

Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications

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Abstract

Nearly 85% of South Coast renosterveld, a fire-prone shrubland, has been replaced by agriculture; the remaining areas are small fragments scattered throughout agricultural lands. Because nearly all of the remaining vegetation is required to fulfil a modest reservation target, conservation of these fragments will be central to any implementation plan. To assess the condition and, therefore, the conservation potential of these fragments, we investigated the community patterns, species diversity and representation of biological attributes in 23 renosterveld fragments. Communities in large fragments were more similar to each other than those in small fragments. There were no significant linear relationships between species diversity and fragment area. We found weak fragmentation effects in attribute representation. Numbers of alien graminoid species and total alien species, and frequency of individuals of geophyte species increased with decreasing fragment size. Frequency of individuals and percentage cover of species with seeds that are dispersed for short distances, increased with decreasing fragment size, while percentage cover of perennial graminoids decreased. Small fragments are highly disturbed by grazing, trampling, crop spraying and frequent fires, but retain a similar community structure to large fragments that presumably represent the pre-agricultural matrix vegetation. Therefore, all remnants of renosterveld, irrespective of fragment size, should be considered conservation-worthy. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Cape Floristic Region, which is extremely rich in plant species, is dominated by fire-prone shrublands: fynbos on infertile substrata and renosterveld on moderately fertile substrata (Cowling and Holmes, 1992). While mountain habitats are mostly pristine and well-conserved, lowland regions have been severely impacted by alien plants, agriculture and urbanisation, resulting in the fragmentation of natural habitat over large areas (Rebelo, 1992). On the shale-derived soils of both the west and south-west coastal lowlands, renosterveld has been reduced by agriculture (largely cereal- and pasture-crops) to <10% of its original extent (McDowell, 1988; Rebelo, 1992; Kemper 1997). Fynbos is being increasingly fragmented by urbanisation [especially in the greater Cape Town metropolitan area where 92 species are currently threatened with extinction (Rebelo, 1992)] and alien plant invasions (Richardson et al., 1996). The

current proportion of lowland fynbos and renosterveld that is formally conserved is 5 and 1.6%, respectively (Low and Rebelo, 1996).

Using as their study system “islands” of fynbos in a “sea” of non-flammable, temperate rainforest, Bond et al. (1988) showed that fragments of <600 ha had significantly fewer species than similar-sized areas of extensive habitat. The low frequency of short-lived and fire-dependent species in “island” relative to “mainland” floras suggested that the absence of regular fires on fragments was responsible for most species loss. Using a similar approach, Cowling and Bond (1991) studied the community structure of endemic-rich and edaphically-specialized fynbos associated with limestone outcrops in a matrix of fynbos on acid sands. In this case, both the fragments and the surrounding landscape are subject to identical disturbance regimes and support structurally and functionally similar fynbos vegetation. They demonstrated a weak fragmentation effect: only fragments smaller than c. 4 ha had significantly fewer species than similar-sized areas on an extensive limestone area. There has been no research in the Cape Floristic Region on fragmentation effects in an

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agricultural landscape, where matrix conditions differ fundamentally from that experienced in the pre-transformation landscape.

This paper aims to fill this gap in our knowledge by investigating the impacts of fragmentation on the community structure of renosterveld. The study system is South Coast renosterveld (Low and Rebelo, 1996) a small-leaved, grassy shrubland associated with fine-textured and moderately-fertile soils on the south coastal forelands of the Cape Floristic Region (Fig. 1). While not as rich in local endemics as fynbos, renosterveld is nonetheless extremely species-rich, especially in geophytes (Cowling, 1990). Renosterveld has been used for natural grazing for centuries by livestock belonging to Khoi-Khoi pastoralists, and later to Dutch settlers. Over the past century, but especially since the 1920s (Kemper, 1997), renosterveld has been extensively transformed by agriculture, and an estimated 160 000 ha of natural vegetation have been transformed to cereals and artificial pastures between 1918 and 1990 (Cowling et al., 1986; Hoffman, 1997). Today, c. 15% of this habitat remains as a series of small (median size, 30 ha) fragments in a matrix of cereal- and pasture-lands that are subjected to grazing, trampling, crop spraying and frequent burning (Kemper, 1997).

