negatively with % clay. Axis 2 reflected soil nutrient levels and was weakly positively correlated with pH and negatively with total nitrogen and available phosphorus. The most important variables were rockiness, bare ground, available phosphorus, topsoil depth and % clay, while the least important variables were % silt, % sand and pH. Three small fragments were associated with very rocky soils, whereas most large fragments were associated with clayey soils.

3.4.4 DCA

The eigenvalues of axes 1 and 2 of the DCA for the 20 sites used in the ordination were 0.495 and 0.256 respectively. These axes account for 22.7% of the total species-environment relationship expressed in the ordination (Table 3.4). Fragments of different size classes were interspersed as with the PCA. No distinct groups of sites were evident, although large fragments appeared more clustered than either small or medium fragments (Figure 3.3). The pattern of fragment distribution in the ordination was similar to the classification pattern (Figure 3.1).

Axis 1 represented a soil texture gradient. It was positively correlated with % silt and negatively correlated with % sand. Axis 2 described fragmentation, disturbance and soil nutrients gradients. Bare ground, area and perimeter were positively correlated and disturbance and total nitrogen negatively correlated with axis 2. No environmental variable dominated the species-environment relationship. The most important variables were area, perimeter, area to perimeter ratio (all fragmentation variables), disturbance and total nitrogen. Area and perimeter were negatively correlated with disturbance, indicating that disturbance tended to be higher on small fragments. Isolation, rockiness and pH were the least important variables. Large fragments were associated with heavier (clayey and silty) soils, with small and medium fragments found on a range of soils.

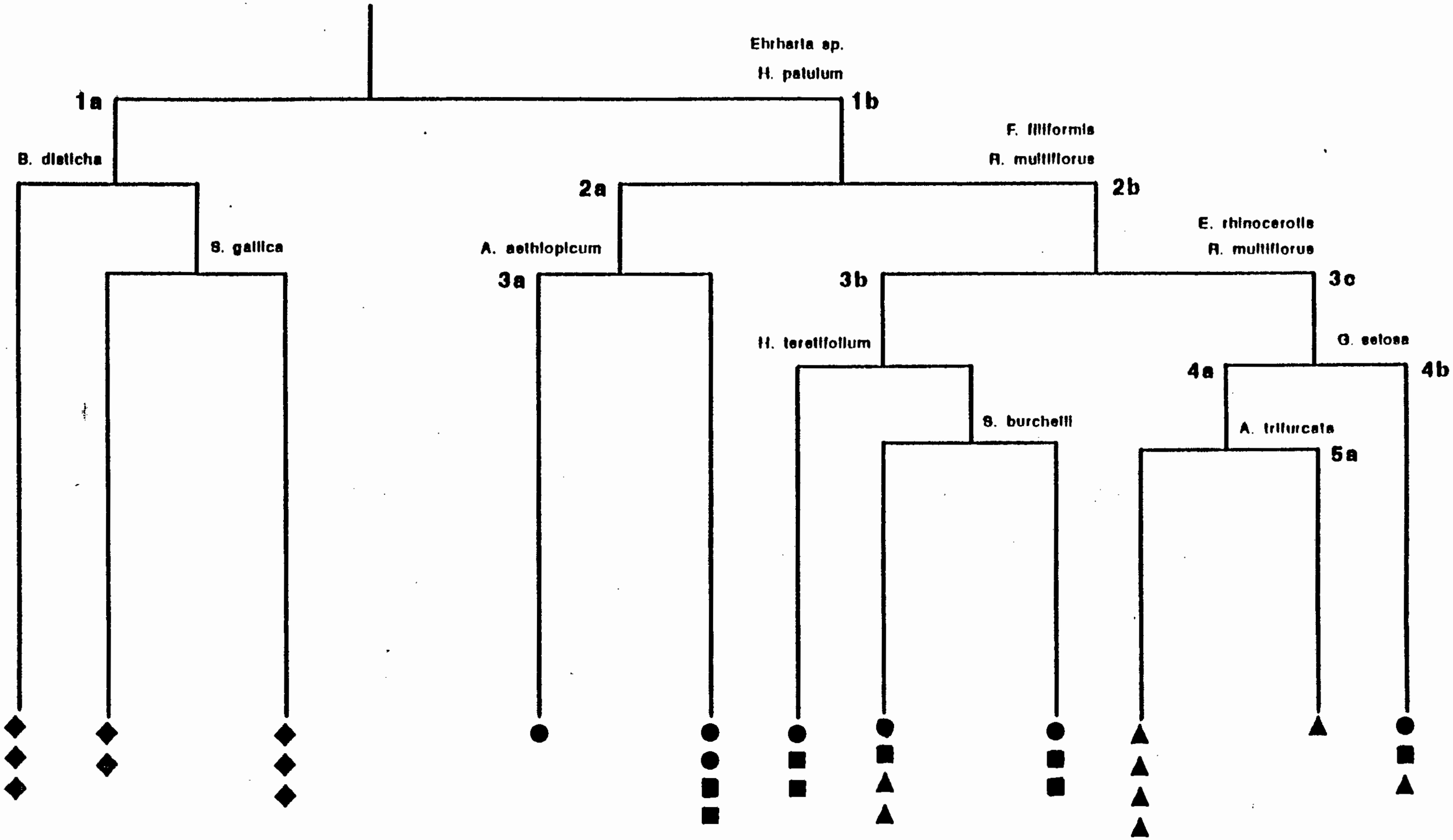

Figure 3.1 TWINSPAN dendogram based on plant cover values on 23 sites. For full species names refer to text. Site codes for fragment size classes: ● = small, ■ = medium, ▲ = large, ◆ = wheatfield. Numbers indicate groups of sites in the text

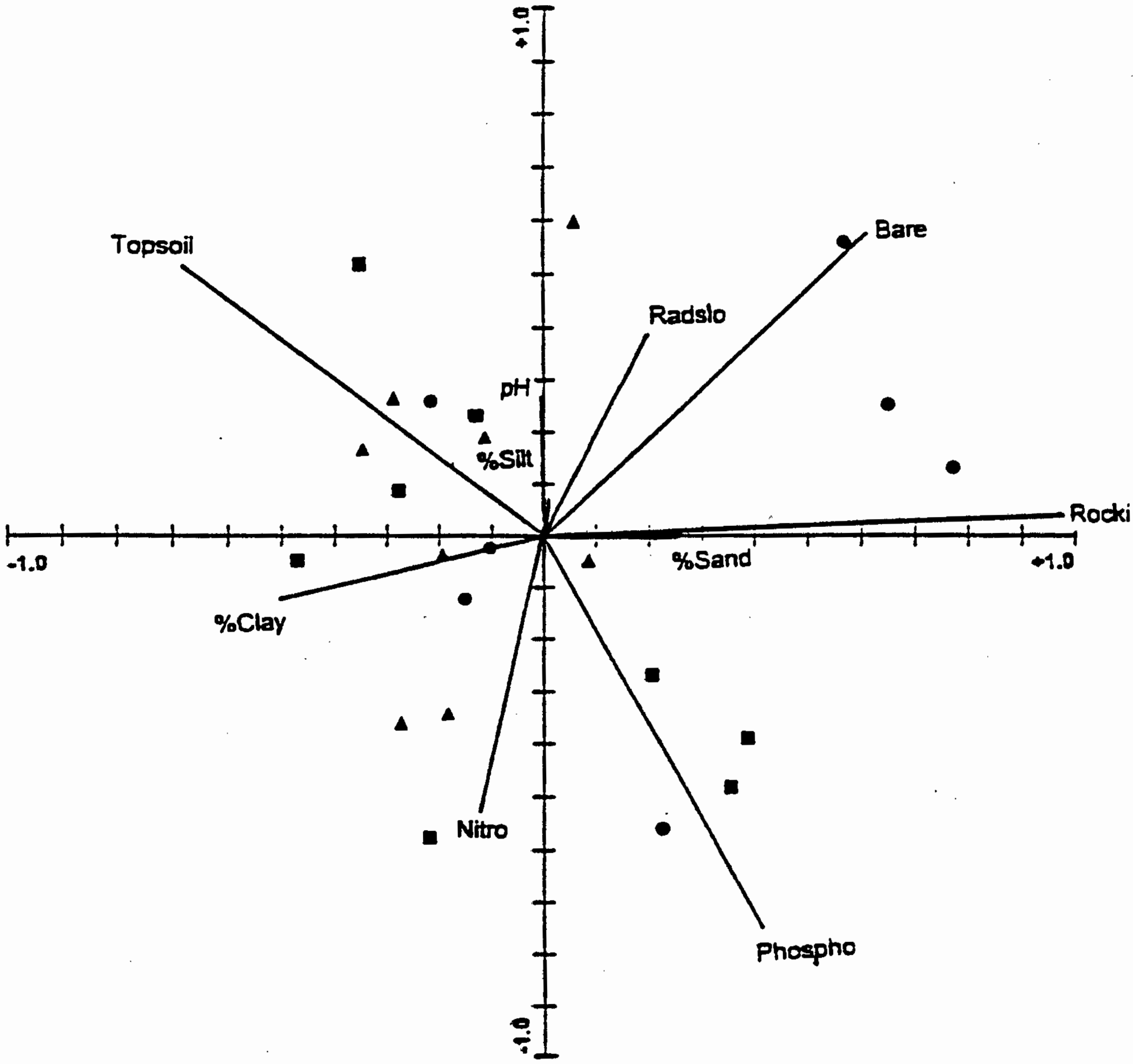

Figure 3.2 PCA biplot of 23 sites and 10 environmental variables. For details of environmental variables refer to Table 3.1. Site codes for fragment size classes: = small, ■ = medium, ▲ = large.

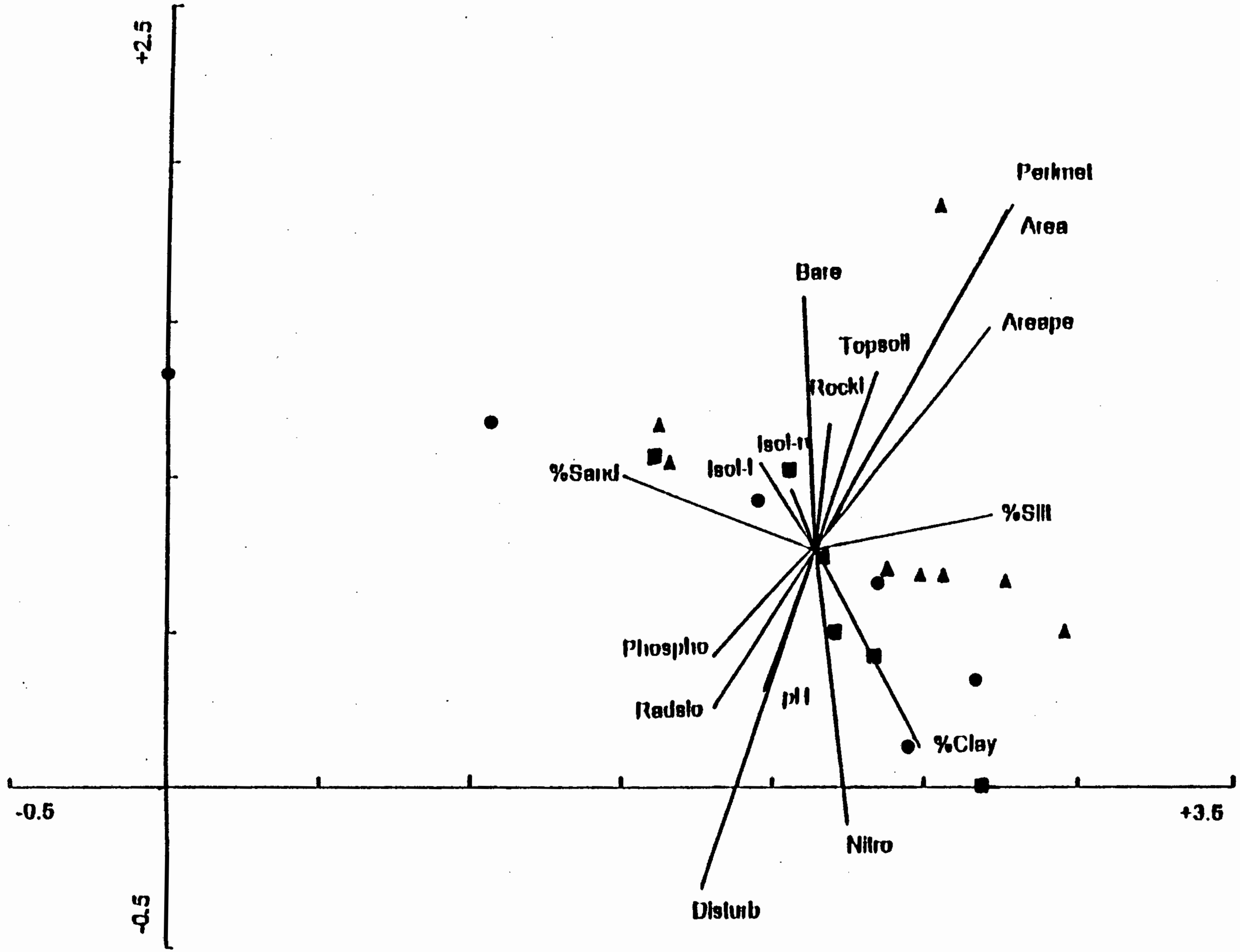

Figure 3.3 DCA biplot of 20 sites and 16 environmental and fragmentation variables. For details of environmental variables refer to Table 3.1. Site codes for fragment size classes: ● = small, ■ = medium, ▲ = large.

Table 3.2 Mean (± SE) values for all measured fragment and environmental variables. Significance levels for one-way ANOVAs are reported. Means that share the same superscript letters do not differ significantly (Tukey Multiple Range test).

Variable	Fragment Size Class			F-Ratio
	Small	Medium	Large	
Area	0.61 ± 0.7[a]	6.20 ± 3.7[a]	70.5 ± 45.1[b]	16.382 ***
Perimet	405.2 ± 244.6[a]	1836.7 ±1120.6[a]	5181.9 ±2384.0[b]	18.737 ***
Areape	12.5 ± 6.8[a]	35.0 ± 12.4[a]	136.3 ± 64.0[b]	22.327 ***
Isol-n	0.37 ± 0.13	0.45 ± 0.36	0.33 ± 0.25	0.432 NS
Isol-l	0.54 ± 0.4	0.61 ± 0.4	0.34 ± 0.3	1.409 NS
Radslo $^{\alpha}$	240.4 ± 324.9	68.7 ± 85.7	25.1 ± 20.0	2.763 NS
Disturb	2.29 ± 0.5[a]	2.50 ± 0.56[a]	0.96 ± 0.81[b]	13.091 ***
Bare	1.53 ± 0.9	0.96 ± 0.6	1.13 ± 0.53	1.265 NS
Topsoil	20.6 ± 7.4	28.0 ± 17.4	32.4 ± 13.1	1.451 NS
Rocki	1.48 ± 1.4	0.63 ± 0.9	0.38 ± 0.6	2.567 NS
pH	5.30 ± 0.2[a]	5.09 ± 0.3[ab]	5.01 ± 0.1[b]	4.086 *
Nitro	0.216 ± 0.03	0.213 ± 0.04	0.210 ± 0.04	0.070 NS
Phospho	10.5 ± 3.0	10.7 ± 4.7	8.1 ± 2.7	1.311 NS
% Clay	15.5 ± 2.9	17.8 ± 5.2	17.3 ± 3.8	0.611 NS
% Silt	39.3 ± 7.7	37.3 ± 6.8	42.9 ± 5.1	1.532 NS
% Sand	48.8 ± 9.1	48.1 ± 11.6	42.2 ± 5.3	1.163 NS

$^{\alpha}$ square-root transformed. Back-transformed means are reported.

Table 3.3 Eigenvalues and cumulative percentage variance of environmental data for the four PCA axes.

Axes	1	2	3	4
Eigenvalues	0.436	0.177	0.152	0.102
Cumulative percentage variance				
of environmental data	43.6	61.3	76.5	86.7

Table 3.4 Eigenvalues, species-environmental correlations, and cumulative percentage variance of species data and species-environment relationship for the four DCA axes.

Axes	1	2	3	4
Eigenvalues	0.495	0.256	0.098	0.072
Species-environment correlation	0.817	0.978	0.969	0.976
Cumulative percentage variance				
of species data	22.4	34.0	38.4	41.6
of species-environment relationship	15.1	22.7	0.0	0.0

3.4.5 Nestedness

The results show that fragments were only weakly nested, with fragments ranked by area less nested than when ranked by species richness (C = 0.259 and 0.315 respectively).

3.5 Discussion

3.5.1 Species patterns

The classification of 31 sites showed marked differences in vegetation composition between wheatfields and fragments of natural vegetation. Since these fields are ploughed, planted with cereals and burned annually, they offer virtually no chance for the recolonisation and establishment of plant species from neighbouring vegetation patches. The classification of fragments shows that large fragments appear to be more similar to each other in terms of vegetation composition, with small and medium fragments having more variable compositions. This could imply that vegetation patterns and processes have been affected by fragmentation to some degree, with large fragments appearing more stable, and small and medium fragments more dynamic, possibly reflecting a range of extinction and edge effect patterns. Alternatively, this pattern may mirror the influence of other environmental variables (see below).

3.5.2 Species-environment relationships

PCA showed that fragments of different sizes are well interspersed in the multivariate space defined by their environmental variables. DCA showed similar trends. One-way analysis of variance supports this finding, with only disturbance and pH (apart from the specifically selected fragmentation variables area, perimeter and area to perimeter ratio) differing significantly with fragment size class. Slightly higher levels of total nitrogen and available phosphorus on small and medium fragments could possibly be the result of fertiliser pollution arising from matrix-management.

Closer inspection of the ordinations, however, reveals that the small fragments have more outlier sites, both in terms of environment and vegetation composition. Furthermore, the DCA showed that disturbance is strongly negatively correlated with the three fragmentation variables; area, perimeter, area to perimeter ratio. This suggests that disturbance increases directly with fragmentation, which can be attributed to intense (though seasonal) grazing pressure on small fragments (see Chapter 1).

Isolation was shown to be an unimportant fragmentation variable in explaining floristic composition. This may be ascribed to the large distances (in terms of dispersal and pollination and hence immigration) that separate most fragments. This supports my hypothesis that inter-patch pollination and dispersal are unlikely to be affecting vegetation composition at this scale of investigation.

The ordinations showed that large fragments, set aside as natural grazing camps, were generally closely associated with heavier soils. Small and medium fragments represent islands of poor, often rocky soils surrounded by crops planted on deeper soils. This agrees with the general notion that the process of fragmentation is selective (Hobbs 1987, Usher 1987, Norton *et al.* 1995).

Only 22.7% of the total species-environment relationship could be explained by the axes of the DCA. This may be an artifact of using all variables in the ordination, although some variables showed high inflation values, which indicate multicollinearity (ter Braak 1987). Alternatively, additional environmental factors not considered here could explain the species-environment relationship better. These factors include time since fragmentation (Saunders *et al.* 1991), post-fire vegetation age and differences in historical fire regimes (see Chapter 1).

