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Bryophyte Diversity Patterns In A Fragmented Landscape: A Case Study Of South African West Coast Renosterveld

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- 3 -
ABSTRACT

Renosterveld, a distinctive vegetation type forming part of the Cape Floristic Region, is well known for the richness of its flora. This vegetation type has been fragmented extensively by agriculture. The extent of this fragmentation in terms of overall habitat loss due to human activities, fragment sizes, and the effect of habitat parameters on bryophyte diversity have not been described previously, thereby limiting the development of conservation strategies for this vegetation type. Today the remaining natural vegetation exists as small habitat remnants. The most affected region is West Coast renosterveld; of the original 7280 km² only 3% remains with 187 plant species listed in the red data book. Although the angiosperm flora is well known, the bryophyte flora of this vegetation type, like that of most others in Southern Africa, is very poorly documented. This study examines the effects of fragmentation on bryophyte diversity in renosterveld vegetation of South Africa’s west coast. The main objectives of this study are to: Document bryophyte species assemblages in remnant fragments of renosterveld vegetation, investigate the effect of fragment size, isolation and heterogeneity on bryophyte diversity patterns in renosterveld, determine the extent to which fragments are nested and evaluate the extent to which existing conservation measures are appropriate for the long-term survival of the bryophyte flora in this vegetation type. Seventy-two bryophyte species were recorded from 23 fragments ranging from 0.1 to 102 hectares. The bryophytes that occurred in small patches were relatively similar to those in large patches; no species were recorded from all fragments. Using multiple regression models, Bryophyte species are observed to increase with increasing fragment size and bryophytes species communities that were occurring in very small patches were found to be subsets of communities in larger fragments. Both isolation and heterogeneity showed significant relationship with bryophyte species diversity. There was no association between mean area of the surrounding patches and species diversity. This practical framework may facilitate a step forward to what could be the next to alleviate the general threat of bryophytes and its habitat vegetation. This could be achieved by laying management strategies for the existing fragments irrespective of its size.

Keywords: Fragmentation, Diversity, Conservation, Renosterveld, Bryophytes, Species-area relationship, Landscape heterogeneity, Nested subsets, Fragment, metapopulation, Alpha diversity, Beta diversity, Gamma diversity.
CHAPTER 1: GENERAL INTRODUCTION

Renosterveld, a distinctive vegetation type forming part of the Cape Floristic Region (CFR), is well known for the richness of its flora. While not as rich in local endemics as fynbos, renosterveld is nonetheless extremely species-rich, especially in its geophyte flora (Cowling, 1990) which includes about 200 species in 70 genera and nine families. Other dominant elements of this vegetation (Kemper, 1997, Harison, 2003) include: *Elytropappus rhinocerotis* (Asteraceae), ericoids, *Helichrysum spp* and a grassy component composed mainly of *Ehrharta spp* and *Themeda triandra*. Renosterveld has been used for natural grazing for centuries by livestock belonging to Khoi-Khoi pastoralists and later to European settlers. Over the past century, but especially since the 1920s (Kemper, 1997), renosterveld has been extensively transformed by agriculture, and an estimated 160000ha of natural vegetation have been transformed to cereals and artificial pastures between 1918 and 1990 (Cowling et al., 1986; Hoffman, 1997). As discussed below, this vegetation type is highly fragmented by human activity, and currently is amongst the most threatened in the CFR.

Although the angiosperm flora is well known, the bryophyte flora of this vegetation type, like that of most others in Southern Africa is very poorly documented. Preliminary data available at the moment (e.g. Perold, 1999; Magill, 1987; Magill and Van Rooy, 1998 and Hedderson unpub.) suggest that renosterveld may harbour substantial bryophyte diversity. The dominant bryophyte groups in the region appear to be Archidiaceae, Aytoniaceae, Bartramiaceae, Bryaceae, Ditrichaceae, Fissidentaceae, Funariaceae, Grimmiaceae, Pottiaceae and Ricciaceae. Little is known of how this (or indeed any other) bryophyte flora might be affected by fragmentation so the conservation status of the many unique bryophytes is very uncertain. The overall goal of this thesis is therefore to provide baseline data on the bryophyte flora of west coast renosterveld and to document patterns of bryophyte diversity in the remaining patches of this vegetation.