Remnant patches of renosterveld have high conservation value (*sensu* Pressey et al., 1994, 1996), since almost all remaining habitat is required to meet a modest reservation goal of 10% of the pre-colonial extent of this vegetation type. Furthermore, owing to the relatively high agricultural value of renosterveld soils, the

remaining fragments are vulnerable to clearance (McDowell, 1988). For these reasons, renosterveld is a major conservation priority in South Africa. However, the question arises of whether all surviving fragments are representative of the original renosterveld and are worth conserving. We approached this question by investigating the relationships between fragmentation and diversity of plants and their biological attributes, viz. origin, life form, life cycle, pollination, dispersive ability and local abundance.

2. Methods

2.1. Study area

Fieldwork was carried out on Fairfield Farm (34°50'S 19°46'E), a c. 9000 ha property east of Cape Town (Fig. 1). The major crop is wheat; 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. Mean annual rainfall is 390 mm, with June–August being the wettest months, and December–January the driest months. Renosterveld occurs on shale-derived duplex soils (sandy loam over clay), low in available phosphorus (mean, 9.7 mg/kg). The renosterveld on Fairfield Farm is typical of South Coast renosterveld (Low and Rebelo, 1996). Members of the Asteraceae are common, particularly *Elytropappus rhinocerotis*; other ericoid-leaved shrubs include *Metalasia* spp. and *Helichrysum* spp.

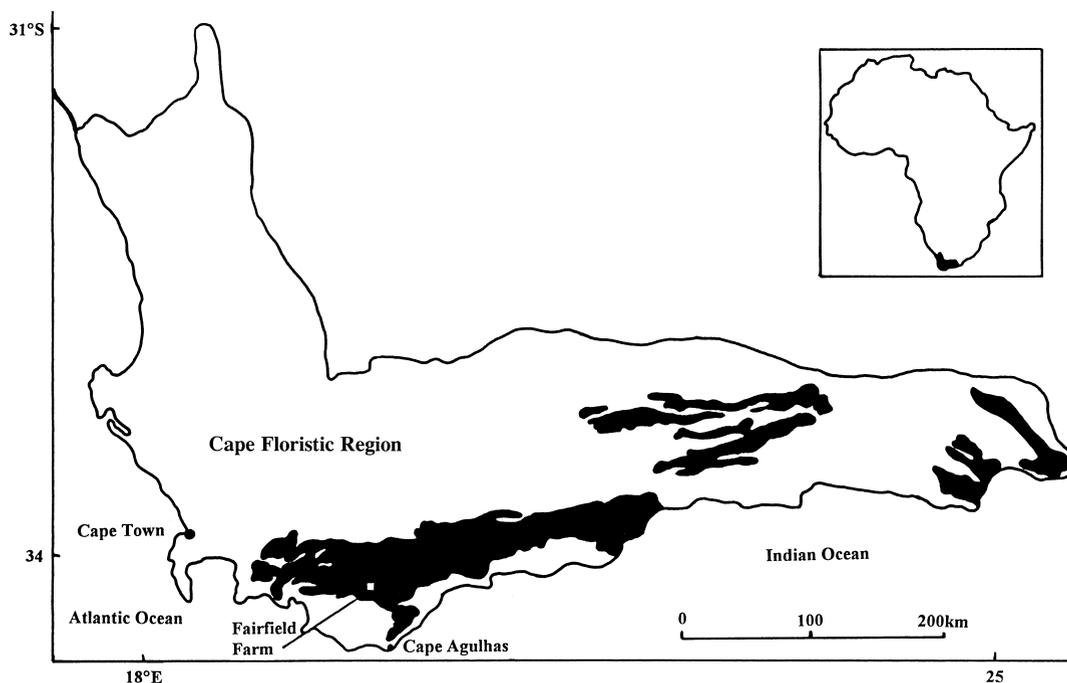


Fig. 1. Original extent (black areas) of South Coast renosterveld within the Cape Floristic region, South Africa (adapted from Rebelo, 1997), and location of study area.