3.5.3 Nestedness

The array of fragments produced a weak pattern of nestedness of species assemblages. Nestedness theory assumes that larger islands support more species. This was not found in this study, probably because I focused on the local scale. It is therefore clear that no systematic loss of species is taking place in similar habitats in this system. Fragments are less nested with respect to area than richness, a result which largely agrees with the findings of Cook (1995). This means that large sites are not more species-rich than small sites; yet nestedness is weak even when the data are ordered by species richness.

3.5.4 The role of patchiness

Fragmentation theory is based on the concept of a species-area relationship, where fragmentation invariably leads to predictable species loss. Such species loss would produce a nested pattern, where smaller sites would be species-poor subsets of larger species-rich sites. These predictions may hold true if species were distributed uniformly across the landscape. The patchy occurrence of species in a continuous landscape, brought about by multi-scale ecological processes (O'Neill *et al.* 1986) and historical factors (Schluter and Ricklefs 1993), is, however, likely to lead to complex and unpredictable distribution patterns in remnants following fragmentation (Bierregaard *et al.* 1992, Norton *et al.* 1995). The distribution and abundance of species in fragmented systems therefore depends both on their spatial arrangement before fragmentation and on the impact of fragmentation itself. Weak nestedness is, in fact, expected in patchy systems due to the observed negative correlations between beta diversity and nestedness indices (Wright and Reeves 1992).

The southwestern part of the Cape Floristic Region has exceptionally high levels of regional diversity, despite only moderate levels of local or point diversity (Cowling *et al.* 1992). These differences are due to high beta turnover along subtle environmental gradients; high gamma turnover within similar habitats; and patchiness caused by historical and unique fire-related changes in vegetation composition (e.g. hot versus cool fires, different fire seasons etc. (Cowling 1987)). The high degree of patchiness in this system is possibly the product of extensive and varied historical landuse, including fire and grazing (see Chapter 1). Subsequent fragmentation of this area has therefore produced patches with variable species composition. This makes it virtually impossible to distinguish between pre-and post fragmentation patterns. A further level of complexity is that not all species or functional types will respond in the same way to fragmentation. The stratification of the experimental design has removed most environmental and habitat gradients on vegetation composition. Any differences in local composition must, therefore, be interpreted in terms of fragmentation, gamma-diversity effects or differences in disturbance (fire, grazing) regimes. My results therefore suggest that either (1) fragmentation has not (yet) changed vegetation composition of South Coast Renosterveld or (2) any fragmentation effects have been masked by gamma diversity patterns and/or fire and grazing regime effects.

3.6 Conclusion

In conclusion, two main findings emerge from this study: firstly, the sites chosen for this study show no systematic bias in terms of underlying ecological gradients, with only fragment size (area, perimeter, shape) distinguishing them. Secondly, vegetation patterns were not strongly correlated with fragment size, suggesting that these patterns are not the result of predictable species loss or invasion processes. Any true fragmentation effect may, however, have been overridden by the patchy species distribution found naturally in South Coast Renosterveld. Although no conclusive fragmentation-related patterns could be found at the broad community composition scale, an investigation into the effects of fragmentation at the plant guild or population scale may provide a better understanding of any vegetation patterns and processes affected by fragmentation (see next two chapters).

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Chapter 4

Plant species diversity and guild structure

4.1 Abstract

Species diversity is predicted to decrease with fragmentation owing to the high extinction risk associated with small population sizes. Species which differ in invasive and persistence potential, pollination and dispersal modes as well as distributions should react differently to fragmentation. I investigated species richness and diversity, as well as the proportional representation of plant guilds in 23 fragments of three different fragment sizes at a local scale. I also compared mean species numbers, cover and number of individuals per guild for each fragment size class. There were no significant differences in species richness (S), heterogeneity (N1), dominance (N2) or evenness (E) between fragment size classes. Guild proportionality differed greatly between wheatfields and natural vegetation, but was similar between different-sized fragments. Medium fragments had significantly more species and individuals of alien taxa than large fragments. The results indicate that small and medium fragments appear to be structurally intact after being isolated for up to 60 years. The loss of habitat diversity is, however, likely, but was not investigated. Fragmentation may have been too recent for effects of fragmentation processes to have been translated to recruitment failure. Naturally small populations, exposed to a range of historical disturbance processes (fire, grazing) may have made renosterveld species more resistant to extinction. Even small fragments may represent valuable areas of natural vegetation. Although these may be too small to be integrated into formal reserve networks, small fragments should be retained as biodiversity "stepping stones".

4.2 Introduction

Fragmentation subjects the native biota to reduced habitat area, increased isolation and increased edge effects. Chapter 1 gives a detailed overview of the theory of fragmentation and illustrates how the combination of these processes results in a high probability of low population sizes and hence extinction risk on small fragments. Fragmentation effects, together with disturbances accompanying matrix management (for example fire, grazing, pollution) can change species richness (through extinctions and invasions) and abundances (Saunders 1991). Population sizes and therefore extinction risks are strongly influenced by species attributes (Saunders 1991, Meffe and Carroll 1994). Consequently, plant guilds differ in their susceptibility to fragmentation. It is postulated that species which differ in origin (invasive potential), life-form (persistence potential), pollination and dispersal modes, as well as distributions, differ in their susceptibility to extinction. Each attribute is discussed separately below:

Species of different origins (i.e. native or alien) may respond differently to fragmentation, with alien species often having high invasive potential (Meffe and Carroll 1994) and an ability to eliminate native taxa (Richardson and van Wilgen 1986, Vlok 1988, Richardson *et al.* 1989, McIntyre and Lavorel 1994). A number of studies have investigated the role of invasions in fragmented systems. Forest fragmentation has been shown to significantly increase the number and dominance of exotic plants in the Potomac Floodplain (Pyle 1995). Brazilian pepper trees (*Schinus terebinthefolius*) have heavily invaded pine rockland fragments in Florida, causing further changes in natural vegetation structure by shading out wildflowers, and inhibiting combustible understorey growth. As a result, the natural fire cycle has been inhibited, causing the succession of pine rockland to rockland hammocks (Simberloff 1993). Matrix-management has also been shown to promote invasions. Frequent fires, intense livestock grazing and trampling following fragmentation in Australia facilitates the invasion of non-native annual species from surrounding agricultural land (Hobbs 1987, Saunders *et al.* 1993, Prober and Thiele 1995).

Different life-form guilds can be differentially susceptible to fragmentation. Turner *et al.* (1996) reported a 50.9% decrease in species richness over the last century in an isolated lowland tropical rainforest fragment in Singapore. Extinctions were not distributed evenly across all plant life-forms. Significantly more shade-tolerant understorey shrubs than trees became extinct. Epiphytic orchids were also particularly extinction-prone but epiphytic pteridophytes were found to be much less susceptible to local extinction (Turner *et al.* 1994). Fragment management, such as intensive grazing has been shown to affect different life-forms differently. Grazing by sheep or cattle on woodland fragments has been shown to result in a significant loss of native perennial shrub and herb species, while perennial grasses and geophytes were not significantly affected (Pettit *et al.* 1995).

Fragmentation and matrix management also negatively affect pollinator populations (Bawa 1990). It follows that biotically-pollinated species are more prone to long-term demographic consequences or extinction through the disruption of plant-animal interactions (see Chapter 5 for details and references). In Japan, for example, a population of *Primula sieboldii* occurs on a small nature reserve which is flanked by urban areas and golf courses. Washitani *et al.* 1994 have shown that the population is suffering from a severe lack of pollinators. The insect fauna of the reserve is impoverished due to the scarcity of suitable habitat outside the reserve and is exposed to insecticides used on golf courses. Consequently, the population of *Primula sieboldii* is suffering from drastically reduced seed set and is likely to go extinct.

Recolonisation of locally extinct populations and thus persistence of a species in a fragmented system depends on the successful dispersal ability of individuals among populations to maintain a number of viable local populations (metapopulation concept, see Gaston 1994, Hanski 1994, Fahrig and Grez 1996). Successful dispersal depends on dispersal distance, a function of the dispersal vector. If landscape structure restricts dispersal, the probability of extinction is increased (Fahrig and Merriam 1994). Dispersal ability was demonstrated to be as important as fragment size, isolation and shape for the presence and survival of ground beetle species in heathland fragments in the Netherlands (De Vries *et al.* 1996). A study of Swedish pastures showed that pasture area, neighbour pasture area and distance to nearest pasture did not influence total species richness (Eriksson *et al.* 1995), but further analysis revealed that dispersal constrained species distributions. Similarly, the loss of emus (*Dromaius novaehollandiae*) from large areas of the Western Australian wheatbelt may have indirectly influenced native vegetation structure by inhibiting the dispersal of large-seeded species on which they fed (Main 1987).

Widely-distributed and large local populations improve a species chances of survival in a fragmented system. Therefore, species which are geographically restricted, habitat-specific or are naturally sparse are at greater risk of not being able to sustain viable population sizes in a fragmented system (Rabinowitz *et al.* 1986). De Vries (1987 in Thomas 1991) for example showed that butterfly species which have become extinct in Costa Rica were endemics occupying wet/dry transitional forest, almost all of which has been lost to agriculture and plantations.

The preservation of biodiversity is important for maintaining the functioning of an ecosystem (Main 1992, Richardson *et al.* 1995, Walker 1995). The loss of species and guild diversity through fragmentation can therefore further affect ecosystem functioning. It has been suggested that diversity within and among guilds enhances their resilience and their capacity to recover from a disturbance and to maintain their original function (Tilman and Downing 1994, Silver *et al.* 1996). Tilman and Downing (1994), for example, demonstrated that more diverse plant communities were more resistant to drought and recovered more fully. The replacement of perennial shrubs with annual crops in Australia has increased soil erosion levels and has affected water and nutrient regimes (Hobbs 1992). Tilman (1996) showed that diverse systems are more productive and thus more sustainable than less diverse systems. An understanding of the effects of fragmentation on species and guild diversity can thus be used to guide ecosystem conservation and management in a way that minimises further system degradation.

South Coast Renosterveld has been extensively transformed by large-scale agriculture, and approximately 15% natural vegetation remain throughout its extent (see Chapters 1 and 2 for details on fragmentation history and current fragmentation patterns). It now occurs as a series of fragments of different sizes, shapes and connectivity in a matrix of cultivated lands and artificial pastures. Renosterveld has been converted selectively into agricultural lands, and remnants are largely restricted to steep slopes, shallow rocky soils and areas unsuitable for agriculture. Some large fragments are retained as natural grazing camps. These are assumed to represent "intact" areas of natural vegetation with representative samples of the region's biota. Small and medium-sized fragments are managed inclusive of agricultural lands and are therefore subjected to seasonal and intense grazing and trampling, frequent burning and annual crop spraying. A study on the vegetation composition of South Coast Renosterveld on different-sized patches and its relationship with a number of fragmentation and environmental variables have not shown a clear indications of vegetation composition change with increased fragmentation. However small and medium fragments tended to be found on more rocky soils and showed higher levels of grazing and trampling disturbance (Chapter 3).

In this chapter, I investigate the vegetation composition on fragments of different sizes in more detail. Key questions are: (1) do fragments in different size classes differ in richness and diversity (including dominance and evenness) of species; (2) does the proportional representation of different plant guilds differ among fragment size classes; (3) do mean numbers, cover and number of individuals per species in each plant guild differ among fragment size classes; and (4) can the observed patterns be explained in terms of fragmentation theory.

4.3 Methods

4.3.1 Data collection

I chose eight fragments of natural vegetation for each of three fragment size classes, and regularly recorded the plant species on three permanent plots per fragment between April 1994 and November 1995. Three plots on eight wheatfields were sampled once during November 1995. For details on study area, choice of fragments and experimental design refer to Chapters 1 and 3. I used species percent cover as well as counts of number of individuals per species as measures of abundance. They were estimated for each species in each plot, using the following categories: Cover: <1% = 1, 1-2% = 2, 3-5% = 3, 6-10% = 4, 11-20% = 5, 21-50% = 6, >50% = 7. Number of individuals: 1 = 1, 2-10 = 2, 11-50 = 3, 51-100 = 4, 101-200 = 5, 201-500 = 6, >500 = 7. I pooled species data for the three plots per site, and calculated mean percent cover and number of individuals for each species.

I categorised species into guilds using a number of species attributes. The categories were:

- Origin (native, alien)
- Life form (geophyte, forb, graminoid, shrub)
- Life cycle (annual, perennial)
- Pollination syndrome (biotic, wind)
- Potential dispersal distance (short, long)
- Area of occurrence (regional (South-western Cape), Cape Floristic Region (CFR), widespread). Species whose area of occurrence could not be determined (see Appendix 1), were not included in the analyses.
- Local abundance (rare, common, very common). Rare species were defined as those with occurrence on fewer than four sites of a total of 31 sites (including wheatfields), common species occurred on 4-19 sites, very common species on 20 or more sites.

Information on all but the last mentioned attribute was collated from a number of sources. These included Adamson and Salter (1950), Dyer (1975, 1976), Maytham Kidd (1983), Bond and Goldblatt (1984), Gibbs Russell *et al.* (1990) and Arnold and de Wet (1993), as well as various monographs and personal observations. Data on local abundance were derived from the plot data collected for this study.

4.3.2 Data analysis

4.3.2.1 Species diversity

Diversity indices are based on the relative proportional abundance of species. Thus, in two plots with the same species richness, the one with a more even abundance is considered to be more diverse (Magurran 1988). Species richness, S, was calculated as the total number of species per site. In addition, Hill's family of diversity indices were used to describe species diversities of the sites. These indices are transformations of commonly-used diversity indices. These transformations improve interpretation of the results. The indices were calculated for each site using percent cover only (Ludwig and Reynolds 1988). Using number of individuals produced similar trends.

N1 is the exponential of Shannon's diversity index. It is calculated as

$$N1 = \exp(-\sum p_i \ln p_i)$$

where p_i = the proportion of individuals found in the ith species. It is a measure of heterogeneity, which assumes that individuals are randomly sampled from an infinite population, and that all species are represented in the sample.

N2 is the reciprocal of Simpson's dominance index, calculated as

$$N2 = 1 / (\sum (n_i (n_i-1) / N(N-1)))$$

where n_i = the number of individuals in the ith species, N = the total number of species. It is a measure of dominance, weighted towards the abundance of the most common species. It is expressed as the reciprocal of Simpson's index, for the value to increase with increasing diversity (Magurran 1988).

Although N1 takes into account the evenness of the abundance of species, it is possible to calculate a separate additional measure of evenness, the modified Hill ratio, E. This index is less affected by the contribution of rare species and by total species richness (Ludwig and Reynolds 1988). It is calculated as:

$$E = ((N2-1) / (N1-1))$$

One-way analysis of variance was used to examine any significant differences in species richness, diversity, dominance and evenness in different fragment size classes. Significant differences among means were detected with Tukey multiple range tests.

4.3.2.2 Plant guilds

I calculated the proportion of species in each plant guild for each fragment size class and for wheatfields. To test whether certain plant guilds have a higher or lower than expected proportional representation on different fragment size classes, I drew up contingency tables and performed chi-square analysis on the total number of species per fragment size class. Wheatfields were not included in this analysis.

I performed one-way analysis of variance on species number, percent cover and number of individuals per fragment to test for significant differences in guild structure between fragment size classes. Percent cover data were arcsin-transformed. Since this study took place over several months to capture all species, total percentage cover exceeded 100% in some cases. In order to arcsin-transform the data, all percentage cover totals per site were relativised to 100%. Data were tested for normality. Tukey multiple range tests were used to detect significant differences among means.

4.4 Results

4.4.1 Species diversity

Medium fragments were most species-rich (S) and small fragments least species-rich (Table 4.1). Differences in species richness were, however, not significant. Small and medium fragments were more variable in terms of species numbers per site , where S ranged from 30 to 86 on small fragments and 67 to 118 on medium fragments. S ranged between 53 and 77 on large fragments.

Medium fragments had the highest level of heterogeneity (N1) with large fragments the lowest. Large fragments were, however, far less variable in terms of heterogeneity than small or medium fragments. Large fragments were also the least diverse fragments in terms of dominance (N2), with medium fragments the most diverse. This trend was also reflected by the evenness index (E), with medium fragments having more even abundances of species, and large fragments having least even abundances. The values of the three diversity indices were intermediate for small fragments. Differences in diversity indices between fragment size classes were not significant.

4.4.2 Plant guilds

Figure 4.1 shows the proportion of species per plant guild in each of the fragment size classes and for wheatfields (total number of species per fragment size class = 22, 196, 206 and 175 for wheatfield, small, medium and large fragments respectively). Plant guild proportionality was drastically different in wheatfields but similar in fragments of natural vegetation in different fragment size classes. Over 90% of species in natural vegetation were native, whereas 79% of the species found in wheatfields were aliens (Figure 4.1.a). Plant life-forms were distributed in roughly equal proportions in patches of natural vegetation. Sixty percent of the species in wheatfields were forbs and 40% were graminoids; no geophytes or shrubs were present in wheatfields (Figure 4.1.b). A far higher percentage of plants in all three fragment size classes were perennials; this pattern was reversed in wheatfields, where 91% of the species were annuals (Figure 4.1.c). The majority of species found in natural vegetation were pollinated by insects or birds, with approximately 20% of species in any fragment size class wind-pollinated. In wheatfields, pollination syndrome was more evenly distributed, with 56% of species pollinated biotically and 44% abiotically (Figure 4.1.d). Dispersal distance showed a converse trend. Natural vegetation had similar proportions of short and long distance-dispersed species. Wheatfields had a far higher proportion of long distance-dispersed species (Figure 4.1.e). All fragment size classes showed similar proportions of plants restricted to the south-western Cape, Cape Floristic Region and widespread taxa, but all species on wheatfields were widespread (Figure 4.1.f). Rare, common and very common species were distributed in similar proportions in each fragment size class; wheatfields were dominated by very common species. No rare species were found in wheatfields (Figure 4.1.g). Chi-square analyses on the total frequency of species number per plant guild for each fragment size class showed no significant differences (Table 4.2).

Table 4.3 summarises the results of one way analysis of variance on the mean number of species per plant guild in each fragment size class. Medium fragments had significantly more alien species than large fragments. Small fragments had intermediate numbers of alien species. Despite the high number of alien species, medium fragments had the highest number of native species. All fragment size classes had similar mean occurrences of each life form per patch, although medium fragments had significantly more graminoids, particularly annual graminoids, (which in most cases were alien species) than large fragments. The number of biotically-pollinated species did not differ significantly between fragment size classes, but significantly more wind-pollinated species were found on medium patches. Small and large patches had similar numbers of wind-dispersed species. Patches in different fragment size classes did not differ significantly in terms of species with long or short dispersal distance. Significantly more widespread plants were found on medium fragments than on large fragments. Similar numbers of rare, common and very common species were found on patches in different fragment size classes.

One-way analysis of variance on the number of individuals per plant guild generally showed no significant differences between fragment size classes (Table 4.4). The only exception was plant origin, with significantly more alien individuals occurring on medium fragments than on large fragments.

Total plant cover was highest on medium fragments and lowest on small fragments (Table 4.5). No significant differences were detected but the far higher cover of alien species on medium fragments (5.9%) than either small (1.7%) or large (0.3%) fragments is worth mentioning.

Table 4.1: Mean (±SE) values of diversity indices per fragment size class. S = species richness, N1 = species heterogeneity, N2 = dominance, E = evenness. F-ratios and significance levels for one-way ANOVAs are reported. See text for details.