1.1 Fragmentation, species diversity and conservation biology

Habitat fragmentation has long been recognised as one of the most important threats to global biodiversity and a major concern in conservation biology. Fragmentation has implications for reserve design (Diamond and May, 1976; Wilcox and Murphy, 1985), the
understanding of species-area relationships (e.g. Temple and Wilcox, 1986), island biogeography theory (Galli et al., 1976; Wiens, 1994), and related ecological issues (Saunders et al., 1991). It has been described as a process where “a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original” (Wilcove et al., 1986). It is invariably associated with land systems where conservation competes poorly with other forms of land use such as agriculture, urbanisation and forestry.

One of the chief impacts of fragmentation is the change from continuous habitat to the formation of distinct habitat patches (islands), sometimes having different habitat parameters. Such islands are well known in ecological theories and much has been done to describe the dynamics of such systems. A particularly well-known concept is that of the equilibrium theory of island biogeography (MacArthur, 1967), which describes the number of species on an island as a function of size and isolation, and factors that affect extinction and immigration rates respectively.

A key prediction from island biogeographic theory is that reduction in the area of a habitat patch can decrease its suitability for both plants and animals to a disproportionately greater degree than the actual reduction in area (Johnson, 2001). It is obvious that the number of species is likely to decline if the habitat size is reduced. Fragmentation effects imply that the value of the remaining habitat also is diminished.

The population dynamics of any species within a system of habitat islands may be viewed at two levels, at the within-island level (within a fragment) and at the between-islands level (between fragments). The species within the island level are governed by well-established rules of growth, reproduction and mortality. The species in the between-island patterns are determined by the ability to cross barriers between the islands (fragments), ability to establish on the island and the risk of disappearing from the island (Levens, 1969). In contrast to the within-island population, the sum of populations over a set of islands has been termed a “metapopulation” (Levens, 1969) and metapopulation-level dynamics are also known to affect interspecific interactions (Levens and Culver, 1971; Bengtsson, 1991) and the genetic structure of populations (Levens, 1969; Gilpin, 1991). In the simplest case, one can assume that dynamics within habitat patches are fast enough to be ignored if between-patch dynamics are being studied. The proportion of
patches colonised is dependent only on the relationship between immigration and extinction.

There are three types of fragmentation effects distinguished by earlier researchers: patch size effects, edge effects, and isolation effects (e.g. Faaborg et al., 1993; Johnson and Winter, 1999). Patch–size effects are those that result from differential use or reproductive success associated with habitat patches of different sizes. Some of the patch–size effect may be induced by edge effects (such as avoidance, predation, pairing success, interspecific competition). Finally, isolation from similar habitat can influence the use of a particular habitat patch because of reduced dispersal opportunities.

When the patches are close to one another they tend to have the same microhabitats, but some of the patches will not necessarily be suitable for plant species because of the loss of habitats. So patch size and isolation may interact. However, the effects of small patches are likely to be more pronounced in landscapes where similar habitats are scarce than the landscapes where such habitat is common. Andrén (1994) suggested that “the decline in population size of a species living in the original habitat seems to be linearly related to the proportion of original habitat lost, at the initial stages of habitat fragmentation. At some threshold, area and isolation of patches of original habitat will begin to influence the population size in the original habitat patches.” The probability that certain species will occur in small patches has been found to depend on how many suitable habitats are there and the nature of the surrounding landscapes. However, effects of fragmentation may not occur until the original habitat is reduced by 70-90% (Andrén, 1994). Each of these factors can affect the occurrence, density, and reproductive success of both fauna and flora in a habitat patch.

As an example, a study of fynbos “islands” in a “sea” of non-flammable, temperate rainforest, (Bond et al., 1988; Kemper, 1999) showed that fragments of less than 600 ha had significantly fewer species than similar–sized areas within extensive habitat. The lower 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.
Tropical montane cloud forests are another ecosystem with high species diversity threatened by fragmentation through deforestation. In some regions the deforestation rate exceeds that of tropical rainforest (Hamilton et al., 1995). At least in this system, the way in which fragmentation affects species richness is expected to vary greatly depending on the scale at which one studies the phenomenon (Haila, 2002; Laurence et al., 2002; Arellano and Halffter, in press from Pinada and Halffter, 2003). Both the remaining fragments of forest and plant communities generated by human activities which surround them participate in the species dynamics of the landscape (Gustafson and Gardner, 1996; Gascon et al., 1999). To understand the heterogeneity of the modified landscape it is important to realize that, from the perspective of organisms that inhabit it, the landscape is not environmentally uniform (Haila, 2002).