Grasses are abundant and include widespread species (for example *Themeda triandra*), as well as Cape elements such as species of *Pentstemon* and *Ehrharta*. Geophytes form an important component of this vegetation type, with Iridaceae and Oxalidaceae particularly well-represented. Fairfield Farm is divided into a series of fenced camps, or holdings.

Large tracts of renosterveld are used as natural grazing camps; others consist of cereal fields or artificial pastures with scattered fragments of renosterveld. Fragments that are included within agricultural fields have a different disturbance regime to the larger fragments that are used as grazing camps. These smaller fragments are more heavily grazed, more frequently burnt and subject to aerial crop spraying.

2.2. Data collection

We chose 23 fragments of natural vegetation, maximally one per camp, ranging in area from 0.06 to 153 ha. Distances between fragments ranged from 0.03 to 1.1 km. Sites were selected with similar aspects (E–SE), on moderate slopes and on shallow duplex soils with mature vegetation. Three permanent plots, each measuring 10×5 m, were located near the centre of each fragment and were situated 5–10 m apart. Plant species were recorded regularly on each plot between April 1994 and November 1995. We used percentage cover of individual species as well as numbers of individuals of each species per plot as measures of abundance. To make field sampling easier, we used a category system; category values were, however, converted back to percentages for the analyses: Cover: 1 = 0.1–0.9%, 2 = 1–2%, 3 = 3–5%, 4 = 6–10%, 5 = 11–20%, 6 = 21–50%, 7 = 51–100%. Number of individuals: 1 = 1, 2 = 2–10, 3 = 11–50, 4 = 51–100, 5 = 101–200, 6 = 201–500, 7 = 501–1000. We pooled species data for the three plots per site and, using the mean percentage value for each

category, calculated percentage cover and number of individuals for each species for each fragment. Indirect gradient analyses (PCA, DCA) showed that the sites chosen do not show any bias in terms of underlying environmental gradients (Kemper, 1997).

We categorized species according to biological attributes that reflect their ability to persist on fragments (Table 1) (see also Bond et al., 1988; Cowling and Bond, 1991). Information on all attributes except local abundance 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. (1991) and Arnold and de Wet (1993), as well as various monographs and personal observations. Nomenclature follows Arnold and de Wet (1993). Data on local abundance were derived from the plot data collected for this study.

2.3. Data analysis

2.3.1. Community analysis

TWINSPAN cluster analysis (Hill, 1979) was used to test the similarity of species sets from each fragment. The analysis was run using percentage cover values of the full species list.

2.3.2. Species diversity

We used species richness S and three measures of diversity: $N1$, the exponential of Shannon's diversity index

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

$N2$, the reciprocal of Simpson's index

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

and E , a measure of evenness

Table 1
Fifteen biological attributes of plant species in six categories chosen for this study

Category	Expected fragmentation effect
Origin (native, alien)	High alien invasion potential from surrounding agricultural landscape and high replacement potential of native species
Life form (geophyte, shrub, forb, graminoid)	High disturbance (fire, grazing, trampling) tolerance in geophytes and forbs; low disturbance tolerance in graminoids and shrubs (Bond et al., 1988)
Life cycle (annual, perennial)	High probability of annual species colonisation and establishment in a disturbed system owing to larger seedbank persistence (Hester and Hobbs, 1992)
Pollination syndrome (biotic, wind)	Low seed set owing to the disruption of plant–pollinator interactions (Bond, 1994)
Dispersal distance (short, long)	Low rate of (re)colonisation in short-distance dispersers (Bond et al., 1988)
Local abundance ^a (rare, common, very common)	Low probability of maintaining viable population sizes and (re)colonisation potential in rare species (Hanski, 1994)

^a Rare species were defined as those occurring on fewer than four sites, common species on 4–15 sites, very common species on 16 or more sites.