Diversity Index	Fragment Size Class			F-Ratio
	Small	Medium	Large	
S	62.7 ± 3.3	80.0 ± 2.2	66.1 ± 0.9	2.249 NS
N1	14.6 ± 1.2	20.8 ± 1.4	13.7 ± 0.3	1.800 NS
N2	5.4 ± 0.4	8.7 ± 0.6	5.2 ± 0.2	2.474 NS
E	0.35 ± 0.01	0.37 ± 0.01	0.33 ± 0.01	0.393 NS

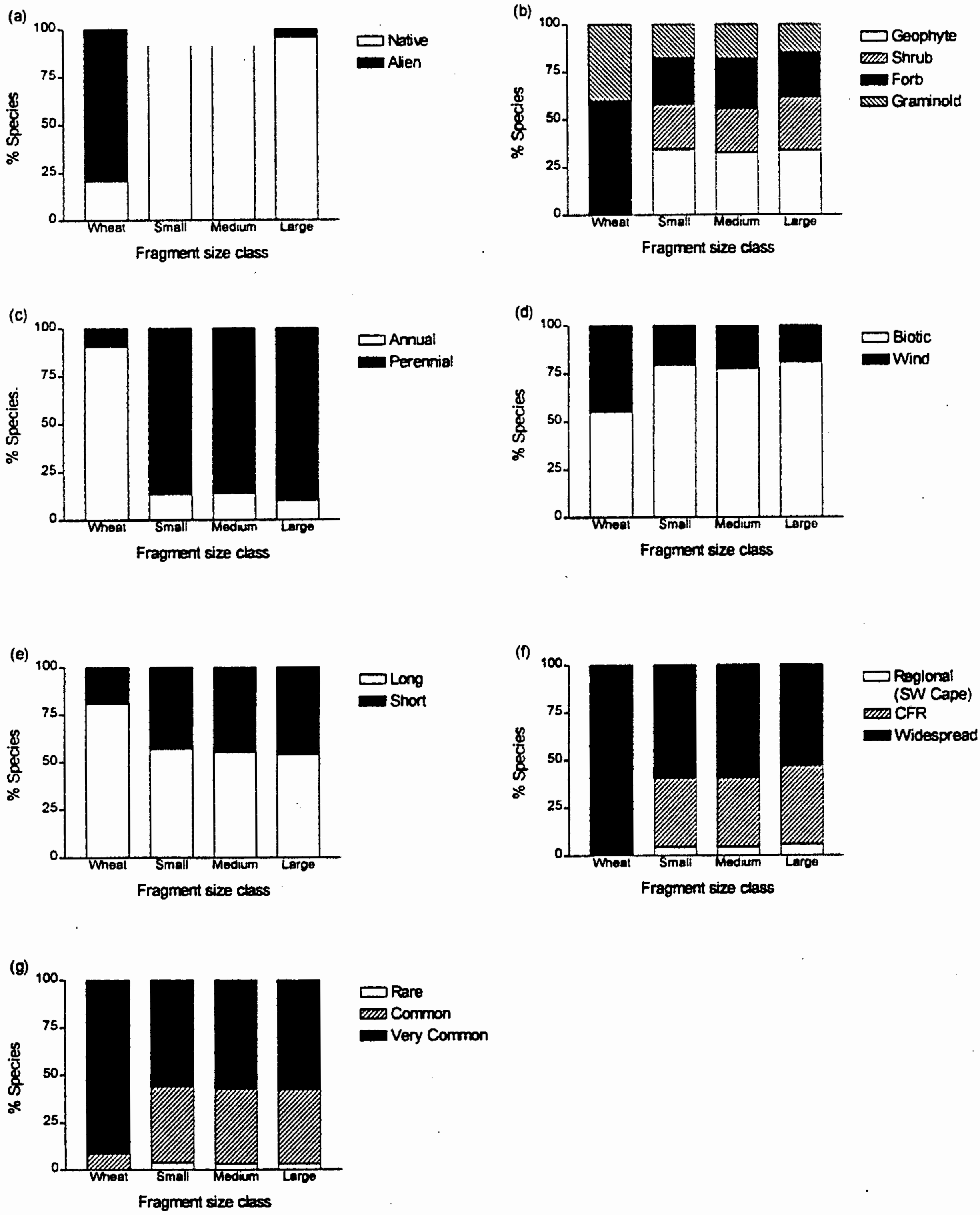

Figure 4.1: Percentage representation of each guild per fragment size class. Categories are: (a) origin, (b) life form, (c) life cycle, (d) pollination syndrome, (e) potential dispersal distance, (f) area of occurrence, (g) local abundance.

Table 4.2: Chi-square analysis on total number of species per fragment size class. Number in brackets shows percentage of total.

(a) Origin			
	Small	Medium	Large
Native	185 (94)	191 (93)	166 (95)
Alien	11 (6)	15 (7)	9 (5)
	$\chi^2 = 0.87$, df = 2, p = 0.648		
(b) Growth form			
	Small	Medium	Large
Geophyte	74 (38)	70 (34)	55 (31)
Shrub	44 (22)	54 (26)	56 (33)
Forb	29 (15)	33 (16)	25 (14)
Graminoid	49 (25)	49 (24)	39 (22)
	$\chi^2 = 4.78$, df = 6, p = 0.573		
(c) Life cycle			
	Small	Medium	Large
Annual	26 (13)	24 (12)	19 (11)
Perennial	170 (87)	182 (88)	156 (89)
	$\chi^2 = 0.54$, df = 2, p = 0.764		
(d) Pollination Syndrome			
	Small	Medium	Large
Biotic	166 (83)	164 (80)	145 (83)
Wind	33 (17)	42 (20)	30 (17)
	$\chi^2 = 1.74$, df = 2, p = 0.783		
(e) Dispersal Distance			
	Small	Medium	Large
Long	102 (52)	110 (53)	94 (54)
Short	94 (48)	96 (47)	81 (46)
	$\chi^2 = 0.12$, df = 2, p = 0.941		

Table 4.2 continued

(f) Area of occurrence

	Small	Medium	Large
Regional (SW Cape)	9 (5)	13 (6)	10 (6)
CFR	85 (43)	86 (42)	80 (45)
Widespread	102 (52)	107 (52)	85 (49)
	$\chi^2 = 1.17$, df = 4, p = 0.882		

(g) Local abundance

	Small	Medium	Large
Rare	21 (11)	18 (9)	13 (8)
Common	109 (56)	117 (57)	98 (55)
Very common	64 (33)	71 (34)	66 (37)
	$\chi^2 = 1.81$, df = 4, p = 0.771		

Table 4.3: Mean (±SE) number of species per guild per fragment size class. F-ratios and significance levels for one-way ANOVAs are reported.

Category	Attribute	Fragment size class			F-ratio
		Small	Medium	Large	
Origin	Native	58.3 ± 3.1	74.4 ± 2.3	63.8 ± 1.0	1.825 NS
	Alien	4.4 ± 0.3[ab]	5.6 ± 0.3[a]	2.4 ± 0.2[b]	5.169 *
Life form	Geophyte	23.4 ± 1.8	26.4 ± 0.8	22.3 ± 0.6	0.509 NS
	Shrub	12.6 ± 2.3	18.8 ± 1.1	19.0 ± 1.1	1.795 NS
	Forb	15.7± 1.0	21.0 ± 0.7	15.3 ± 0.4	2.611 NS
	Graminoid	11.0 ± 0.6[ab]	14.5 ± 0.2[a]	10.1 ± 0.3[b]	5.152 *
Life cycle	Annual	9.0 ± 0.6	11.0 ± 0.4	6.6 ± 0.4	3.397 NS
	Perennial	53.7 ± 2.8	69.0 ± 2.2	59.5 ± 1.2	1.764 NS
	Ann. forb	5.3 ± 0.4	6.4 ± 0.2	4.6 ± 0.2	1.464 NS
	Peren. forb	10.4 ± 0.7	14.6 ± 0.7	10.6 ± 0.2	2.394 NS
	Ann. graminoid	3.6 ± 0.3[ab]	4.6 ± 0.2[a]	2.0 ± 0.2[b]	5.017 *
	Peren. graminoid	7.4 ± 0.4	9.9 ± 0.3	8.1 ± 0.3	1.999 NS
Pollination syndrome	Biotic	50.3 ± 2.7	62.6 ± 2.0	53.6 ± 0.9	1.455 NS
	Wind	12.4 ± 0.6[a]	17.3 ± 0.4[b]	12.5 ± 0.4[a]	4.571 *
Dispersal distance	Long	35.3 ± 1.7	44.8 ± 1.5	36.1 ± 0.9	2.017 NS
	Short	27.4 ± 1.8	35.1 ± 0.9	30.0 ± 0.4	1.741 NS
Area of occurrence	Regional (Sw Cape)	2.7 ± 0.2	4.0 ± 0.3	4.0 ± 0.2	1.507 NS
	CFR	24.0 ± 1.6	29.5 ± 1.3	27.6 ± 0.9	0.635 NS
	Widespread	36.0 ± 1.7[ab]	46.5 ± 1.1[a]	34.5 ± 0.3[b]	4.896 *
Local abundance	Rare	3.1 ± 0.5	2.9 ± 0.2	2.1 ± 0.1	0.385 NS
	Common	25.3 ± 1.7	32.6 ± 1.8	26.3 ± 1.0	0.960 NS
	Very common	34.3 ± 1.9	44.5 ± 0.5	37.6 ± 0.5	3.226 NS

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

Table 4.4: Mean (±SE) frequencies of individuals per guild per fragment size class. F-ratios and significance levels for one-way ANOVAs are reported.

Category	Attribute	Fragment size class			F-ratio	
		Small	Medium	Large		
	Total	906.2 ± 63.3	938.0 ± 52.7	891.1 ± 42.0	0.028	NS
Origin	Native	863.7 ± 66.8	876.8 ± 50.6	886.5 ± 42.0	0.006	NS
	Alien	42.5 ± 4.6^{ab}	61.1 ± 4.6^{a}	4.7 ± 0.6^{b}	3.788	*
Life form	Geophyte	197.8 ± 16.1	147.4 ± 7.9	117.8 ± 8.4	1.785	NS
	Shrub	111.9 ± 8.4	100.8 ± 4.2	117.5 ± 4.6	0.303	NS
	Forb	297.8 ± 57.8	387.7 ± 49.9	192.4 ± 49.82	0.679	NS
	Graminoid	298.7 ± 34.4	302.1 ± 24.0	463.5 ± 40.4	1.039	NS
Life cycle	Annual	249.5 ± 50.6	176.7 ± 23.5	137.9 ± 19.9	0.403	NS
	Perennial	656.7 ± 42.6	761.3 ± 43.7	753.3 ± 41.9	0.228	NS
	Ann. forb	212.5 ± 49.9	133.2 ± 19.1	121.3 ± 18.5	0.343	NS
	Peren. forb	85.3 ± 11.7	254.5 ± 34.5	71.1 ± 6.4	2.770	NS
	Ann. graminoid	36.9 ± 7.5	43.5 ± 5.7	16.6 ± 2.3	0.918	NS
	Peren. graminoid	261.8 ± 34.7	258.7 ± 26.8	447.0 ± 41.1	1.270	NS
Pollination syndrome	Biotic	565.3 ± 41.1	595.9 ± 48.2	366.2 ± 18.0	1.135	NS
	Wind	340.9 ± 33.7	347.3 ± 26.4	525.1 ± 40.0	1.252	NS
Dispersal distance	Long	629.6 ± 52.2	719.0 ± 39.9	728.3 ± 47.1	0.173	NS
	Short	276.5 ± 20.2	224.2 ± 14.6	163.0 ± 10.7	1.817	NS
Area of occurrence	Regional (SW Cape)	75.7 ± 11.0	180.9 ± 29.3	21.4 ± 3.1	2.472	NS
	CFR	275.4 ± 43.9	217.1 ± 8.4	284.9 ± 21.6	0.264	NS
	Widespread	555.1 ± 33.2	540.0 ± 28.6	584.8 ± 35.2	0.066	NS
Local abundance	Rare	21.4 ± 4.5	10.6 ± 1.3	9.8 ± 1.7	0.759	NS
	Common	227.2 ± 13.5	343.4 ± 44.9	133.5 ± 7.9	1.799	NS
	Very common	657.6 ± 63.7	583.7 ± 23.7	747.9 ± 41.7	0.486	NS

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

Table 4.5: Relativised mean (±SE) percentage cover per guild per fragment size class. F-ratios and significance levels for one-way ANOVAs on arcsin-transformed data and back-transformed means are reported.

Category	Attribute	Fragment size class			F-ratio
		Small	Medium	Large	
	Total	62.3 ± 1.2	71.7 ± 1.5	63.7 ± 1.63	1.544 NS
Origin	Native	60.5 ± 1.1	65.7 ± 0.6	63.2 ± 1.7	0.602 NS
	Alien	1.7 ± 0.1	5.9 ± 1.2	0.3 ± 0.1	2.108 NS
Life form	Geophyte	11.4 ± 1.5	7.7 ± 0.2	6.3 ± 0.2	1.513 NS
	Shrub	27.5 ± 2.3	23.9 ± 1.1	21.7 ± 1.2	0.480 NS
	Forb	4.8 ± 0.4	9.9 ± 0.5	7.0 ± 0.5	3.198 NS
	Graminoid	18.5 ± 2.3	30.2 ± 1.6	28.7 ± 1.4	1.592 NS
Life cycle	Annual	3.1 ± 0.2	7.5 ± 1.2	2.0 ± 0.1	1.829 NS
	Perennial	59.2 ± 1.3	64.2 ± 0.6	61.7 ± 1.7	0.505 NS
	Ann. forb	1.8 ± 0.2	2.1 ± 0.1	1.4 ± 0.1	1.301 NS
	Peren. forb	3.0 ± 0.2	7.8 ± 0.5	5.6 ± 0.5	3.276 NS
	Ann. graminoid	1.3 ± 0.1	5.4 ± 1.2	0.6 ± 0.1	1.712 NS
	Peren. graminoid	17.2 ± 2.3	24.8 ± 1.0	28.0 ± 1.4	1.547 NS
Pollination syndrome	Biotic	30.1 ± 1.7	31.7 ± 1.3	21.4 ± 0.7	2.430 NS
	Wind	32.2 ± 0.5	40.0 ± 1.3	42.3 ± 1.3	1.704 NS
Dispersal distance	Long	44.0 ± 2.3	60.3 ± 2.2	54.2 ± 1.7	2.837 NS
	Short	18.3 ± 2.0	11.4 ± 0.6	9.5 ± 0.3	2.505 NS
Area of occurrence	Regional (Sw Cape)	8.8 ± 1.7	7.3 ± 0.5	1.8 ± 0.1	1.990 NS
	CFR	12.5 ± 1.3	13.8 ± 0.7	15.0 ± 0.9	0.210 NS
	Widespread	41.1 ± 1.6	50.5 ± 1.5	47.0 ± 1.2	1.382 NS
Local abundance	Rare	0.8 ± 0.2	0.6 ± 0.1	0.5 ± 0.1	0.533 NS
	Common	16.9 ± 2.1	13.3 ± 0.8	11.4 ± 1.0	0.579 NS
	Very common	44.6 ± 2.0	57.7 ± 1.4	51.9 ± 1.5	2.048 NS

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

4.5 Discussion

4.5.1 Species diversity

Apart from their restricted size, small and medium fragments have a higher edge to area ratio and are therefore more susceptible to disturbances stemming from matrix-management (Saunders 1991, Meffe and Carroll 1994). The majority of vegetation fragmentation studies have shown fragmentation to negatively influence species diversity patterns (e.g. Bond *et al.* 1988, Webb and Vermaat 1990, Saunders and Hobbs 1992, Turner 1996, but see Robinson and Quinn 1988, Iida and Nakashizuka 1995). The results from this study indicate that small, medium and large fragments have similar levels of species richness, heterogeneity, dominance and evenness of species. This, therefore, suggests no negative effects of fragmentation on the species diversity of South Coast Renosterveld. However, species richness and diversity values were generally more variable among small and medium fragments. This implies that large fragments may be more stable, while small and medium fragments represent a range of dynamic systems, where extinction and colonisation mechanisms are operating. These results agree with those obtained in Chapter 3, where two-way indicator species analysis showed higher variability in species composition among small and medium fragments. Large sites are heavily grazed throughout the year, possibly resulting in slightly lower diversity levels; small and medium fragments are exposed to sporadic but extremely intense grazing and trampling, which may explain the higher variation in species richness and diversity levels.

4.5.2 Plant guilds

Fragments of natural vegetation differ drastically in species composition and proportional representation of plant guilds from wheatfields. Although this is not a surprising result, it emphasises the high degree of modification of the agricultural matrix encompassing fragments and the sharp boundary between natural vegetation fragments and their surrounding matrix. Only few (usually alien) species can persist or establish in wheatfields, indicating that the matrix does not even provide marginal habitat for some native species. This vastly different and hostile matrix, moreover, hinders dispersal between patches by not providing suitable habitat for movement between patches.

Despite the reduction in habitat area, their position in the landscape and a high potential of edge effects, plant guilds on small and medium fragments do not differ in their proportional representation from large fragments. This does not agree with the hypothesis that species with different attributes are expected to be differentially represented on small and medium fragments. These results differ from those of Pettit *et al.* (1995), but largely mirror results obtained by Bond *et al.* (1988), whose comparison of plant guilds on islands and mainlands of fynbos shrubland only found geophytes, short shrubs and sprouters significantly underrepresented on small fragments, while graminoids were overrepresented.

Similarly, the number of species, individuals and cover for each plant guild generally did not differ between fragment size classes. The only major exception is the number and cover of alien species, which are lower on large fragments. This may be the result of edge effects in small and medium fragments. Despite the significantly higher mean number of alien plant species and their number of individuals on medium islands, high species richness on medium fragments indicates that native vegetation has not been replaced by alien species. It is becoming generally accepted that ecosystems vary in their susceptibility to invasions (Hobbs and Humphries 1995). Studies in the Australian Wheatbelt found that fragments of woodland were far more susceptible to subsequent invasion of non-native annuals than shrub or heathland (Hester and Hobbs 1992, Saunders *et al.* 1993). Coupled with my results, this suggests that shrublands are indeed less invadable by alien annuals.

4.5.3 Proposed mechanisms

South Coast Renosterveld exists as a series of fragments of natural vegetation, which, apart form reduced size and increased isolation, are subjected to the effects of inclusive agricultural management. Nevertheless, small and medium fragments appear to remain structurally relatively intact. These patterns could reflect a number of underlying mechanisms, taking into account the temporal and spatial scale of fragmentation of South Coast Renosterveld. Some of these are discussed below.

Sprouters are able to persist for long periods (Midgley 1996), and include a number of shrubby and bulbous species. Although fragments may not be recruiting new species or individuals, persistent species are able to withstand extinction at least temporarily. Fragmentation of South Coast Renosterveld is a relatively recent event and a lag-phase after fragmentation, related to the persistence of species, may obscure the expression of recruitment failure and ultimately extinction (Buchmann and Nabhan 1996 and references within). Lamont *et al.* (1993), for example, showed that small roadside populations of *Banksia goodii* were too small to attract pollinators, resulting in lower levels of seed set. They concluded that small roadside fragments lack means of regeneration and are therefore functionally extinct. It would have been useful to include regeneration mode (resprouters versus reseeders) as a guild category, since resprouters are persisters which are tolerant to frequent grazing and fire disturbance (Kruger 1983, Midgley 1987). Small and medium fragments are particularly exposed to frequent fires and intense grazing; they may be over-represented by persistent resprouters. Similarly, an analysis of pollinator dependence (selfers versus obligate outcrossers) may have explained the apparent persistence of most species on small and medium fragments. However, data on regeneration and pollination dependence are lacking for most species. Collection of this data should therefore be a priority.