Landscape fragmentation affects species diversity at all levels i.e. it affects the alpha (within community), beta (among communities) and gamma (landscape) diversities. The species richness of the entire fragmented landscape (gamma diversity) is the result of both alpha and beta diversities which reflect the heterogeneity of the landscape (pre- or post-fragmentation). Therefore, gamma diversity is a function of the sensitivity of species to differences in the landscape (Pineda and Halffter, 2003). Therefore in a modified landscape where the original landscape (pre-fragmentation) was homogenous, we expect the total number of species to be similar to the number of species in the richest patch (forest habitat or some other mosaic habitat). In this scenario the species composition in the remaining patches would be subsets of the richest one and consequently, gamma diversity would be more greatly influenced by alpha diversity. On the other hand, species richness in heterogeneous landscapes will be notably higher than that of the richest patch and the number of species for the landscape would be a result of the distinctness or dissimilarity in the composition of the species assemblages of different patches of vegetation that make up the landscape. Thus, high values of beta diversity are expected. This way of portioning the element of diversity is central to understanding the contribution of local and regional processes to species diversity (Schluter and Ricklefs, 1993; Lande, 1996).

Nestedness is fundamentally ordered composition (Patterson, 1984; Patterson and Atmar, 1986). Any factor that favours the assembly or disassembly (Mikkelson, 1993) of species communities from a common pool in a consistent order will produce a nested structure
and is common in ecological communities of almost every kind examined. In (Wright et al., 1998) views, nested subsets constitute a special kind of distribution pattern that is observed in presence / absence matrices and that carries unique information. A group of species assemblages is said to be nested when the species making up smaller biotas are also found in all larger ones. When a number of such biotas are ranked by species richness, they present a nested series. In the presence / absence matrix where sites are arranged in order of decreasing species richness and species are ranked in order of decreasing number of occurrences, species presences in a strongly nested set of communities will fill the upper left of the matrix in a roughly triangular shape. Nested subsets can only be observed at and above the level of a single community or assemblages, and in this sense nestedness is a meta-community or landscape pattern.

There are different causes of nestedness pattern. These include passive sampling, habitat nestedness, distance and area (Wright et al., 1998). Though it has been shown that there are constraints that may limit nestedness these constraints can be put under one theme: homogeneity. Since nestedness reflects homogeneity of species communities, anything that injects heterogeneity reduces the potential of nestedness to form. Patterson and Brown (1991) listed three conditions they believed necessary for the development of nestedness: the islands or sites must be ecologically comparable, species inhabiting these sites must have shared similar biogeographic histories and species must be hierarchically ordered in terms of their niches.

According to (Wright et al., 1998) the heterogeneity in species distributions among sites can result from:

- Evolution. Speciation, local adaptation, and changes in species ranges over evolutionary time give rise to site endemics and biogeographic variation in species pools.
- History. Evolution and community assembly are ongoing and partly stochastic processes, so that the community found at a given site is often influenced by past events. If sites or sources of colonists have different biogeographic histories or undergone divergent processes of community development, heterogeneous species communities are likely to result.
• Spatial heterogeneity in the environment, including patchiness. Differences in environment from place to place can cause geographic variation in the kinds or mix of habitats found at different sites.

The distinctive patterns of species richness and composition in fragments have important implications for conservation. The elevated slopes of species richness changes with area means that insular impoverishment with area reduction is substantially greater on fragments than on islands (Lowlor, 1986).

Nested subsets also have relevance to biological conservation, most obviously in resolving the single large or several small (SLOSS) conundrum. In a perfectly nested archipelago, small reserves each support the same set of species (Patterson and Atmar, 1986). However, few systems are perfectly nested, and nestedness is seldom perfectly correlated with island area. In addition, systems of small reserves, when selected on the basis of fauna or floral dissimilarity, will often preserve more species than the single largest island (Simberloff and Gotelli, 1984). The utility of nestedness in reserve planning appears to be limited, at least when the compositions of all areas are known. “Smart” amalgamation routines invariably perform better than those based on solely on area considerations, whether from small-to-large or large-to-small (Cook, 1995; Lomolino, 1996).