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

using percentage cover (Ludwig and Reynolds, 1988; Magurran, 1988). Analyses using number of individuals gave similar results and are not reported here. We used least squares regression analysis to examine any significant changes in diversity measures with fragment area.

2.2.3. Plant attributes

Scatter diagrams of all patterns that indicated some relationships between fragment area and plant attributes were monotonic. Therefore, least squares regression analysis was used to test for significant linear relationships between fragment area and number of species, frequency of individuals, and percentage cover of species categorised according to biological attributes. Cover values were arcsin-transformed. Other data were tested for normality prior to analysis.

3. Results

We recorded a total of 366 species on Fairfield Farm, 284 of these in the sample plots. The remaining species were collected elsewhere on the farm, including on the 23 selected fragments. Of the total number of species, 44 were locally rare (see Table 1 for definition). Two new geophyte species were collected [*Galaxia melanops* Goldbl. & J.C. Manning (Iridaceae) and *Aristea teretifolia* Goldbl. & J.C. Manning (Iridaceae)]. Three species are listed in the IUCN Red Data categories (Hilton-Taylor, 1996) as globally vulnerable: *Anisodonteia dissecta* (Malvaceae) (low shrub), *Moraea debilis* (Iridaceae) and *Tritoniopsis flexuosa* (Iridaceae) (both geophytes). Another three species are listed as globally rare: *Aspalathus rosea* (Fabaceae) (low shrub), *Diosma passerinoides* (Rutaceae) (small-leaved shrub) and *Sparaxis fragrans* (Iridaceae) (geophyte). Two species are suspected to belong to one of these categories, namely *Athanasia quinquedentata* subsp. *quinquedentata* (Asteraceae) (low shrub) and *Cliffortia monophylla* (Rosaceae) (low shrub).

3.1. Community analysis and species diversity

The TWINSpan classification of 23 sites produced eight groups from four divisions (Fig. 2). The first division separated five small sites (≤ 10 ha), characterized by the absence of *Ficinia filiformis* and *Restio multiflorus*, both graminoids common in the area. From this group, one fragment separated out at the next division on the presence or absence of *Anthospermum aethiopicum*, a shrub only found on this site. The remaining sites were divided into two major groups, with one group of small and large fragments characterized by a lack of the asteraceous shrub *Elytropappus rhinocerotis* and lower

cover values of *Restio multiflorus*. This group subdivided twice more; the indicator species being two asteraceous shrubs *Helichrysum teretifolium* and *Senecio burchellii*. The second major group contained six large fragments (> 29 ha) and two small fragments (< 3 ha). This group subdivided into a group of five large fragments, and a group of two small and one large fragments. *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. This site was characterized by *Athanasia trifurcata*, an asteraceous shrub.

There was no significant relationship between any measure of diversity and fragment area (Fig. 3).

3.2. Plant attributes

Of the 15 plant attributes listed in Table 1, only seven showed significant relationships with fragment area (Fig. 4). Six of these showed a negative relationship with increasing fragment area, namely numbers of all annual and alien species, numbers of annual graminoid species, frequency of individuals of geophyte and short-distance dispersed species, and percentage cover of short-distance dispersed species. Only percentage cover of perennial graminoid species showed a positive relationship with fragment area. Rare species occurrence did not differ significantly with fragment size.

4. Discussion

4.1. Community analysis and species diversity

Although we found no clear relationship between renosterveld fragment size and community composition or diversity, there was greater variability in species composition, richness and diversity in small fragments than in large fragments (Figs. 2 and 3). These results imply that large fragments may be more stable in composition, while smaller fragments are more vulnerable to local extinctions and hence, more open to colonisation by alien and other well-dispersed species. This probably results from the higher grazing (and trampling) intensity, as well as the greater fire frequency, on the smaller fragments (Bond et al., 1988).