Although intensive agriculture is comparatively recent, South Coast Renosterveld has been subjected to disturbance for centuries, when pastoralists began grazing livestock. These activities are thought to have changed renosterveld from grassland to a more shrubby system (see Chapter 1). Simberloff (1993) argues that historical disturbance influences the responsiveness of a system to recent disturbance, where historical disturbance created different, but more "robust" communities. It is thus likely that the most sensitive species have gone extinct with the advent of pastoralism (Khoi) and more recently, settled agriculture (Europeans). The remnants of natural vegetation may now be more resistant to the more recent effects of large-scale fragmentation. Unfortunately, comprehensive historical species lists from this area are lacking, and it is difficult to say how many and which species have gone extinct since pastoralism and agriculture began.

Another reason for the apparent lack of differences in diversity, plant guild proportionality, number and abundance (as indexed by cover and number of individuals), may be that renosterveld is a highly heterogeneous system. Renosterveld shares many species with fynbos, the dominant sclerophyllous shrubland in the Cape

Floristic Region (see Chapter 1). Many fynbos species exist as small, isolated populations, crowded into small areas (Rebelo 1992). Small population sizes may therefore be natural in renosterveld and it is possible that many renosterveld species have already had small and isolated populations resistant to inbreeding depression and loss of heterozygosity prior to fragmentation and are therefore able to withstand extinction processes (e.g. demographic stochasticity) associated with small population size.

The experimental design of this study is limited in that it only tests the effect of area reduction on species diversity and guild structure. It does not take habitat diversity into account. Although small and medium fragments seem to have similar levels of species diversity, with similar proportional representation of plant guilds and plant guild richness and abundances, habitat diversity is bound to be reduced as total habitat area is reduced. The effect of loss of habitat diversity on species diversity was however beyond the scope of this study. P. Hockey (pers. comm.), for example, found a strong fragmentation effect for birds in South Coast Renosterveld, which he attributes to the loss of habitat diversity on small fragments. It is, therefore, likely that a loss in habitat diversity due to the selective nature of clearing has resulted in the immediate and complete loss of species or guilds from renosterveld. This was found in Australia, where non-random clearing for agriculture resulted in fragments containing only a subset of communities. Thus, woodlands, which occur on rich soils in Australia are particularly underrepresented on the remaining fragments (Hobbs 1987).

The observed patterns must also be interpreted in the light of a short-term ("snapshot") study, rather than a long-term study of community dynamics. Ideally, the area should be monitored over a prolonged period, particularly to understand the links between system structure and processes and how these are affected by fragmentation (Wiens *et al.* 1986). This emphasises the need to interpret the results of this study in terms of the spatial and temporal scales under investigation.

4.6 Conclusion

Despite these limitations, some insights were gained on the value of small fragments. The results suggest that even the smallest fragments play an important role in the conservation of the South Coast Renosterveld flora and can provide vital links ("stepping stones") between larger fragments. Studies in the Western Australia wheatbelt have shown that fragments are also important for the control of soil salinisation and mitigation of erosion as well as providing shelter for livestock (Hobbs 1992, 1993). These and other functions were not investigated in this study, but similar functions may well be performed in this system. It has for example been shown that livestock grazing on renosterveld and fynbos provides livestock with trace minerals lacking on natural pastures, and improves livestock health (B. Heydenrych pers. comm.).

Although the potential for establishing nature reserves in very fragmented areas is small due to their fragmented nature and high purchasing costs (McDowell 1988), even the smallest fragments can provide direct services to the farming community. The results of this study should therefore be used as an incentive to managers to retain even small areas of South Coast Renosterveld rather than to convert marginal land into cereal fields or artificial pastures.

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Chapter 5

Reproductive success of two geophytes *Ornithogalum thyrsoides* Jacq. and *Babiana ambigua* (Roemer & Schultes) G.J. Lewis

5.1 Abstract

Fragmentation generally decreases population sizes and potentially disrupts plant-pollinator interactions. This can affect plant reproductive success and ultimately demography. I compared reproductive success, measured by fruit set, seed set, germination success and number of individuals produced per plant, on small, medium and large fragments for two species. I chose two plant species with different reproductive strategies to investigate whether fragment size influences reproductive success, and how reproductive success is influenced by plant life history. In *Ornithogalum thyrsoides* (Hyacinthaceae) reproductive success did not decline with increasing fragmentation. In *Babiana ambigua* (Iridaceae), reproductive success was drastically affected by fragmentation, but in a way contrary to fragmentation theory predictions. Fruit set, seed set and the production of individuals per plant were higher on small fragments. Germination success was, however, higher on large fragments. A number of reasons for these patterns are proposed. The results show that plant reproductive strategy influences the effect of fragmentation on reproductive success. Whereas *O. thyrsoides* is capable of selfing and has a range of common pollinators, *B. ambigua* relies on few pollinators for reproduction. Species with specialised reproductive strategies are therefore more at risk of local extinction. Conservation efforts should focus on such species.

5.2 Introduction

The fragmentation of natural vegetation by agricultural practices results in an array of patches, which are surrounded by vast areas of fundamentally different and generally monospecific vegetation. This potentially influences a number of ecological processes at several scales (Saunders *et al.* 1991), including the population scale (Jennersten 1988). Reports of the negative impact of fragmentation on important population processes such as pollination and seed production are increasing, causing widespread concern about long-term consequences on biodiversity in fragmented systems (Buchmann and Nabhan 1996).

Fragmentation reduces habitat area and isolates populations. This could disrupt plant-animal interactions, which play an essential role in some plant life histories, particularly during the pollination and seed dispersal stages (Aizen and Feinsinger 1994a). Sowig (1989), for example, illustrated that foraging strategies of bumblebees are a function of patch size. Specialised plant-pollinator systems tend to be particularly sensitive to disturbances (Gilbert 1980, Jennersten 1988, Bond 1994) and the breakdown of specialised pollination systems has been shown to have serious consequences for the reproductive success of a plant (Linhart and Feinsinger 1980, Lamont *et al.* 1993).

The process of fragmentation may also influence plant-animal interactions indirectly by reducing the size of populations. Small pollinator populations could decrease pollinator visitation rates (Handel 1983), which reduces the number of pollen grains deposited, resulting in a lower number of fertilised ovules. Studies of oceanic islands show that pollinators were more uncommon on islands than on mainlands (Feinsinger *et al.* 1979, Linhart and Feinsinger 1980), with reduced pollen flow on isolated islands compared to mainland sites (Spears 1987). Severe pollinator limitation on a protected area flanked by agricultural land in the Sonoran Desert of Mexico has drastically reduced reproductive success (in terms of fruit and seed set) of a moth-pollinated cactus, *Peniocereus striatus* (Buchmann and Nabhan 1996). Jennersten (1988) showed that pollinator visitation rates and seed set in anthropogenically fragmented areas was lower than on undisturbed, continuous sites. Geographically isolated plant populations are at risk of genetic isolation, loss of genetic variance, potential expression of deleterious alleles and increased homozygosity (Ledig 1986, Menges 1991, Ellstrand 1992), with low pollen quality as a consequence. Menges (1991) tentatively attributed germination success patterns for *Silene regia* populations to the effects of small population size on population genetics.

Fragmentation changes landscape geometry, often increasing edge to area ratios, which change microclimate by, for example, altering radiation and water runoff, temperature and windspeed (Saunders *et al.* 1991). These microclimatic changes have been shown to affect plant reproduction by shifting flowering times (e.g. Jackson 1966), and could therefore influence reproductive success (Handel 1983). Microclimatic conditions are also hypothesised to influence pollinator activity and behaviour (Handel 1983). This was documented by Herrera (1995), who reported significant differences in pollinator activity with the sunlight regime associated with individual plants.

The management of fragments situated in agricultural lands can further affect plant reproductive success. The widespread use of pesticides in agricultural systems surrounding natural vegetation is known to lead to fruit abortion, reduced fruit development and delayed seed germination (Heitefuss 1988 in Freemark and Boutin

1995) and change pollinator composition and abundance (Kevan *et al.* 1985), thus negatively influencing plant reproductive success.

The brief review above illustrates that fragmentation can and does influence important biological processes. Ultimately, this results in the extinction of populations and species (Meffe and Carroll 1994). It could also cause a cascading effect on the demography of other species in the ecosystem (Gilbert 1980, Ingvarsson and Lundberg 1995).

The degree to which fragmentation will affect reproductive success will depend on the reproductive strategy of the plant (Bond 1994). Studies on oceanic islands have noted a high proportion of wind-pollinated and selfing taxa on islands (Whitehead 1969 in Regal 1982), with insect-pollinated plants usually associated with unspecialised flowers (see Spears 1987). This is assumed to be the result of an island-induced decline in pollinator diversity (Linhart and Feinsinger 1980, Spears 1987). In a multi-species study, Aizen and Feinsinger (1994a) found great variation in fruit and seed set among species. Their results suggest that species with different degrees of pollinator specificity may react differently to fragmentation. These findings suggest that increased fragmentation leads initially to a loss in outcrossing plants, pollinated by specialised animals. Plants with specialised flowers and only one or few pollinator species are therefore apt to be more severely affected by fragmentation than plants with a range of pollinators. Plants which are outcrossers rather than autogamous selfers, and which therefore have to rely on pollination will be similarly affected. Reproductive success is also a function of resource availability (Johnson 1992, Obeso 1993, Aizen and Feinsinger 1994a), which may be changed by fragmentation: reproductive success in isolated fragments may, therefore, not simply be a function of pollination success.

Large tracts of South Coast Renosterveld, a sclerophyllous shrubland in the lowlands of the Cape Floristic Region, South Africa, have been fragmented by agriculture (See Chapter 1 for a description of South Coast Renosterveld and Chapter 2 for an overview of fragmentation patterns). The resulting fragments differ in size, isolation and geometry. Furthermore, small and medium fragments are managed as part of the surrounding agricultural lands and are therefore subjected to crop spraying. Current fragmentation theory predicts that pollination systems and plant reproductive success in renosterveld would therefore vary as a function of fragmentation. I investigated this broad prediction, using two species with different reproductive strategies. This study therefore aimed to address the following key questions: (1) is reproductive success (indexed by pollination, fruit and seed production, and germination) influenced by fragment size, a breakdown in plant-pollinator interactions or the consequences of small population sizes; and (2) how is this pattern influenced by plant life history.

5.3 Methods

5.3.1 Plant species

I investigated two geophyte species, both characteristic species of this vegetation type. *Ornithogalum thyrsoides* Jacq. (Hyacinthaceae) is a widespread geophyte, endemic to the Cape Floristic Region, often occurring in large, dense populations on flats and lower slopes, often in wet areas (Bond and Goldblatt 1984). It bears a number of white dish-like flowers, often with dark centres (3-20), and blooms from October to December. It is pollinated by a range of insects, but most commonly by beetles, particularly several species of monkeybeetle (Order Coleoptera, Tribe Hopliini) and a day-flying moth (Order Lepidoptera, Family Ctenuchidae) (C. Zachariades pers. comm.). The seeds develop in a three-locular capsule and are dispersed for only short distances (<10m) after the dry capsule splits open (pers. obs.). This species, which is suspected to be capable of selfing, was very common at the study site and was sampled during the 1994 flowering season. Hereafter I refer to this species as *Ornithogalum*.

Babiana ambigua (Roemer & Schultes) G.J. Lewis (Iridaceae) is a variable, fairly widespread and common geophyte, also endemic to the Cape Floristic Region (Bond and Goldblatt 1984). It usually has between three and six zygomorphic, fragrant, tubular flowers which range in colour from pale pink to dark purple with white, yellow and dark purple markings near the centre. The flowers are borne close to the ground. I believed *B. ambigua* to be incapable of selfing. It generally occurs on sandy flats and lower slopes, although it often inhabits rocky areas in South Coast Renosterveld (pers. obs.). It flowers from July to September and is exclusively pollinated by solitary bees (Order Hymenoptera, Family Anthophoridae) (J. Manning, pers. comm.). Fewer seeds are produced than for *Ornithogalum* (pers. obs.), and these develop in a three-locular capsule and are shaken out after ripening (short-distance dispersal, <10m). Although far less common than *Ornithogalum*, *B. ambigua* occurred in adequate numbers for this study. Sampling of *B. ambigua* was carried out during the 1995 flowering season. Hereafter I refer to this species as *Babiana*.

Plate 5.1: The two plant species used in the experiment: *Ornithogalum thyrsoides* (Hyacinthaceae) (top) with one of its pollinators, a day-flying moth, and *Babiana ambigua* (Iridaceae) (bottom).

5.3.2 Breeding system experiment

To confirm the breeding system of both species, I transferred 45 potted individuals of each species to Cape Town and bagged each plant with nylon mesh. Plants were randomly allocated to one of three treatments: (1) pollination with pollen from other individuals, (2) pollination with own pollen, (3) no pollination. I recorded fruit set, seed set and germination success for each treatment. Species with fruit set <25% of that following cross-pollination were classified as self-incompatible (Aizen and Feinsinger (1994a).

5.3.3 Pollination Field Experiment

5.3.3.1 *Ornithogalum*

I chose fragments where *Ornithogalum* occurred in adequate densities to provide a satisfactory sample size. This resulted in four fragments per fragment size class (see Chapter 1 for a definition of fragment size classes). On each fragment, I tagged 24 individual plants and assigned them to one of three treatments: (1) Hand- cross-pollination to estimate maximum fruit and seed set of a fragment; unpollinated flowers and buds were removed since it was logistically not possible to hand-pollinated each flower of each plant; (2) No hand-pollination; the number, ratio and position of flowers removed per plant was matched as closely as possible to treatment (1), resulting in paired samples. This was done because the removal of flowers could result in a nutrient resource shift (Obeso 1993) and influence its attractiveness to pollinators (therefore biasing results). Plants in treatment (3) were unmanipulated. Inflorescences were collected after seed set but prior to seed dispersal. Unfortunately this meant that a large proportion of drying inflorescences were removed by seed predators, making a pairwise comparison of treatments (1) and (2) impossible.

5.3.3.2 *Babiana*

Owing to the lower density of *Babiana* in the study area, only three fragments per fragment size class had adequate densities for the field study. Fragments were chosen prior to flowering. However, although all fragments produced enough individuals, not all plants produced flowers. Surprisingly, all three small fragments showed a mass display of flowers, whereas all three large fragments produced very few, scattered flowers, with the medium fragments producing intermediate numbers. For each fragment, 20 individuals were to be marked and assigned to one of the manipulation treatments described for *Ornithogalum*. This was only possible for all small and two medium fragments. An additional 10 inflorescences per fragment were collected prior to seed dispersal.

For each species, a rough estimate of the population size of flowering plants was made on each fragment. Since flowering population sizes varied dramatically, especially in the case of *Babiana*, population size could have influenced fruit and seed set in terms of attractability of a mass-display of flowers, thereby increasing the probability of pollinator visitation. Each fragment was therefore assigned to one of four population size classes: (1) < 20 individuals, (2) 20-50, (3) 51-150, (4) > 150.

5.3.4 Germination trials

I tested seeds collected in the pollination field experiment for germination ability. For each species, I incubated 100 seemingly viable (plump) seeds (25 seeds in four petri dishes) per pollination treatment per fragment on filter paper with 2.5ml water containing 0.075% Benlate, a fungicide. In some cases, seed numbers of *Babiana* were too low, and all available viable seeds were used (at least 10). The petri dishes were placed in controlled environment growth chambers under a dark/light, 10°/20°C cycle regime for 14/10 hours to simulate early spring field conditions. Moisture levels were kept constant throughout the experiment. Germination was defined by the appearance of the radicle. I used the proportion of seeds which germinated to estimate germination success. The experiment was discontinued after 2 months or until all seeds had germinated, whichever happened sooner. I opened ungerminated seeds were to confirm viability by determining the presence of an embryo.

5.3.5 Data analysis

I used one-way ANOVA to compare the mean fruit and seed set for the three pollination treatments in the breeding system experiments. The mean proportion of seed germinating from these treatments, expressed as a percentage, were also compared using one-way ANOVA on arcsin-transformed data.

Two-way ANOVAs using fragment size class and pollination treatment as factors were used to compare the seed set, fruit set, germination success (arcsin-transformed) and individuals produced per plant for the field pollination experiment. Individuals per plant were calculated using the following formula:

$$TS * G / I$$

where:

TS = total number of seeds collected per fragment per treatment. In the case of treatments (1) and (2), where flowers had been removed, total number of seeds was extrapolated for all flowers;

G = germination success, i.e. the proportion of seeds germinated per fragment per treatment;

I = number of individual plants per fragment per treatment.

Because many *Babiana* plants did not flower, the sample size for the *Babiana* pollination experiment was small. The small sample sizes meant that two-way ANOVAs were not possible (in some cases n<3). Two one-way ANOVAs were used to compare the effects of fragment size (using data of unmanipulated plants only) and pollination treatment on fruit set, seed set, germination success (arcsin-transformed) and individuals produced per plant. One-way ANOVAs were used to compare fruit set, seed set, germination success (arcsin-transformed) and individuals produced per plant between population size classes for both species. All data were tested for normality. Significant differences among means were determined using Tukey multiple range tests.

5.4 Results

5.4.1 *Ornithogalum*

The breeding system experiment showed that *Ornithogalum* is self-compatible, with no significant differences recorded for fruit and seed set between plants pollinated with cross-pollen and those pollinated with self-pollen (Figure 4.1). Although excluded plants showed significantly lower levels of fruit and seed set, they were capable of autogamy. Germination success did not differ significantly with any of the three treatments.

The results of the pollination field experiment revealed that fruit set did not change significantly with fragment size (Figure 5.2.a), with a large proportion (>0.85) of flowers producing fruit. Unmanipulated plants, however, yielded 10% fewer numbers of fruits per flower than either of the treatments where flowers were removed. This difference was statistically significant. The interaction between fragment size and treatment was not significant. Seed production did not change significantly with either fragment size or treatment (Figure 5.2.b), although hand-pollinated plants yielded nearly 13% more seeds than unmanipulated ones. The interaction between factors was again not significant.

The germination trials generally produced very high levels of germination success (>80%) (Figure 5.2.c), with most seeds germinating within 4 weeks of incubation. Neither fragment size, pollination treatment, nor the interaction between them had a significant effect on germination success. Overall reproductive output (calculated as the number of individuals produced per plant) was significantly higher on medium-sized fragments (Figure 5.2.d), with roughly 40% more individuals produced on medium fragments than on either small or large ones. Neither pollination treatment nor the interaction with fragment size were significant.

Correlation analysis showed that population size was not correlated with fragment size (Spearman rank correlation coefficient -0.00, NS, n=36). Further analysis (Figure 5.3) revealed a significant difference in seed set between populations of 20-50 plants and populations greater than 150 plants. Germination success was on average 18% higher in populations of 20-50 plants than in populations of 50-100 plants. Large populations produced significantly more individuals per plant than very small or intermediate-sized populations.