Fragmentation of natural habitats is a problem for conservation planning. This is because remnants of natural habitat tend to have high conservation value and are highly vulnerable to a wide array of threats (Saunders et al., 1991; Fahrig and Merriam, 1994). Thus, many remnants qualify as priorities for conservation action despite their lack of appeal to conservation authorities and lobby groups (Pressey, 1994; Balmford, 1996). The high conservation value of fragments is associated with high irreplaceability. As a result of large-scale habitat loss each fragment potentially can make a high contribution to a reservation goal or the loss of a fragment may greatly restrict options for attaining a representative reserve (Pressey et al., 1994, 1995). Their location in an agricultural matrix makes fragments highly vulnerable to a wide array of processes that threaten the long-term maintenance of biodiversity (Terborgh and Winter, 1980; Gilpin and Soulé, 1986).
Renosterveld, a fire-prone, small-leaved and grassy shrubland (Low & Rebelo, 1996), is one of the diverse natural vegetation types of South Africa's Cape Floristic Region (CFR). The CFR, recognised by Meyers (1990) as one of the world's hotspots of plant diversity and endemism, is perhaps best known for its fynbos vegetation. Whilst highest levels of endemism appear to be concentrated in fynbos, local endemics are also relatively common in renosterveld. It is particularly renowned for its spectacularly rich geophyte flora (Cowling, 1990; Johnson, 1992). Unlike fynbos, the dominant vegetation type in the CFR, renosterveld lacks restioids, and proteoids are very rare (Cowling and Richardson, 1995). It is largely associated with shale-derived, fertile and lowland soils, making this type of vegetation highly suitable for cereal cultivation (Hoffman, 1997).

Renosterveld is very highly fragmented. However, estimates of the amount of loss of natural vegetation are crude (Moll and Bossi, 1984; Low and Rebelo, 1996) and no exact account of the number and size of renosterveld exists. Most of the area has been grazed by livestock for at least the last century, ploughed for cereals and other crops or devoted to forestry (Rebelo, 1995). Moll and Bossi (1984), Kemper (1997) estimated that only 15% of the original renosterveld in South Africa remains as a series of small (medium size, c 30 ha) fragments in a matrix of cereal and pasture lands that are subjected to grazing and burning, while (Rebelo, 1995) reports a surface area of 1,923,260 ha, of which only 0.22% is under protection. Apart from agriculture, urban development, pastoral activities (Azorin, 1992; Rebelo, 1992) and spread of aliens (Richardson et al., 1992) exacerbate the effects of fragmentation, resulting in remnants of natural habitat surrounded by man made vegetation.

In recent years, the flora and the dynamics of renosterveld vegetation have been the focus of considerable research attention. In particular, a number of studies have considered the effects of fragmentation (Kemper, 1997; Donaldson et al., 2002) and grazing (Savory and Scott, 1986). In terms of conservation and utilization, Cowling et al. (1986) suggested that the establishment of a vigorous grassy sward would be the most effective long-term conservation strategy in this vegetation since utilisation would be compatible with conservation. Therefore, management models should consider the biological attributes of key species in order to improve the grazing status of the vegetation.
West Coast renosterveld, apparently more fragmented than South Coast renosterveld (Cowling et al., 1986; Rebelo, 1995), is the focus of this thesis. It covers an undulating coastal plain north of Cape Town and is located at an elevation between 100-350 m with annual rainfall of 400-600 mm. It has been extensively transformed by cereal and pasture crops, with only 3% of the original 7,280 km$^2$ remaining in 1988 as isolated fragments largely on lands too steep for agriculture (Hall and Veldhuis, 1985; McDowell and Moll, 1992; McDowell, 1988; Heydenreych and Littlewort, 1995). Cowling and Richardson (1995) report 1406 plant species on the red data list in the fynbos biome, of which 187 are found in the west coast renosterveld (Rebelo, 1992).

1.3 Bryophytes and their diversity patterns in fragmented landscapes

The bryophytes are a diverse group of 'lower' land plants with some 23,000 described species worldwide, making it the largest group of land plants apart from the angiosperms (Mishler, 1997). This group of plants consists of three distinct lineages (i.e. mosses (Bryopsida), hornworts (Anthoceropsida) and liverworts (Hepaticopsida) encountered in a broad range of terrestrial habitats including tropical rain forests, streams, mesic forests, arctic tundra and desert boulders. The physical structure and physiological attributes of bryophytes (such as desiccation resistance or drought tolerance, nutrient-capturing ability) allow them to play a major role in many of the world’s ecosystems, affecting water and mineral fluxes, controlling surface run-off and erosion and at the same time providing food and habitat for a wide range of organisms (Newton et al., 2000). Like other plants, bryophytes play a vital role in more complex ecosystems, such as absorbing nutrients in precipitation, dust and litter before they can be taken up by higher plants (Oechel and Van Clave, 1986).