4.2. Plant attributes

Diversity per se is a poor measure of fragmentation effects. Of greater relevance are changes in community structure as reflected in the frequency of individuals and species with different biological attributes (Saunders et al., 1991; Holt et al., 1995). If processes associated with small population size are predominant in determining structure, then one would expect an over-representation

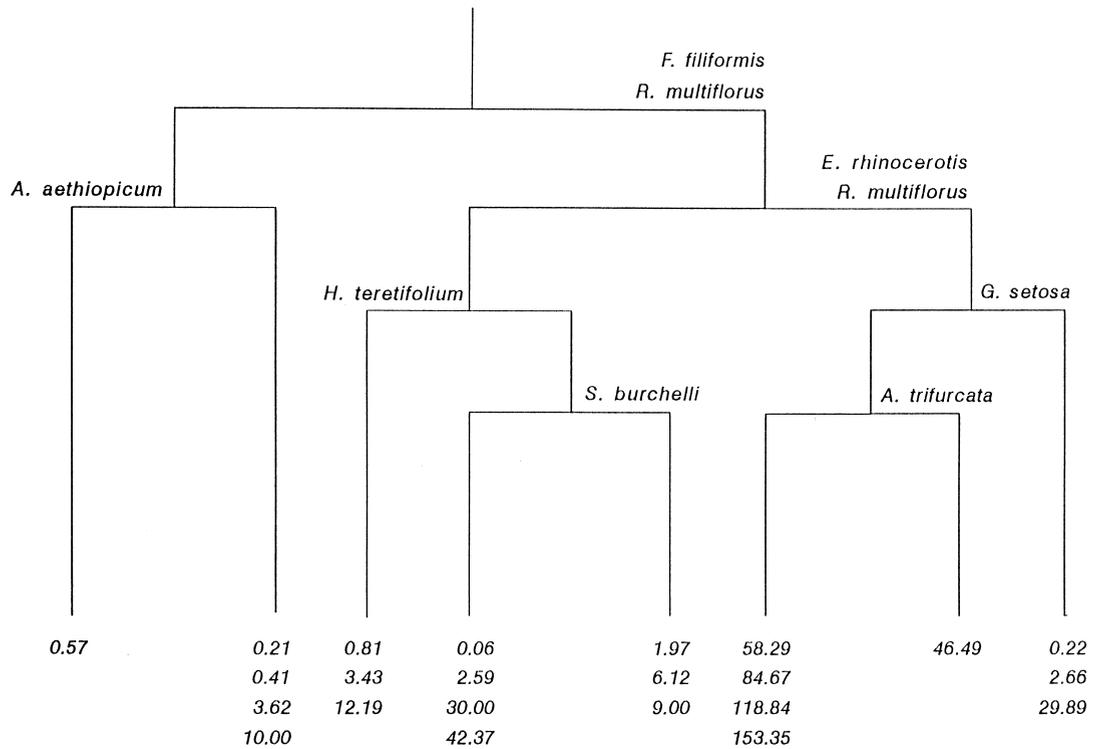


Fig. 2. TWINSpan dendrogram based on plant cover values in 23 fragments of renosterveld. For full species names refer to text. Numbers at base of dendrogram indicate areas (ha) of fragments in each subdivision.