5.4.2 *Babiana*

Because of its deep-rooted corm, *Babiana* did not react well to the transplantation procedure, and all 45 plants died during the course of the breeding system experiment. However, it is believed (G. Duncan pers. comm.) that *B.* ambigua is either self-compatible to a far lesser degree than *Ornithogalum*, if not completely self-incompatible, a trend observed in many members of the Iridaceae.

Fruit set varied significantly with fragment size class (Figure 5.4.a), with large fragments producing roughly two thirds fewer fruits per flower than small fragments (means of 0.80, 0.60 and 0.28 for small, medium and large fragments respectively). Fruit set changed with pollination treatment (Figure 5.5.a); hand-pollinated plants had the highest fruit set and unmanipulated plants the lowest. Seed set in *Babiana* differed with fragment size class (Figure 5.4.b), with small fragments producing nearly three times as many seeds per fruit as large fragments. Although hand-pollination increased seed set by an average of 25% over natural pollination, this was not significant (Figure 5.5.b).

Virtually all (96.3%) viable seeds from large fragments germinated, significantly more than from seeds from small (36.0%), or medium (4.3%) fragments (Figure 5.4.c). Although unmanipulated plants had better average germination success (45.6%) than either of the manipulation treatments (3% and 12.6% respectively), this was not statistically significant (Figure 5.5.c). All opened ungerminated seeds contained embryos, confirming that all seeds used in the germination experiment were potentially viable. Overall reproductive success showed that small fragments produced significantly more individuals per plant (16.8) than medium (0.5) or large fragments (5.1) (Figure 5.4.d). Pollination treatment did not influence overall reproductive output significantly (Figure 5.5.d), but unmanipulated flowers produced more individuals (7.5) than the manipulated plants (1.9 and 4.1 respectively).

Population size was highly significantly negatively correlated with fragment size (Spearman rank correlation coefficient -0.939, $p<0.001$, $n=19$). Fruit set in large flowering populations was roughly twice as high as in small populations (Figure 5.6.a), and seed set increased approximately threefold from 7.3 seeds per fruit in small populations to nearly 19 in large populations (Figure 5.6.b). Germination success in small populations (72.8%) was significantly higher than in populations of 20-50 plants (5.7%), 51-150 plants (22.3%) and >150 plants (16.3%) (Figure 5.6.c). However, the number of individuals produced per plant did not differ significantly with population size (Figure 5.6.d).

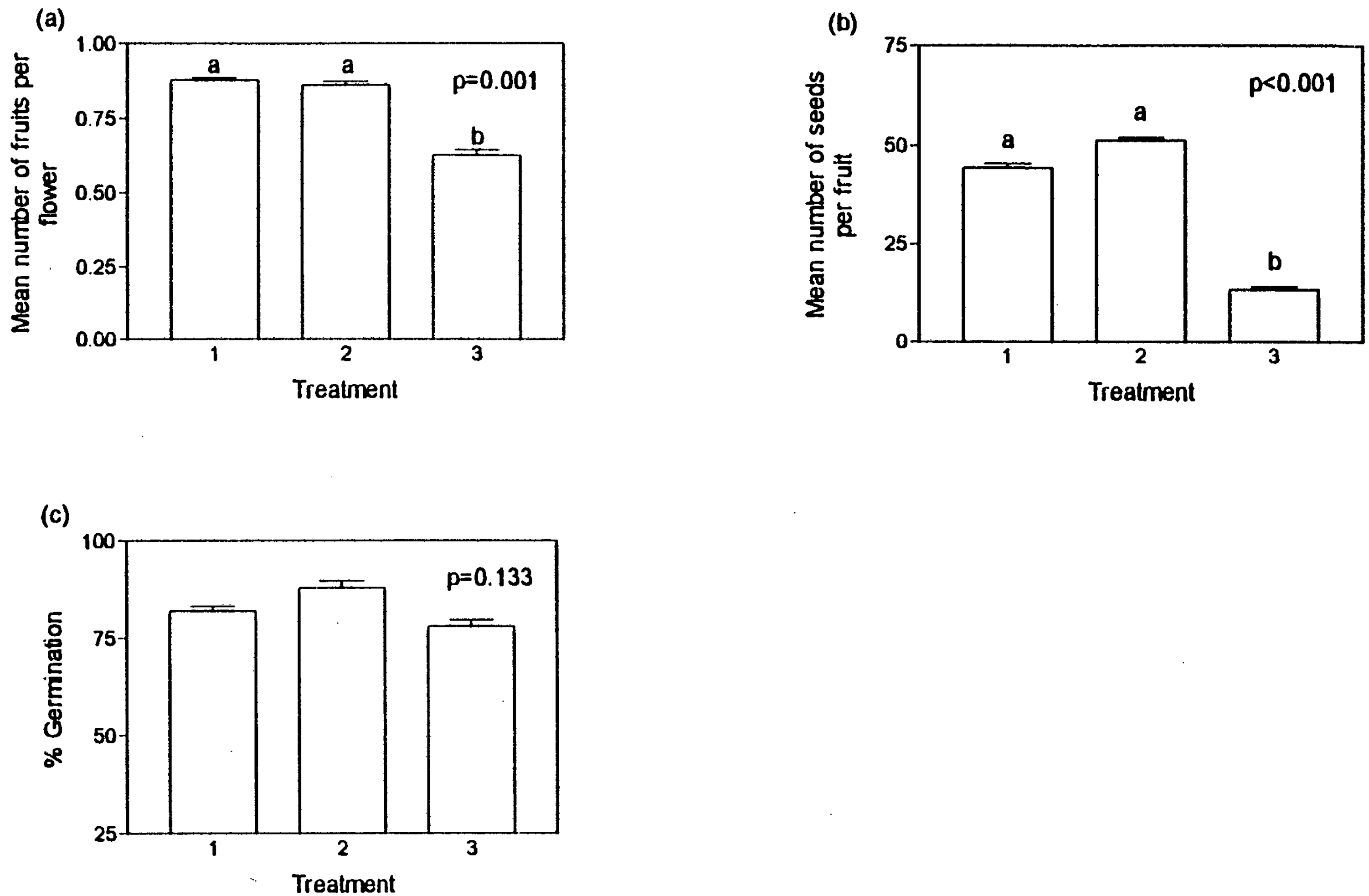

Figure 5.1: Mean (± SE) number of (a) fruits per flower, (b) seed per fruit, and (c) germination success (arcsin-transformed) for *Ornithogalum* under three pollination treatments performed on potted plants (breeding system experiment). Treatments: (1) cross-pollination, (2) self-pollination, (3) exclusion. Significance levels for one-way ANOVAs and back-transformed means are reported. Means that share the same superscript letter do not differ significantly (Tukey Multiple Range test).

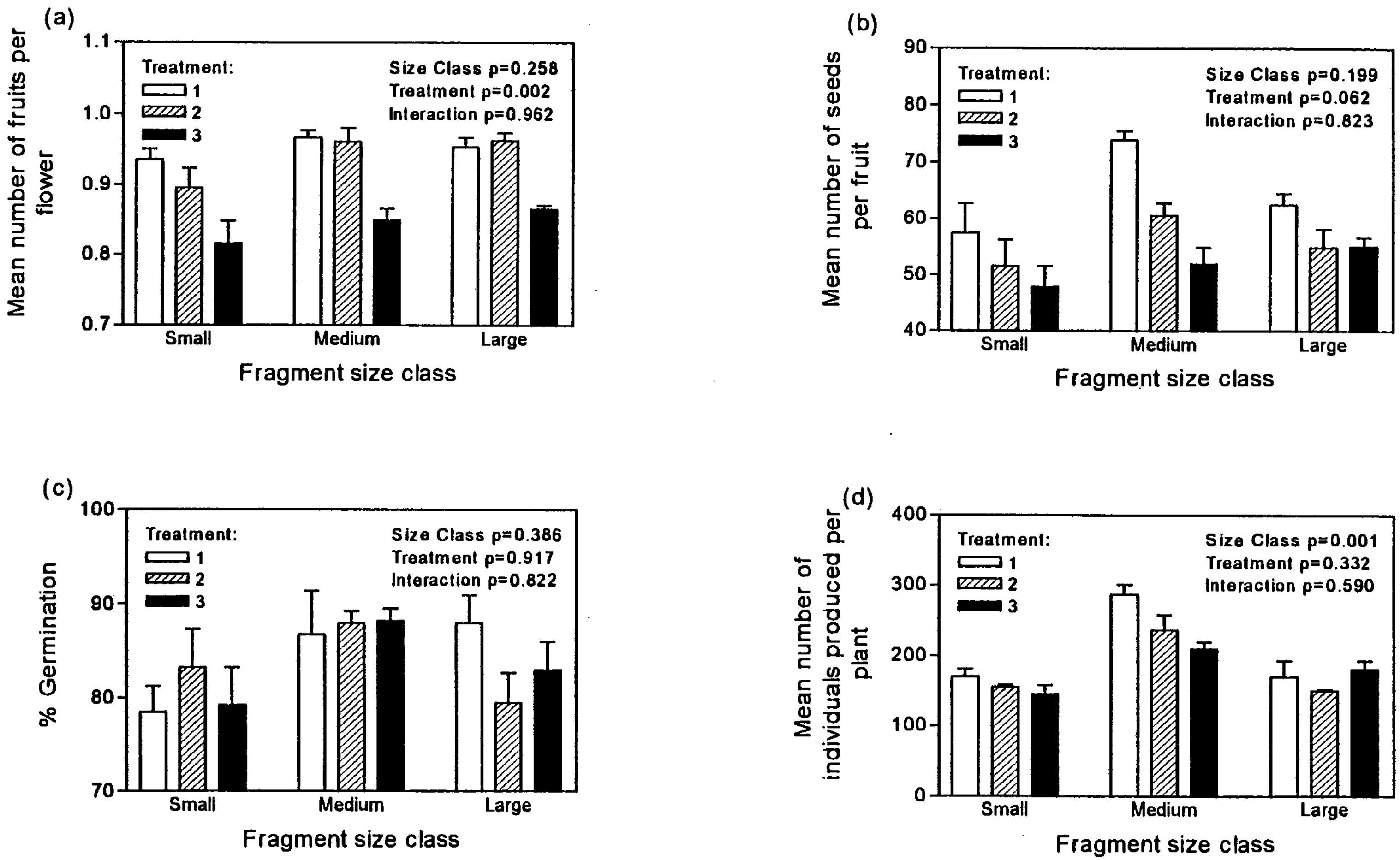

Figure 5.2: Mean (± SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success (arcsin-transformed), and (d) individuals produced per plant, for *Omithogalum* for three fragment size classes and three pollination treatments used in the pollination field experiment. Treatments: (1) cross- hand-pollination and removal of flowers, (2) no pollination and removal of flowers, (3) no manipulation. Significance levels for two-way ANOVAs and back-transformed means are reported.

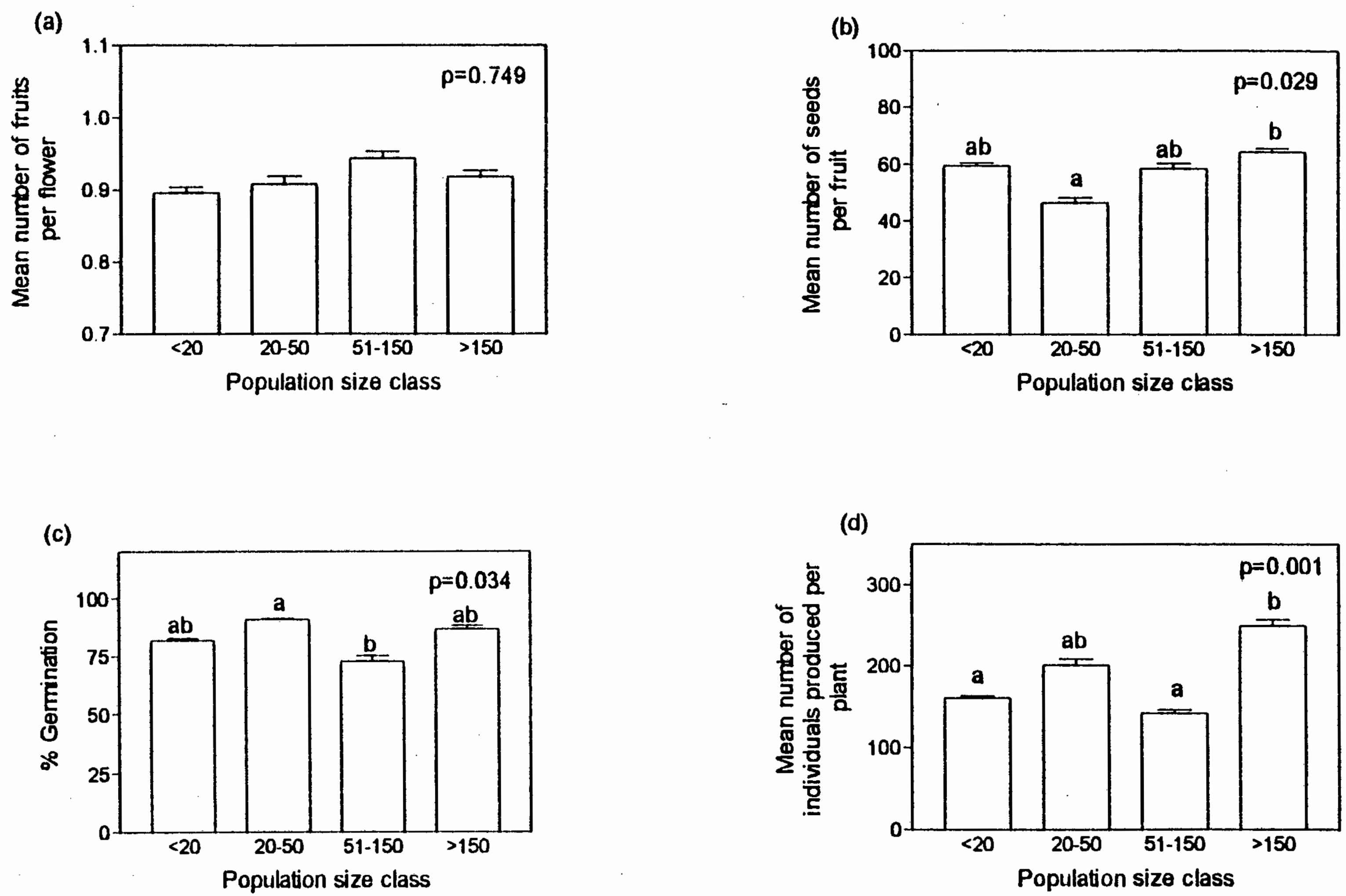

Figure 5.3: Mean (± SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success (arcsin-transformed), and (d) individuals produced per plant, for *Ornithogalum* for four population size classes (pollination field experiment). Significance levels for one-way ANOVAs and back-transformed means are reported. Means that share the same superscript letter do not differ significantly (Tukey Multiple Range test).

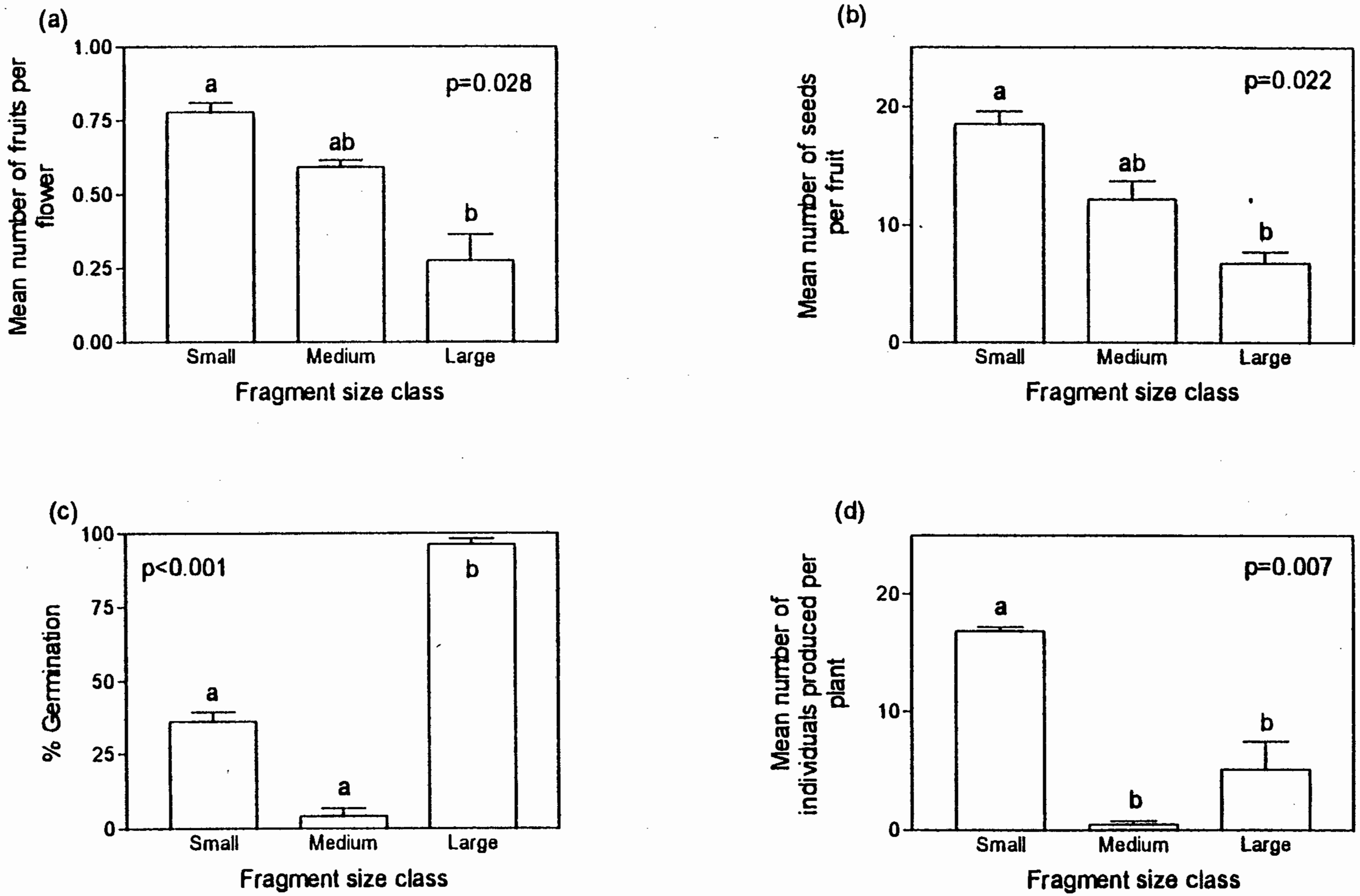

Figure 5.4: Mean (± SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success (arcsin-transfomed), and (d) individuals produced per plant, for *Babiana* , for three fragment size classes (pollination field experiment). Significance levels for one-way ANOVAs and back-transformed means are reported. Means that share the same superscript letter do not differ significantly (Tukey Multiple Range test).