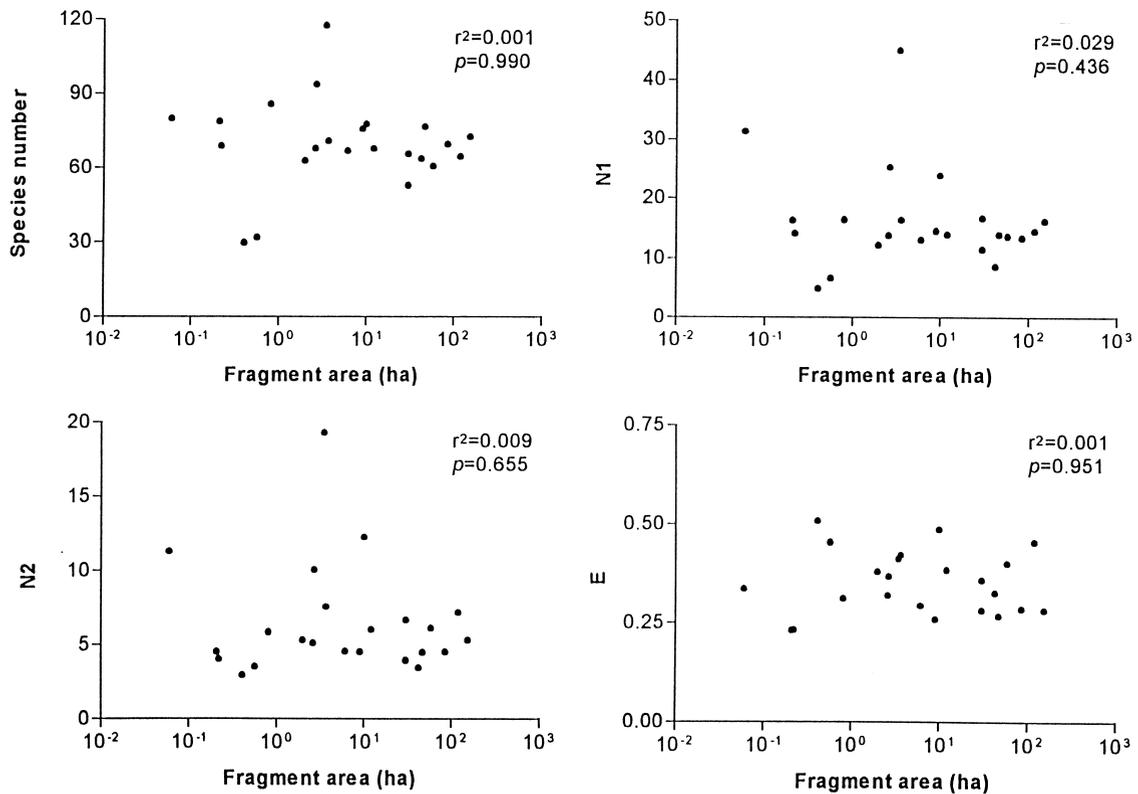


Fig. 3. Relationships between four diversity indices and fragment area in a fragmented renosterveld landscape. Data are mean values from three 5×10 m plots located on similar soils, slopes and aspects in each of 23 fragments (N1, Shannon's diversity index; N2, reciprocal of Simpson's index; E, evenness).