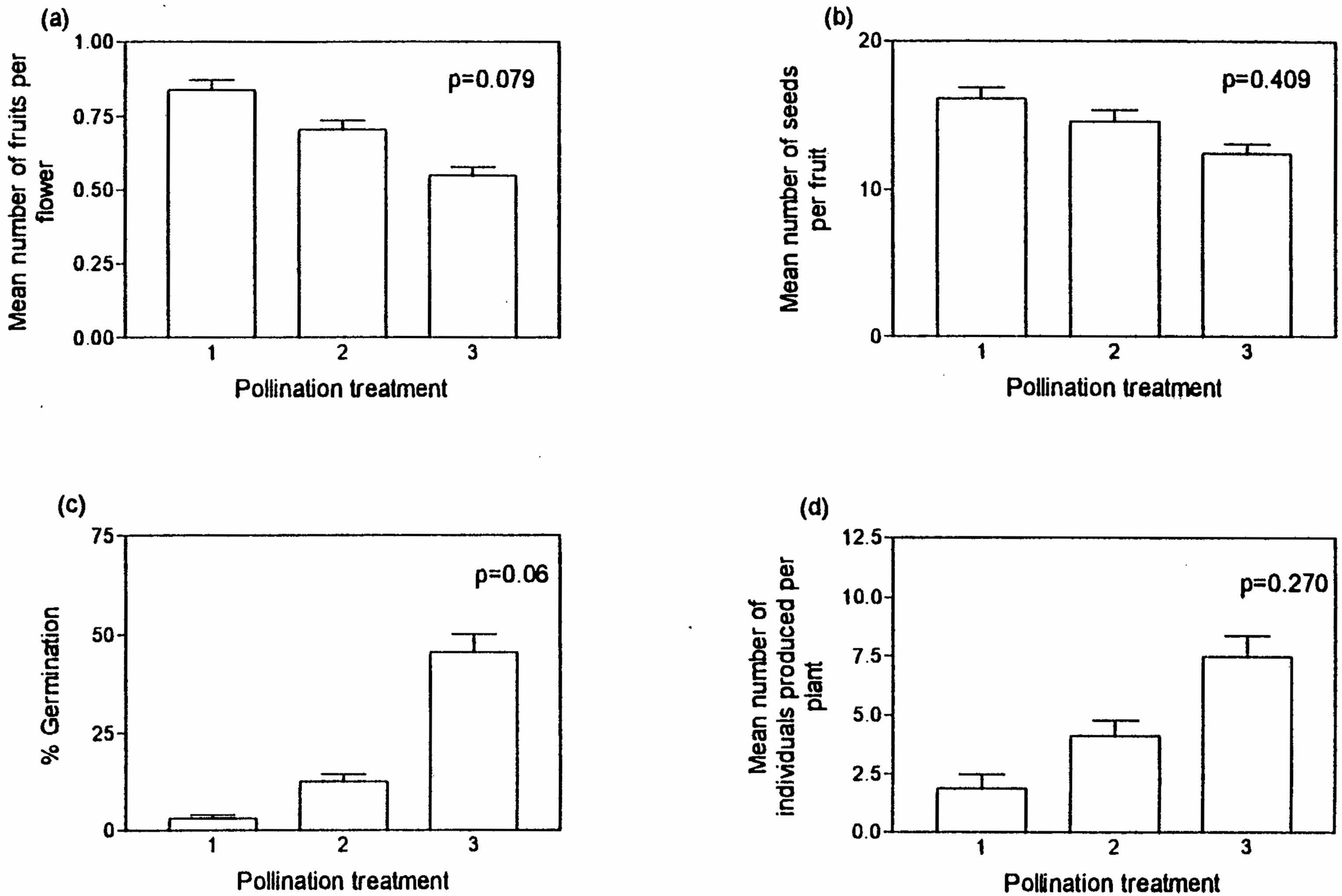

Figure 5.5: Mean (± SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success (arcsin-transformed), and (d) individuals produced per plant, for *Babiana* , under three pollination treatments performed in the pollination field experiment. Treatments: (1) cross- hand-pollination and removal of flowers, (2) no pollination and removal of flowers, (3) no manipulation. Significance levels for one-way ANOVAs and back-transformed means are reported. Means that share the same superscript letter do not differ significantly (Tukey Multiple Range test).

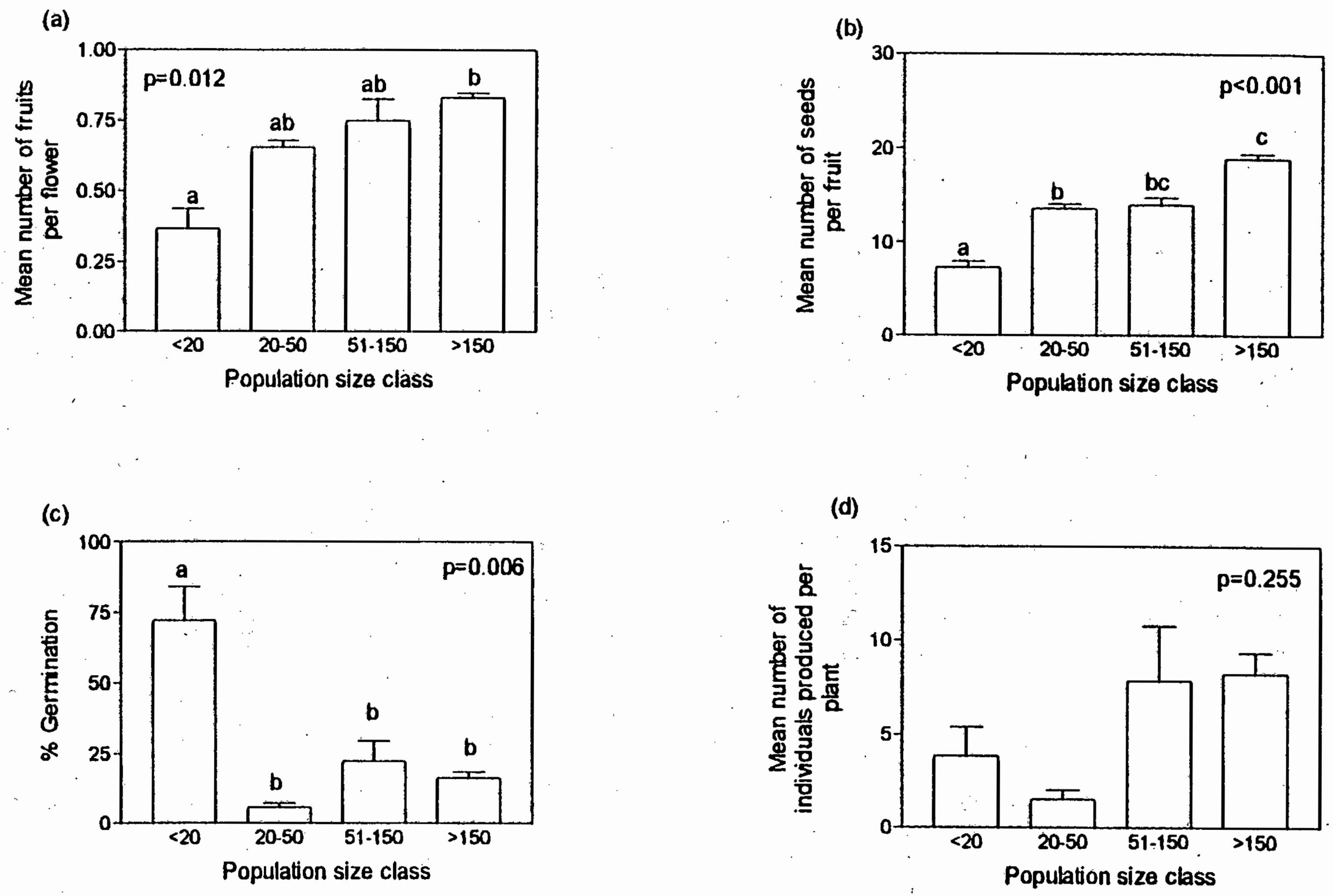

Figure 5.6: Mean (± SE) number of (a) fruits per flower, (b) seeds per fruit, (c) germination success (arcsin-transformed), and (d) individuals produced per plant, for *Babiana* for four population size classes (pollination field experiment). Significance levels for one-way ANOVAs and back-transformed means are reported. Means that share the same superscript letter do not differ significantly (Tukey Multiple Range test).

5.5 Discussion

5.5.1 *Ornithogalum*

Neither fruit set, seed set nor germination success declined with increasing fragmentation. This pattern contrasts with the results by Spears (1987), Menges (1991), and Jennersten (1988), who all found that reproductive success of plants on islands was lower relative to that in large areas. However, Aizen and Feinsinger (1994a) partially attributed some variations in fruit and seed set among species to their association with different pollination-guilds. Since *Ornithogalum* is pollinated by a range of insects common to the study area, a complete breakdown of pollinator-plant relationships either due to pesticides or isolation is unlikely. Moreover, a large proportion of flowers produced fruits on all fragment sizes, suggesting no disruptive shift in microclimatic conditions on small fragments. Overall high seed output across all fragments suggests no limitations in either pollen quantity or quality

The similar results of the two pollination treatments where flowers and buds were removed, show that maximising pollination did not increase average fruit production. Unmanipulated plants however showed a significant decline in fruit set relative to both manipulated treatments. This implies that unmanipulated plants across all fragment size classes did not maximise fruit production. Stephenson (1981) has shown that the percentage of pollinated flowers that produce fruits decreases as the number of pollinated flowers increases. The artificial thinning of hand-pollinated and non-pollinated plants, therefore, increases the probability that the remaining flowers will produce fruit. This pattern is therefore likely to be the result of maternal resource allocation rather than pollen limitation (Johnson 1992, Obeso 1993). The results therefore suggest that *Ornithogalum* is not pollinator-limited and is hence resilient to the impacts of fragmentation on pollinator availability. Although no stage of reproduction measured differed with fragmentation, overall reproductive success revealed that fragmentation does have a statistically significant effect on the reproductive success in *Omithogalum*, with medium-sized fragments producing fewer individuals than either large or small fragments. However, the biological meaning of this pattem is not clear.

The high germination success across treatments suggests good pollen quality. This may, however, be misleading, since the breeding system experiment showed that selfing, autogamous plants still had a germination success of 78%, only 10% lower than the germination success recorded from seed from the pollination field experiment, Therefore, any negative effect of fragmentation on reproductive output could have been successfully compensated by autogamy and selfing. Although population size did not influence fruit production, seed set, germination success and overall reproductive success were affected. The nature of the variation with population size however suggests that these results have little biological meaning.

5.5.2 *Babiana*

Fruit production was dramatically affected by fragmentation, but contrary to predictions of fragmentation theory: small fragments produced significantly more fruits per flower than large ones. Seed set showed a similar pattem, with the mean number of seeds produced on large fragments only one third of those produced on small fragments. Moreover, fragment size was negatively correlated with flowering population size. Small fragments produced a mass-display of flowers, whereas flowering individuals on large fragments were widely scattered. The difference in fruit/seed production could therefore be the result of a difference in pollen quantity, where pollinator attraction was maximised on small fragments, ensuring high levels of fertilisation. On large fragments, owing to low flower numbers and densities, attraction was low, resulting in lower fertilisation rates and hence a decrease in fruit and seed set (see Handel 1983). The overall high fruit and seed set on small and medium fragments suggests no breakdown in plant-pollinator relationships due to fragmentation (providing *Babiana* is indeed self-incompatible).

The various pollination treatments did not significantly affect fruit or seed set, although both fruit and seed set were marginally lower in unmanipulated plants. These results should be treated with caution, since none of the large fragments, and only two of the medium fragments received treatment (1) and (2). This could, therefore, skew the results towards fruit or seed set in small fragments.

The results from the germination trials are counter-intuitive, with a far larger percentage of seeds from large fragments germinating than from either medium or small fragments. This may reflect differences in pollen quality, with scattered flowers on large fragments receiving out-crossed pollen from far (and therefore potentially unrelated) individuals (Handel 1983). Conversely, populations on small and medium fragments perhaps are showing signs of inbreeding, since the probability of receiving pollen from another population decreases with increasing population size (Handel 1983). Alternatively, it may be a consequence of pesticide pollution (which is greater on small and medium fragments), resulting in the overall lower fitness of seeds.

Despite poor germination success, owing to the high numbers of seeds produced, overall reproductive success was nevertheless highest in small fragments. Johnson (1992) points out that in order to separate nutrient and pollinator limitations, this type of experiment should ideally be carried out over at least two years. High reproductive output in some plant groups (Zimmerman and Mitchell Aide 1989) have resulted in flowering depression the following year, due to repleted resources. This may have been the situation with *Babiana* populations on large fragments, where only a small proportion of the population flowered; in this case, overall reproductive output on large fragments over a number of years, could be significantly higher on large fragments. Overall reproductive output of *Ornithogalum* and variable results from fruit set, seed set and germination success in *Babiana* show that plant reproductive success can be influenced by a variety of factors at any stage in the reproductive processes, and should therefore not be measured in terms of any one of these indices, but should rather be measured through overall reproductive success.

A reduction in habitat area, a breakdown in plant-pollinator interactions and small population sizes all potentially threaten plant reproductive success. In a parallel study, Donaldson *et al.* (in prep.) showed that fragmentation has significantly affected the pollinator fauna of South Coast Renosterveld, particularly monkey beetles and some bee species. This study generally did not reveal clear impacts of fragmentation on plant reproductive output, although *Babiana* appeared to be more sensitive, showing a strong dependence on mass displays. However, any highly significant effects may have been buffered by the compensation for any impacts through the plant's breeding system. Although reliant on seed production, *Ornithogalum* does not depend on pollinators for reproduction and has a host of pollinators, two factors which protect against local extinction. *Babiana*, on the other hand, appears to lack the ability to self, and relies on few pollinators. It is therefore far more reliant on successful pollination for its reproductive success and any breakdown could have serious consequences on the long-term demography of the species. Both species are geophytes ("persisters"), which, therefore, delays extinction (Bond 1994, Midgley 1996). Therefore, although our results are not startling, we conclude that *Babiana* and species with similar reproductive strategies are more at risk than species such as *Ornithogalum*.

5.6 Conclusion

Events at other stages of a plant's life cycle can influence demography. This study did not consider the effects of fragmentation on seed dispersal and seedling establishment, which are other vital components of reproduction (Aizen and Feinsinger 1994a, Chambers and MacMahon 1994). Seed bank persistence could also play an important role as it could benefit population persistence by decreasing the probability of extinction during years where reproductive success is low (Kalisz and McPeek 1993). Overgrazing, trampling (Hobbs 1987, Aizen and Feinsinger 1994a), a change in burning regime (Bond *et al.* 1988), the role of exotic pollinator invasion on natural pollinator composition (e.g. Aizen and Feinsinger 1994b) and increased seed predation (Johnson 1992, van Wyk 1995) may be equally devastating to plant reproductive success. Ultimately though, in terms of reproductive success, this study has shown that conservation efforts should be prioritised towards plants with specific pollinators, as well as self-incompatible, short-lived, seed-dependent species (Bond 1994).

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Chapter 6

General Conclusion

6.1 Preamble

This chapter highlights the major findings and limitations of this study and makes suggestions for future research. I used a hierarchical approach to investigate the effects of fragmentation on the vegetation patterns and some processes in South Coast Renosterveld. I concentrated on the landscape, community and population levels of organisation. Saunders *et al.* (1991) criticised current fragmentation research, arguing that a balance between single-species studies and community/ecosystem studies as well as a balance between theoretical studies and field experimentation is needed in order to provide practical answers for managing fragmented systems. I believe that the approach of my thesis was a successful attempt at achieving this balance. It provided some understanding of a system which has received little attention in the past. It also yielded some useful answers for the formulation of conservation guidelines, aimed at effectively maintaining and managing fragments within an agricultural setting and for prioritising future research strategies.

The specific aims of the study were to:

- provide a descriptive inventory of South Coast Renosterveld fragments throughout its former extent and to link fragment patterns to agricultural potential

- investigate in how far vegetation composition, diversity and guild structure has been negatively impacted by fragmentation

- examine to what extent plant reproductive success is altered by fragmentation

The major findings of my study are discussed in the context of each objective.

6.2 Major findings and practical implications

6.2.1 Fragmentation patterns at the landscape scale

Two main findings emerged from this study. Firstly, over 80% of South Coast Renosterveld has been transformed. This confirms the urgent need for the formal conservation of this vegetation type. Secondly, fragmentation levels decrease significantly along a west-east gradient, with large areas of natural vegetation still occurring towards the eastern parts of its extent. This pattern, therefore, suggests that there is potential for large reserves in the east, as well as for north-south corridor reserves, linking the Langeberg Mountains and the Indian Ocean. The western part of South Coast Renosterveld is very fragmented, but greater species richness in the west suggests that small reserves will be needed here. Renosterveld extent is correlated with landscape topography, and to a lesser extent with rainfall seasonality. The remaining areas of South Coast Renosterveld are restricted to steep slopes and, therefore, face little danger of future cultivation.

6.2.2 Vegetation composition and guild structure

On the whole, the comparison of small (<2 ha), medium (2.5-12 ha) and large (>25 ha) fragments only yielded few differences in terms of vegetation composition, species diversity and guild structure. TWINSPAN classification of fragments, however, showed that large fragments were most similar to each other. Small and medium fragments were more variable. This could reflect processes related to fragmentation, such as extinctions, invasions and edge effects, operating on small and medium fragments. In addition, large fragments, set aside as natural grazing camps tended to occur on deeper soils, while small and medium fragments were found on rocky soils with low agricultural potential. In terms of species diversity and guild structure, small and medium fragments appear (at least structurally) relatively intact, with the exception of higher numbers and cover of alien plants on medium fragments. These results underline the conservation value of small and medium fragments which sustain high levels of biodiversity and are therefore vital dispersal links between large fragments. Future research needs to explore the potential value of small fragments to farmers (e.g. grazing value and erosion control) and should create an awareness of farmers on how to manage these.

6.2.3 Plant reproductive success

The effects of fragmentation plant reproductive success was investigated using two geophyte species. This experiment highlighted the importance of reproductive strategy in buffering the effects of fragmentation (fragment size, population size and plant-pollinator interactions) on reproductive success. Reproductive success of *Ornithogalum thyrsoides*, a geophyte with a host of common pollinators and which readily selfs, was not affected by fragmentation. The reproductive success of *Babiana ambigua*, a geophyte served by only a few pollinator species and not capable of selfing, appears to have been influenced by fragmentation, albeit in an unexpected and contradictory way. The results, therefore, indicate that species with a specialised reproductive strategy should be given top conservation priority. This may be vital information for identifying target species when selecting reserves.

6.2.4 South Coast Renosterveld and fragmentation theory

"An ecosystem is not an ecosystem, is not an ecosystem, and fragmentation is not fragmentation is not fragmentation" (Haila *et al.* 1993, pg 45). This statement questions the relevance of applying fragmentation theory universally to any system. Although fragmentation theory can serve as a guideline to formulate research hypotheses and can create an awareness of research priorities, the history and dynamics of a system and the life history strategies of species within that system must be taken into account when interpreting results and formulating conservation strategies in already fragmented systems. South Coast Renosterveld appears to be a low risk vegetation type, compared to a system like, for example, tropical forests, with many species able to persist for a long time. As a result, many of my results do not agree with fragmentation theory, and some stand in direct contrast. I suggest asking a number of fundamental questions about the system to roughly identify high- and low-risk vegetation types (and therefore to assess the relevance of fragmentation theory to that particular system) and to help in formulating research hypotheses (see Figure 6.1). Specifically, the following questions should be addressed: Is fragmentation at a spatial scale that influences species? Has enough time elapsed since fragmentation for species composition to change? Are species able to persist or do they need to recruit regularly to sustain viable populations? Do recruiters depend on pollinators or dispersers? Does the nature and management of the transformed matrix differ vastly from that of natural vegetation?