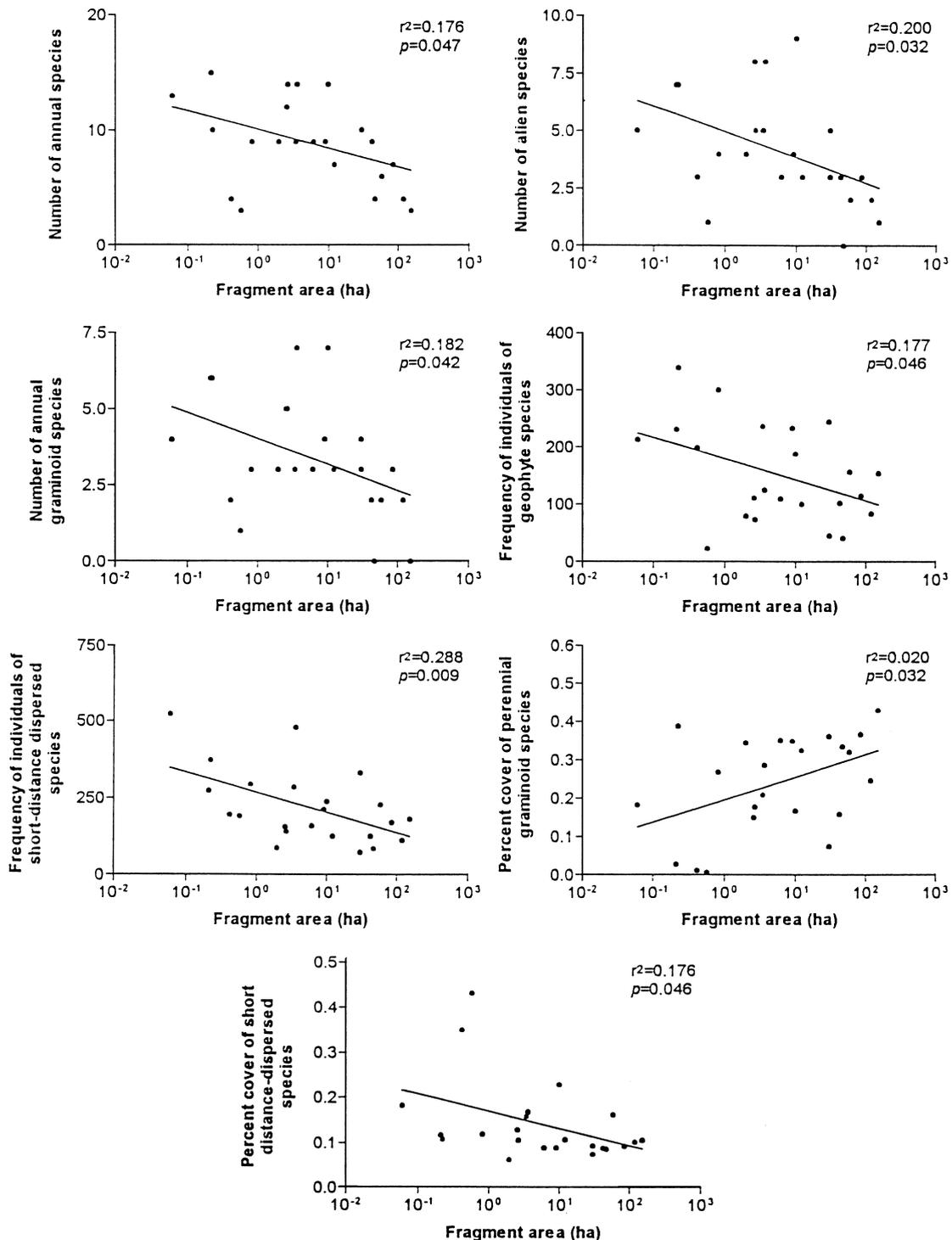


Fig. 4. Significant linear relationships between abundance of plant attributes and fragment area in a fragmented renosterveld landscape. Data are mean values from three 5×10 m plots located on similar soils, slopes and aspects in each fragment.

on small fragments of attributes promoting persistence and colonization (e.g. great longevity, long-distance dispersal, etc.) (Bond et al., 1988; Templeton et al., 1990; Fahrig and Merriam, 1994). If the selective processes are deterministic, one would expect to find high representation of attributes that reflect an ability to

cope with the new disturbance regime (Sloan Denslow, 1985; Hobbs, 1987; Bond et al., 1988; Pettit et al., 1995).

The significantly higher number of annual, alien and annual graminoid (largely alien) species on smaller fragments is largely a function of greater edge effects (most aliens are recruited from adjacent agricultural

land) and more intense disturbance in these areas (Hester and Hobbs, 1992; Scougall et al., 1993). The decrease in numbers of geophyte individuals with increase of fragment size is mainly the result of the large contribution from widespread, self-compatible and “weedy” species such as *Ornithogalum thyrsoides* (Hyacinthaceae) (Kemper, 1997), which thrive in disturbed sites throughout the Cape Floristic Region (pers. obs.). This may also explain the apparently counter-intuitive decline with increasing fragment size in the density and cover of individuals that have short-distance dispersal: weedy geophytes have relatively large and passively dispersed seeds. The significant decline in cover of perennial grasses with decreasing fragment size is likely to be a result of more intense grazing in the smaller fragments (Cowling et al., 1986). Overall, changes in the representation of plant attributes in relation to fragmentation of renosterveld can be explained in terms of changes in disturbance regime rather than the effects of population size.

4.3. Why such a weak fragmentation effect?

The majority of studies on fragmentation have shown that it negatively influences species diversity (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). There are at least three explanations for the weak fragmentation effect observed here. First, most renosterveld species resprout after fire (pers. obs.) or have wind-dispersed seeds (Cowling et al., 1994). Sprouters are able to persist for long periods (Midgley, 1996), so the relatively recent fragmentation of this vegetation type (the last 70 years) may obscure the expression of recruitment failure (Lamont et al., 1993; Buchmann and Nabhan, 1996). Wind-dispersal may enable the propagules of many of the dominant asteraceous shrubs (*Elytropappus rhinocerotis*, *Athanasia* spp., *Helichrysum* spp.) to disperse among fragments, thus avoiding local extinction (Fahrig and Merriam, 1994).

Secondly, the 2000 year history of livestock grazing (Deacon, 1992), has caused the conversion of much of the renosterveld habitat from a shrubby grassland to grassy shrubland, dominated by unpalatable species (Cowling et al., 1986; Scholtz, 1986). Thus, the long history of disturbance may have predisposed renosterveld species to withstand the deterministic impacts of fragmentation (see also Simberloff, 1993). This is in contrast to fynbos, where the vegetation has always been relatively unpalatable (Johnson, 1992) and not subject to heavy grazing impacts now and in the past (Deacon, 1992).

Thirdly, like fynbos, renosterveld does have a number of locally rare plant species. These small and isolated, but entirely natural, populations may well have been

resistant to inbreeding depression and loss of heterozygosity prior to fragmentation (Rebello, 1992). Thus, they may have been able to withstand extinction processes associated with small population size.

4.4. Conservation

Our study has shown that even very small renosterveld fragments (<1 ha) do not support vegetation that is substantially different in terms of composition and diversity from large ones (>30 ha). In addition, the high total number of species recorded is an impressive tally for a landscape dominated by cereal and pasture crops. Therefore, these renosterveld fragments represent “islands of hope” for the maintenance of plant biodiversity; they have “high irreplaceability” and conservation value (Pressey et al., 1994) and should not be ignored in any plan for improving the conservation status of this endangered vegetation type.

Given the high land value and fragmented nature of these landscapes, the prospect for establishing formal reserves containing South Coast renosterveld is very low (McDowell, 1988). However, towards the eastern limit of its original extent, where up to 34% of renosterveld remains, reserve establishment is more feasible (Kemper, 1997).

Where formal reserves are not feasible, every effort must be made to demonstrate the benefits to farm-scale economies of retaining and managing fragments, especially the larger ones, since “on-farm” conservation is the only option. Included in these benefits are mitigation of erosion and maintenance of hydrological processes provided by this natural habitat (Hobbs, 1992, 1993). Anecdotal evidence suggests that livestock health is improved (and veterinary costs reduced) when animals have access to the rich mixture of micronutrients associated with renosterveld grazing (B. Heydenrych, pers. comm.). Furthermore, these remnants provide a reservoir of biodiversity for restoring natural pastures should environmental change or economic factors result in cropping becoming unsustainable. Therefore, not only are the fragments the only option for conserving renosterveld, they may also be of direct economic value both now and in the future. The challenge for research is to demonstrate the economic benefits of the services which these fragmented ecosystems provide (Daily, 1997; Noss and Csuti, 1994).

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