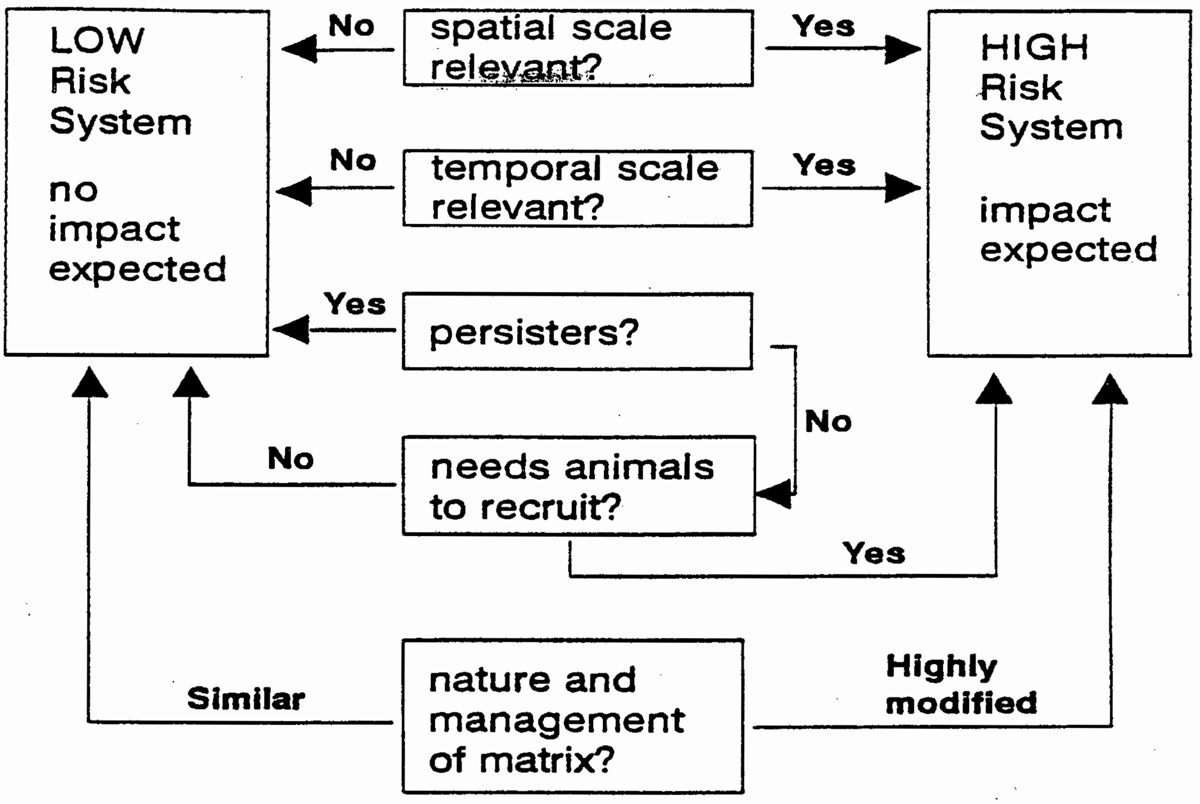

Figure 6.1: Checklist of fundamental questions to broadly assess fragmentation risk on different vegetation types

6.3 Limitations

The most important limitation of this study, as is the case with many projects of this nature, is the time constraint. Clearly, fragmentation is a process that can modify ecosystem patterns and processes over decades. My study only took place over two years and therefore only provided a glimpse at vegetation patterns and some processes. Secondly, the large-scale fragmentation of South Coast Renosterveld is comparatively recent. Although small fragments appear to be structurally diverse, many species are persisters. This may mask any lack of recruitment on small fragments.

Ideally, it would have been useful to compare pre- and post-fragmentation patterns and processes and to continue monitoring these fragments over several years.

Finally, the experimental design only allowed an investigation of fragmentation at the local scale. The loss of habitat diversity through fragmentation is an important issue in terms of conservation planning. It is impossible to reconstruct the original structure of South Coast Renosterveld, and it is likely that whole habitats have been transformed by agriculture. It is, therefore, possible that the remaining fragments only support a fraction of its original plant diversity. Future research should be directed towards assessing habitat diversity in South Coast Renosterveld.

Many questions regarding the effects of fragmentation on patterns and processes of South Coast Renosterveld remain unanswered. These include the direct effects of crop-spraying on natural vegetation and the effects of fragment size and isolation on population genetics. Lastly, the potential and viability or restoring natural vegetation and to create a corridor network along road verges, contour lines or fences to connected fragments needs to be investigated.

6.4 References

Haila, Y., Saunders, D.A. and Hobbs, R.J. 1991. What do we presently understand about ecosystem fragmentation? *In:* Saunders, D.A., Hobbs, R J. and Ehrlich P.R. eds., *Nature conservation 3: Reconstruction of fragmented ecosystems.* Surrey Beatty and Sons; Sydney. pp. 45-55.

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Appendix 1

Species list of Fairfield Farm. Species marked with an asterix were not found in the study plots. Species attributes are given for species recorded in a study plot (see Chapter 4 for details on category definitions).

	Origin	Life form	Life cycle	Area of occurrence	Local abundance	Pollination syndrome	Potential dispersal distance
Alliaceae							
Tulbaghia capensis L.	native	geophyte	perennial	CFR	common	biotic	long
Amaryllidaceae							
*_Boophane guttata_ (L.) Herb.							
*_Brunsvigia orientalis_ (L.) Ait.							
Gethyllis cf. _afra_ L.	native	geophyte	perennial	CFR	rare	biotic	long
*_Haemanthus sanguineus_ Jacq.							
*_Nerine humilis_ (Jacq.) Herb.							
Strumaria tenella (L. f.) Snijman	native	geophyte	perennial	CFR	rare	biotic	long
Araceae							
Zantedeschia aethiopica (L.) Spreng.	native	geophyte	perennial	widespread	common	biotic	long
Asparagaceae							
Protasparagus capensis (L.) Oberm.	native	shrub	perennial	widespread	very common	biotic	long
Protasparagus rubicundus (Berg.) Oberm.	native	shrub	perennial	CFR	very common	biotic	long
Asphodelaceae							
Anthericum (L.) _sp._	native	geophyte	perennial	?	common	biotic	short
Bulbinella barkerae P.L. Perry	native	geophyte	perennial	CFR	common	biotic	short
Bulbinella cf. _chartacea_ P.L. Perry	native	geophyte	perennial	CFR	common	biotic	short
*_Bulbinella trinervis_ (Bak.) P.L. Perry							
Bulbinella triquetra (L. f.) Kunth	native	geophyte	perennial	widespread	common	biotic	short

Trachyandra hirsuta (Thunb.) Kunth	native	geophyte	perennial	CFR	very common	biotic	short
Trachyandra muricata (L. f.) Kunth	native	geophyte	perennial	widespread	common	biotic	short

Colchicaceae

Onixotis punctata (L.) Mabberly	native	geophyte	perennial	CFR	common	biotic	short
Wurmbea variabilis B. Nordenstam	native	geophyte	perennial	CFR	rare	biotic	short

Cyperaceae

Ficinia filiformis (Lam.) Schrader	native	graminoid	perennial	widespread	very common	wind	long
Ficinia nigrescens (Schrader) Raynal	native	graminoid	perennial	widespread	rare	wind	long
Schoenoxiphium ecklonii Nees	native	graminoid	perennial	CFR	rare	wind	long
Tetraria burmannii (Schrader) C. B. Clarke	native	graminoid	perennial	CFR	rare	wind	long

Eriospermaceae

•*Eriospermum dielsianum* Schltr. ex V. Poelln.							
Eriospermum Jacq. ex Willd. *sp.*	native	geophyte	perennial	widespread	common	biotic	long

Haemodoraceae

Wachendorfia paniculata L.	native	geophyte	perennial	CFR	common	biotic	short

Hyacinthaceae

Albuca L. *sp.*	native	geophyte	perennial	?	rare	biotic	long
Eucomis regia (L.) L'Her.	native	geophyte	perennial	widespread	very common	biotic	short
•*Lachenalia orchioides* (L.) Aiton							
Lachenalia salteri W. Barker	native	geophyte	perennial	regional	common	biotic	long
Massonia depressa Houtt.	native	geophyte	perennial	widespread	common	biotic	long
Ornithogalum dubium Houtt.	native	geophyte	perennial	widespread	common	biotic	long
Ornithogalum thyrsoides Jacq.	native	geophyte	perennial	widespread	very common	biotic	long
Tenicroa exuviata (Jacq.) Speta	native	geophyte	perennial	widespread	common	biotic	short
Urginea Steinh. *sp.*	native	geophyte	perennial	?	common	biotic	long

Hypoxidaceae

Pauridia minuta (L. f.) Durand & Schinz	native	geophyte	perennial	CFR	common	biotic	short
Spiloxene aquatica (L. f.) Fourc.	native	geophyte	perennial	widespread	rare	biotic	short
Spiloxene capensis (L.) Garside	native	geophyte	perennial	CFR	common	biotic	short

Spiloxene ovata (L. f.) Garside	native	geophyte	perennial	CFR	common	biotic	short
•*Spiloxene schlechteri* (Bolus) Garside							
Spiloxene serrata (Thunb.) Garside	native	geophyte	perennial	CFR	common	biotic	short

Iridaceae

Aristea teretifolia Goldbl. & J.C. Manning	native	geophyte	perennial	regional	common	biotic	short
Babiana ambigua (Roemer & Schultes) G.J. Lewis	native	geophyte	perennial	CFR	common	biotic	short
•*Babiana patersoniae* L. Bol.							
•*Babiana stricta* (Ait.) Ker-Gawl. var. *stricta*							
Babiana stricta (Ait.) Ker-Gawl. var. *sulphurea* (Jacq.) Bak.	native	geophyte	perennial	CFR	common	biotic	short
Bobartia gladiata (L. f.) Ker-Gawl. subsp. *teres* Strid.	native	forb	perennial	regional	common	biotic	long
Galaxia fugacissima (L. f.) Druce	native	geophyte	perennial	widespread	common	biotic	short
Galaxia melanops Goldbl. & J.C. Manning	native	geophyte	perennial	regional	rare	biotic	short
Geissorhiza heterostyla L. Bol.	native	geophyte	perennial	widespread	very common	biotic	short
•*Geissorhiza nana* Klatt							
Geissorhiza ovata (Burm. f.) Asch & Graeb.	native	geophyte	perennial	CFR	common	biotic	short
Gladiolus gracilis Jacq.	native	geophyte	perennial	CFR	common	biotic	long
Gladiolus liliaceus Houtt.	native	geophyte	perennial	CFR	very common	biotic	long
Gladiolus maculatus Sweet subsp. *maculatus*	native	geophyte	perennial	widespread	rare	biotic	long
•*Gladiolus vaginatus* Bolus f.							
Hesperantha falcata (L. f.) Ker-Gawl.	native	geophyte	perennial	widespread	common	biotic	short
Hesperantha radiata (Jacq.) Ker-Gawl.	native	geophyte	perennial	widespread	common	biotic	short
Hexaglottis lewisiae Goldbl.	native	geophyte	perennial	widespread	very common	biotic	short
Hexaglottis lewisiae Goldbl. subsp. *lewisiae*	native	geophyte	perennial	widespread	rare	biotic	short
•*Hexaglottis longifolia* ((Jacq.) Vent.							
Homeria elegans(Jacq.) Sweet	native	geophyte	perennial	CFR	rare	biotic	short
•*Homeria miniata* (Andrews) Sweet							
Ixia micrandra Bak. var. *micrandra*	native	geophyte	perennial	CFR	common	biotic	short
Ixia polystachya L.	native	geophyte	perennial	CFR	very common	biotic	short
Ixia stricta (Eckl. ex Klatt) G.J. Lewis	native	geophyte	perennial	regional	very common	biotic	short
Lapeirousia corymbosa (L.) Ker-Gawl. subsp. *corymbosa*	native	geophyte	perennial	CFR	rare	biotic	
Micranthus junceus (Bak.) N.E. Br.	native	geophyte	perennial	CFR	common	biotic	short
Moraea bituminosa (L. f.) Ker-Gawl.	native	geophyte	perennial	CFR	common	biotic	short

Moraea debilis Goldbl.	native	geophyte	perennial	regional	rare	biotic	short
Moraea fergusoniae L. Bol.	native	geophyte	perennial	CFR	rare	biotic	short
Moraea gawleri Sprengel	native	geophyte	perennial	widespread	common	biotic	short
•*Moraea papilionaceae* (L. f.) Ker-Gawl.							
Moraea Mill. *sp.* (subgenus Monocephalae)	native	geophyte	perennial	CFR	common	biotic	short
Moraea tripetala (L. f.) Ker-Gawl.	native	geophyte	perennial	widespread	very common	biotic	short
Romulea flava (Lam.) De Vos var. *minor* (Beg.) D.	native	geophyte	perennial	widespread	common	biotic	short
Romulea hirsuta (Eckl.) ex Klatt var. *cuprea* (Beg.) De Vos	native	geophyte	perennial	CFR	common	biotic	short
•*Romulea minutiflora* Klatt							
Romulea rosea (L.) Eckl. var. *australis* (Ewart) De Vos	native	geophyte	perennial	CFR	rare	biotic	short
Romulea rosea (L.) Eckl. var. *reflexa* (Eckl.) Beg. De Vos	native	geophyte	perennial	CFR	common	biotic	short
Sparaxis bulbifera (L.) Ker-Gawl.	native	geophyte	perennial	regional	common	biotic	short
•*Sparaxis* cf. *fragrans* (Jacq.) Ker-Gawl.							
•*Sparaxis* cf. *grandiflora* (Delaroche) Ker-Gawl. subsp. *violacea* (Eckl.) Goldbl.							
•*Therelanthus bracteolatus* (Lam.) G.J. Lewis							
Tritoniopsis antholyza (Poir.) Goldbl.	native	geophyte	perennial	CFR	common	biotic	long
Tritoniopsis flexuosa (L. f.) G.J. Lewis	native	geophyte	perennial	regional	common	biotic	long
Watsonia aletroides Ker-Gawl. (red and pink forms)	native	geophyte	perennial	CFR	common	biotic	long
Species 1	native	geophyte	perennial	CFR	common	biotic	short

Juncaceae

Juncus bufonius L.	native	graminoid	annual	widespread	common	wind	long

Orchidaceae

•*Disperis capensis* (L.) Swartz							
Monadenia bracteata (Swartz) Dur. & Schinz	native	geophyte	perennial	widespread	common	biotic	long
Pterygodium alatum (Thunb.) Swartz	native	geophyte	perennial	CFR	common	biotic	long
Pterygodium catholicum (L.) Swartz	native	geophyte	perennial	CFR	very common	biotic	long
Satyrium bicorne (L.) Thunb.	native	geophyte	perennial	widespread	rare	biotic	long
•*Satyrium coriifolium* Swartz							
Satyrium humile Lindl.	native	geophyte	perennial	CFR	common	biotic	long

Poaceae

Aira cupaniana Guss.	alien	graminoid	annual	widespread	very common	wind	long
Anthoxanthum dregeanum (Nees) Stapf	native	graminoid	perennial	CFR	common	wind	long
Avena barbata Brot.	alien	graminoid	annual	widespread	very common	wind	long
Brachypodium distachyon (L.) Beauv.	alien	graminoid	annual	widespread	very common	wind	long
Briza maxima L.	alien	graminoid	annual	widespread	very common	wind	long
Briza minor L.	alien	graminoid	annual	widespread	very common	wind	long
Bromus hordaceus L. subsp. *molliformis* (J. Loyd) Maire & Weiller	alien	graminoid	annual	widespread	common	wind	long
Bromus pectinatus Thunb.	native	graminoid	annual	widespread	very common	wind	long
Bromus rigidus Roth	alien	graminoid	annual	widespread	very common	wind	long
Cymbopogon marginatus (Steud.) Stapf ex Burtt Davy	native	graminoid	perennial	widespread	common	wind	long
•*Cymbopogon plurinodis* (Stapf) Stapf ex Burtt Davy							
•*Ehrharta* cf. *bulbosa* J.E. Sm.							
Ehrharta calycina J.E. Sm.	native	graminoid	perennial	widespread	very common	wind	long
Ehrharta capensis Thunb.	native	graminoid	perennial	CFR	common	wind	long
Ehrharta melicoides Thunb.	native	graminoid	perennial	widespread	common	wind	long
Ehrharta ottonis Kunth ex Nees	native	graminoid	perennial	widespread	common	wind	long
Ehrharta Thunb. *sp.*	native	graminoid	perennial	widespread	rare	wind	long
•*Eragrostis curvula* (Schrad.) Nees							
Festuca scabra Vahl	native	graminoid	perennial	widespread	common	wind	long
Helictotrichon hirtulum (Steud.) Schweick.	native	graminoid	perennial	widespread	common	wind	long
Karroochloa curva (Nees) Conert & Tuerpe	native	graminoid	perennial	widespread	common	wind	long
Koeleria capensis (Steud.) Nees	native	graminoid	perennial	widespread	very common	biotic	short
Lolium multiflorum Lam. / *L.m.* x *perenne* L.	alien	graminoid	annual	widespread	common	wind	long
Lophochloa cristata (L.) Hyl.	alien	graminoid	annual	widespread	common	wind	long
Melica racemosa Thunb.	native	graminoid	perennial	widespread	common	wind	long
•*Merxmuellera disticha* (Nees) Conert							
Merxmuellera stricta (Schrad.) Conert	native	graminoid	perennial	widespread	common	wind	long
Pentaschistis cf. *colorata* (Schrad.) Stapf	native	graminoid	perennial	CFR	very common	wind	long
Pentaschistis curvifolia (Schrad.) Stapf	native	graminoid	perennial	widespread	common	wind	long
Pentaschistis eriostoma (Nees) Stapf	native	graminoid	perennial	CFR	common	wind	long
•*Pentaschistis pallida* (Thunb.) Linder							
Phalaris minor Retz.	alien	graminoid	annual	widespread	common	wind	long

Themeda triandra Forssk.	native	graminoid	perennial	widespread	very common	wind	long
•*Tribolium alternans* (Nees) Renvoize							
Tribolium hispidum (Thunb.) Desv.	native	graminoid	perennial	widespread	common	wind	long
Tribolium uniolae (L. f.) Renvoize	native	graminoid	perennial	widespread	very common	wind	long
Vulpia bromoides (L.) S.F. Gray	alien	graminoid	annual	widespread	common	wind	long
cf. *Holcus lanatus* L.	alien	graminoid	perennial	widespread	common	wind	long

Restionaceae

Restio multiflorus Spreng.	native	graminoid	perennial	CFR	very common	wind	long

Tecophilaeaceae

Cyanella hyacinthoides L.	native	geophyte	perennial	widespread	common	biotic	short
Cyanella lutea L. f.	native	geophyte	perennial	widespread	very common	biotic	short

Aizoaceae

•*Tetragonia* L. *sp.*

Anacardiaceae

Rhus angustifolia L.	native	shrub	perennial	CFR	common	biotic	short
•*Rhus laevigata* L.							
Rhus rehmannia Engl. var. *glabrata* (Sond.) Moffett	native	shrub	perennial	widespread	common	biotic	short
Rhus rosmarinifolia Vahl	native	shrub	perennial	CFR	common	biotic	short
•*Rhus tomentosa* L.							
•*Rhus* cf. *undulata* Jacq.							

Apiaceae

Arctopus echinatus L.	native	forb	perennial	CFR	very common	biotic	short
Itasina filifolia (Thunb.) Raf.	native	forb	perennial	CFR	common	biotic	short
Lichtensteinia lacera Cham. & Schlechtd.	native	forb	perennial	regional	rare	biotic	short

Asclepiadaceae

Microloma tenuifolium (L.) K. Schum.	native	forb	perennial	widespread	very common	biotic	long
Xysmalobium gomphocarpoides (E. Mey.) D. Dietr.	native	forb	annual	widespread	rare	biotic	long

Asteraceae

Arctotis acaulis L.	native	forb	perennial	CFR	very common	biotic	long
Arctotis cf. *macrosperma* (DC.) Beauv.	native	forb	perennial	?	rare	biotic	long
Arctotis pinnatifida Thunb.	native	forb	perennial	CFR	common	biotic	long
**Athanasia quinquedentata* Thunb. subsp. *quinquedentata*							
Athanasia trifurcata (L.) L.	native	shrub	perennial	CFR	common	biotic	long
Athrixia capensis Ker Gawler	native	shrub	perennial	CFR	very common	biotic	long
Berkheya armata (Vahl) Druce	native	forb	perennial	CFR	very common	biotic	long
Berkheya rigida (Thunb.) Adamson & T.M. Salter	native	forb	perennial	CFR	very common	biotic	long
Berkheya Ehrh. *sp.*	native	forb	perennial	widespread	rare	biotic	long
**Castalis nudicaulis* (L.) T. Nord var. *nudicaulis*							
Chrysocoma ciliata L.	native	shrub	perennial	widespread	common	biotic	long
**Conyza scabrida* DC.							
Corymbium cymosum E. Meyer ex DC.	native	forb	perennial	CFR	very common	biotic	long
Corymbium villosum L. f.	native	forb	perennial	CFR	common	biotic	long
Cotula ceniifolia DC.	native	forb	annual	CFR	very common	biotic	long
**Cotula turbinata* L.							
Elytropappus rhinocerotis (L. f.) Less.	native	shrub	perennial	widespread	very common	wind	long
**Eriocephalus paniculatus* Cass.							
Eriocephalus racemosus L.	native	shrub	perennial	CFR	common	biotic	long
Felicia aculeata Grau	native	shrub	perennial	CFR	common	biotic	long
**Felicia filifolia* (Vent.) Burtt Davy subsp. *filifolia*							
Felicia hyssopifolia (Berg.) Nees subsp. *polyphylla* (Harv.) Grau	native	shrub	perennial	widespread	common	biotic	long
Felicia tenella (L.) Nees subsp. *cotuloides*	native	forb	annual	CFR	common	biotic	long
Felicia Cass. *sp.*	native	forb	perennial	CFR	common	biotic	long
Gazania krebsiana Less. subsp. *krebsiana*	native	forb	perennial	widespread	common	biotic	long
Helichrysum cymosum (L.) D. Don subsp. *cymosum*	native	shrub	perennial	widespread	very common	biotic	long
Helichrysum patulum (L.) D. Don	native	shrub	perennial	regional	very common	biotic	long
**Helichrysum rosum* (Berg.) Less. var. *rosum*							
Helichrysum teretifolium (L.) D. Don	native	shrub	perennial	widespread	common	biotic	long
Helichrysum Mill. *sp.* 1	native	shrub	perennial	?	rare	biotic	long
Helichrysum Mill. *sp.* 2	native	forb	perennial	?	rare	biotic	long

Hypochoeris glabra L.	alien	forb	annual	widespread	common	biotic	long
Metalasia acuta Karis	native	shrub	perennial	CFR	common	biotic	long
Metalasia densa (Lam.) Karis	native	shrub	perennial	widespread	common	biotic	long
Oedera capensis (L.) Druce	native	shrub	perennial	CFR	common	biotic	long
Oedera genistifolia (L.) Anderb. & Bremer	native	shrub	perennial	widespread	common	biotic	long
Osteospermum imbricatum L.	native	shrub	perennial	widespread	common	biotic	long
Osteospermum spinosum L.	native	shrub	perennial	CFR	common	biotic	long
Osteospermum tomentosum (L. f.) Norlindh	native	shrub	perennial	CFR	common	biotic	long
Printzia polifolia (L.) Hutch.	native	shrub	perennial	CFR	very common	biotic	long
**Pseudognaphalium undulata* (L.) Hilliard & Burtt							
Senecio burchellii DC.	native	forb	perennial	CFR	very common	biotic	long
**Senecio cymballariifolius* (L.) Less.							
Senecio erubescens Aiton	native	forb	perennial	widespread	common	biotic	long
Senecio pubigerus L.	native	shrub	perennial	CFR	very common	biotic	long
Senecio rosmarinifolius L. f.	native	shrub	perennial	widespread	very common	biotic	long
**Senecio* cf. *spiriifolius* Thunb.							
Stoebe bruniades (Reichb.) Levyns	native	shrub	perennial	regional	common	biotic	long
Stoebe cf. *ensorii* Compton	native	shrub	perennial	regional	common	biotic	long
Stoebe plumosa (L.) Thunb.	native	shrub	perennial	widespread	common	wind	long
Ursinia anthemoides (L.) Poir. subsp. *anthemoides*	native	shrub	perennial	widespread	common	biotic	long
Ursinia dentata (L.) Poir.	native	shrub	perennial	CFR	common	biotic	long
Ursinia discolor (Less.) N.E. Br.	native	shrub	perennial	CFR	common	biotic	long
Ursinia heterodonta (DC.) N.E. Br.	native	shrub	perennial	CFR	rare	biotic	long
Vellerophyton dealbatum (Thunb.) Hilliard & B.L. Burtt	native	forb	annual	CFR	common	biotic	long

Boraginaceae

**Lobostemon echioides* Lehm.

Brassicaceae

Brassica rapa L.	alien	forb	annual	widespread	common	biotic	long
Lepidium africanum (Burm. f.) DC.	alien	forb	annual	widespread	common	wind	long

Campanulaceae

**Grammatotheca bergiana* (Cham.) Presl							
**Lightfootia diffusa* Buek							
Roella cuspidata Adamson var. *cuspidata*	native	shrub	perennial	regional	rare	biotic	long
Caryophyllaceae							
Cerastium capense Sonder	alien	forb	annual	widespread	common	biotic	long
Polycarpon tetraphyllum L. f.	alien	forb	annual	widespread	common	biotic	long
**Petrorhagia prolifera* (L.) Ball & Heywood							
Silene burchellii Otth ex DC.	native	forb	perennial	widespread	common	biotic	long
Silene gallica L.	alien	forb	annual	widespread	common	biotic	long
Spergularia rubra (L.) J. & C. Presl	alien	forb	annual	widespread	common	biotic	long
Celastraceae							
Maytenus heterophylla (Eckl. & Zeyh.) N. Robson	native	shrub	perennial	widespread	common	biotic	long
Crassulaceae							
Crassula capensis (L.) Baill. var. *capensis*	native	geophyte	perennial	CFR	very common	biotic	short
**Crassula* cf. *glomerata* Berg.							
Crassula ciliata L.	native	forb	perennial	widespread	common	biotic	short
Crassula saxifraga Harvey	native	forb	perennial	widespread	common	biotic	short
Crassula subulata L. var. *subulata*	native	shrub	perennial	widespread	rare	biotic	short
Dipsacaceae							
Scabiosa columbaria L.	native	forb	perennial	widespread	very common	biotic	long
Droseraceae							
Drosera pauciflora Banks ex DC.	native	forb	perennial	CFR	very common	biotic	short
Ericaceae							
**Erica bruniifolia* Salisb.							
**Erica lasciva* Salisb.							
Erica setaceae Andr.	native	shrub	perennial	CFR	common	biotic	short
Euphorbiaceae							

Clutia polifolia Jacq.	native	shrub	perennial	CFR	common	biotic	short
•*Clutia pubescens* Thunb.							
Clutia tomentosa L.	native	shrub	perennial	CFR	common	biotic	short
Euphorbia ecklonii (Klotzsch & Garke) Haessler	native	forb	perennial	CFR	common	wind	long
Euphorbia erythrina Link	native	forb	perennial	widespread	very common	wind	long

Fabaceae

•*Amphithalea ericifolia* Eckl. & Zeyh. subsp. *erecta* Granby							
Argyrolobium pumilum Eckl. & Zeyh.	native	shrub	perennial	CFR	rare	biotic	short
Aspalathus biflora E. Mey. subsp. *biflora*	native	shrub	perennial	widespread	common	biotic	short
•*Aspalathus* cf. *ciliaris* L.							
Aspalathus hispida Thunb.	native	shrub	perennial	widespread	common	biotic	short
Aspalathus hispida Thunb. subsp. *hispida*	native	shrub	perennial	CFR	common	biotic	short
Aspalathus lanceifolia Dahlg.	native	shrub	perennial	CFR	common	biotic	short
Aspalathus millefolia Dahlg.	native	shrub	perennial	CFR	common	biotic	short
Aspalathus nigra L.	native	shrub	perennial	CFR	common	biotic	short
•*Aspalathus rosea* Garab. ex Dahlg.							
Aspalathus spinosa L. subsp. *spinosa*	native	shrub	perennial	widespread	very common	biotic	short
Aspalathus submissa Dahlg.	native	shrub	perennial	CFR	common	biotic	short
Aspalathus L. *sp.*	native	shrub	perennial	?	rare	biotic	short
Indigofera cf. *digitata* Thunb.	native	shrub	perennial	CFR	common	biotic	short
Indigofera heterophylla Thunb.	native	shrub	perennial	widespread	very common	biotic	short
Indigofera incana Thunb.	native	shrub	perennial	CFR	rare	biotic	short
Lotus subbiflorus Lag.	alien	forb	annual	widespread	common	biotic	short
•*Psoralea alata* (Thunb.) Salter							
•*Sutherlandia* cf. *frutescens* R. Br.							
Trifolium angustifolium L.	alien	forb	annual	widespread	common	biotic	short
Trifolium campestre Schreb.	alien	forb	annual	widespread	common	biotic	short
Vicia bengalensis L.	alien	forb	annual	widespread	common	biotic	short

Fumariaceae

Cysticapnos cracca (Cham. & Schldl.) Liden	native	forb	annual	widespread	common	biotic	long
Fumaria muralis Sond. ex Koch	alien	forb	perennial	widespread	common	biotic	long

Gentianaceae

Sebaea aurea (L. f.) Roemer & Schultes	native	forb	annual	CFR	very common	biotic	long
Sebaea exacoides (L.) Schinz	native	forb	annual	CFR	very common	biotic	long

Geraniaceae

**Erodium moschatum* (L.) L'Her.							
Pelargonium alchemilloides (L.) L'Her.	native	forb	perennial	widespread	very common	biotic	long
**Pelargonium dipetalum* L'Her.							
Pelargonium lobatum (Burm. f.) L'Her.	native	geophyte	perennial	CFR	rare	biotic	long
Pelargonium myrrhifolium (L.) L'Her. var. *myrrhifolium*	native	forb	perennial	widespread	common	biotic	long
Pelargonium pilosellifolium (Eckl. & Zeyh.) Steud.	native	geophyte	perennial	CFR	rare	biotic	long
**Pelargonium pinnatum* L'Her.							
**Pelargonium proliferum* (Burm. f.) Steud.							
**Pelargonium* L'Her. *sp.* (section Polyactum)							

Lamiaceae

**Salvia africana-caerulea* L.							
**Salvia runcinata* L. f.							
Stachys aethiopica L.	native	forb	perennial	widespread	very common	biotic	short

Lobeliaceae

Cyphia digitata (Thunb.) Willd.	native	forb	perennial	CFR	rare	biotic	long
Cyphia linaroides Presl	native	forb	perennial	widespread	rare	biotic	long
Cyphia phyteuma (L.) Willd.	native	forb	perennial	CFR	common	biotic	long
Cyphia volubilis Willd. var. *volubilis*	native	forb	perennial	widespread	very common	biotic	long
Cyphia zeyheriana Presl ex Eckl. & Zeyh.	native	forb	perennial	CFR	common	biotic	long
**Cyphia* Berg. *sp.*							
Lobelia erinus L.	native	forb	annual	widespread	very common	biotic	short

Malvaceae

Anisodontea dissecta (Harv.) Bates	native	forb	perennial	CFR	rare	biotic	short
Hibiscus aethiopicus L.	native	forb	perennial	widespread	common	biotic	short
Hibiscus pusillus Thunb.	native	forb	perennial	widespread	common	biotic	short

Mesembryanthemaceae

**Ruschia* Schwant. *sp.*							
**Trichodiadema fergusionae* L. Bol.							
Species 1	native	forb	perennial	?	common	biotic	short
Species 2	native	forb	perennial	?	common	biotic	short
*Species 3							
*Species 4							

Montiniaceae

**Montinia caryophyllacea* Thunb.

Oxalidaceae

Oxalis glabra Thunb.	native	geophyte	perennial	CFR	common	biotic	short
Oxalis heterophylla DC.	native	geophyte	perennial	widespread	very common	biotic	short
Oxalis obtusa Jacq.	native	geophyte	perennial	widespread	common	biotic	short
**Oxalis pardalis* Sond.							
Oxalis pes-caprae L.	native	geophyte	perennial	widespread	common	biotic	short
Oxalis purpurea L.	native	geophyte	perennial	widespread	very common	biotic	short
Oxalis tomentosa L. f.	native	geophyte	perennial	?	common	biotic	short
Oxalis zeekoevleyensis Knuth	native	geophyte	perennial	CFR	common	biotic	short
Oxalis L. *sp.1*	native	geophyte	perennial	?	very common	biotic	short
Oxalis L. *sp.2*	native	geophyte	perennial	?	rare	biotic	short
Oxalis L. *sp.3*	native	geophyte	perennial	?	common	biotic	short
Oxalis L. *sp.4*	native	geophyte	perennial	?	common	biotic	short
Oxalis L. *sp.5*	native	geophyte	perennial	?	very common	biotic	short
Oxalis L. *sp. 6*	native	geophyte	perennial	?	very common	biotic	short
Oxalis L. *sp.7*	native	geophyte	perennial	?	common	biotic	short
Oxalis L. *sp.8*	native	geophyte	perennial	?	rare	biotic	short
Oxalis L. *sp.9*	native	geophyte	perennial	?	very common	biotic	short
Oxalis L. *sp.10*	native	geophyte	perennial	?	rare	biotic	short

Plantaginaceae

Plantago lanceolata L.	alien	forb	perennial	widespread	very common	wind	long

Polygalaceae

**Muraltia* Juss. *sp.*

Polygala lehmanniana Eckl. & Zeyh.	native	forb	perennial	CFR	common	biotic	short
Polygala L. *sp.*	native	forb	perennial	?	common	biotic	short
Polygonaceae							
Polygonum undulatum (L.) Berg.	native	shrub	perennial	widespread	common	biotic	short
Rumex acetosella L.	alien	forb	perennial	widespread	common	wind	long
Primulaceae							
Anagallis arvensis L.	alien	forb	annual	widespread	very common	biotic	long
Proteaceae							
Leucadendron teretifolium (Andr.) I. Williams	native	shrub	perennial	CFR	common	wind	short
Leucadendron salignum Berg.	native	shrub	perennial	widespread	common	wind	short
Rhamnaceae							
Phylica calcarata Pillans	native	shrub	perennial	regional	rare	wind	short
**Phylica nigrita* Sond.							
Rosaceae							
Cliffortia monophylla Weim.	native	shrub	perennial	regional	common	biotic	short
Rubiaceae							
Anthospermum aethiopicum L.	native	shrub	perennial	widespread	common	biotic	short
Anthospermum galioides Reichb. subsp. *galioides*	native	shrub	perennial	CFR	common	wind	short
Galium capense Thunb. subsp. *capense*	native	forb	perennial	widespread	common	biotic	long
Rutaceae							
Adenandra marginata (L. f.) Roem. & Schultes subsp. *humilis* (Eckl. & Zeyh.) Strid	native	shrub	perennial	regional	common	biotic	short
**Agathosma* Willd. *sp.*							
Diosma hirsuta L.	native	shrub	perennial	CFR	common	biotic	short
Diosma passerinoides Steud.	native	shrub	perennial	CFR	common	biotic	short
Santalaceae							

Thesium frisea L.	native	shrub	perennial	CFR	common	biotic	short
Thesium spinulosum A. DC.	native	shrub	perennial	widespread	rare	biotic	short

Scrophulariaceae

**Harveya purpurea* (L. f.) Harv.							
Hemimeris montana L. f.	native	forb	annual	widespread	very common	biotic	long
**Nemesia lucida* Benth.							
**Nemesia versicolour* E. Mey. ex Benth.							
Phyllopodium cordatum (Thunb.) Hilliard	native	forb	annual	CFR	common	biotic	long
**Sutera hispida* (Thunb.) Druce							
Zaluzianskya divaricata Walp.	native	forb	annual	CFR	rare	biotic	short
*Species 1							

Selaginaceae

(Genus *Selago* under revision)							
Selago corymbosa L.	native	shrub	perennial	widespread	common	biotic	short
Selago dregei Rolfe	native	shrub	perennial	CFR	rare	biotic	short
Selago fruticulosa L.	native	shrub	perennial	CFR	rare	biotic	short
**Selago* cf. *polystachya* L.							
Selago ramosissima Rolfe	native	shrub	perennial	CFR	rare	biotic	short
Selago scabrida Thunb.	native	shrub	perennial	CFR	common	biotic	short

Solanaceae

(Genus *Lycium* under revision)

**Lycium* cf. *afrum* L.

**Lycium* cf. *ferocissimum* Miers

Sterculiaceae

**Hermannia alnifolia* L.							
**Hermannia confusa* Salter							
Hermannia decumbens Willd. ex Spreng.	native	shrub	perennial	CFR	common	biotic	long
Hermannia diversistipula Presl ex Harv. var. *diversistipula*	native	shrub	perennial	CFR	common	biotic	long
Hermannia flammula Harv.	native	shrub	perennial	widespread	common	biotic	long
Hermannia hyssopifolia L.	native	shrub	perennial	CFR	common	biotic	long

Hermannia ternifolia Presl ex Harv.	native	shrub	perennial	regional	common	biotic	long
Thymelaeaceae							
Gnidia fourcadei Moss	native	shrub	perennial	CFR	common	biotic	short
Gnidia cf. *laxa* (L. f.) Lam.	native	shrub	perennial	regional	common	biotic	short
•*Gnidia sericea* L.							
Gnidia setosa Wikstr.	native	shrub	perennial	CFR	common	biotic	short
•*Struthiola ciliata* (L.) Lam.							
Struthiola dodecandra (L.) Druce	native	shrub	perennial	CFR	common	biotic	short
Struthiola L. *sp.*	native	shrub	perennial	?	common	biotic	short
Species 1	native	shrub	perennial	?	common	biotic	short