At all taxonomic levels, bryophytes tend to have distributional ranges that correspond to those of tracheophytes, but most species of bryophytes are more widely distributed (Watson, 1971). Like other spore producing plants, bryophytes generally tend to have broad ranges and this suggests that long distance dispersal of spores or other propagules is an important factor explaining their distribution (Shaw, 1995). Many families are cosmopolitan (Sim, 1918), and even at the species level may occur throughout different climatic regions. The list of cosmopolitan species is quite large (reviewed in Watson,
1971). However, many exhibit disrupted or narrow ranges. This is perhaps particularly true of the Cape Region of South Africa, where numerous endemic bryophyte genera and species are present. For example *Riccia* has over 50 species in the Cape, most of which are endemic, and a large number occur in renosterveld and succulent karroo (Perold, 1999).

Bryophyte habitats are patchy, both in time and space (Herben, 1994). This means that within a landscape any species is able to grow only in certain limited regions (habitat patches) and growth is impossible in the rest of the landscape. The metapopulation dynamics of bryophytes species are determined by the ability to disperse and a particular structure of the environment, which will be a landscape of non-continuous habitat patches (Söderström and Herben, 1997).

Dispersal of bryophytes may involve anything from diaspores landing within a few centimetres from the parent colony to trans-oceanic dispersal. If the diaspores are transported only short distances, they contribute mainly to local population growth while diaspores that are dispersed over long distances contribute mainly to between-patch dynamics (distance dispersal). The dispersal distance is however, a result of the interaction between species characteristics (e.g. spores size, seta length) and environment (above-ground height of bryophyte habitat, exposure to wind and wind velocity). A major factor influencing dispersal is diaspore size, with small diaspores being transported more easily over long distances. Sexually produced spores are usually small (8-20µm) among bryophytes but 100-200µm in some species (e.g. *Riccia* and *Archidium* spp.). The height of diaspore release is another factor in dispersal distance (Raynor et al., 1975). In bryophytes, this is both affected by seta length and habitat type. For species growing near the ground, seta length is thus an important factor determining dispersal ability. The longer the seta, the greater will be the wind velocity around the capsule.

In addition, the longevity of spores varies. Some bryophytes spores may survive for a considerable time without germinating. Spores of some epiphytic hepatics in Lejeuneaceae survive only a few hours (Fulford, 1951) whereas relatively xerophytic Marchantioids e.g. *Mannia fragrans* (Balbis) Frye and Clark and various *Riccia* spp may remain viable for several years (Inoue, 1960). When spores stay longer in particular area, reproductive
successes and growth rate takes longer thus affecting the spread of spores. This delay in growth may affect bryophyte reaching other habitat patches.

Bryophyte diversity in fragmented landscapes will be influenced by the interaction between the species biology and habitat, that is the gametophyte longevity and its reproductive effort, spore size and spore number. Species with large spores or prevalence of vegetative growth is likely to be successful within a patch. However, the ability of such species to disperse may be diminished (fewer spores, lower reproductive effort), and the species may be unsuccessful at the between-patch level. This is true both for the annual shuttle species and the perennial stayers (sensu During, 1992). Species with small spores and/or less vegetative spread will be able to rely more on dispersal to the other habitat patches, and be less vulnerable to disturbance at the already colonised patch.

The size of the habitable patch varies with the substrate type and thus between habitat patches of the same kind. The patch size determines the maximum population size at each locality and is a parameter within patch dynamics (Söderström and Herden, 1997). Minimum population size increases with patch size and large population size decreases the probability for chance extinction and thus increases the stability of local populations. Furthermore, larger habitat patches will also be larger ‘target areas’ for dispersing diaspores and hence will receive more diaspores from the outside.

Species-area relationships can be explained by two ecological hypotheses. (1) The habitat heterogeneity hypothesis predicts higher species numbers because of higher heterogeneity. (2) The area per se or equilibrium hypothesis considers colonisation-extinction dynamics to cause increasing species numbers with increasing habitat area independent of habitat heterogeneity (Rosenzweig, 1995). Habitat area and habitat heterogeneity are often closely correlated (Kohn and Walsh, 1994; Rosenzweig, 1995). As we were much more interested generally in composition of the whole vegetation, equal sized plots were ignored in this case. Notably, equal sample sizes should reduce the habitat heterogeneity effect, making it possible to test separately for area per se effects (Kelly et al., 1989; Köchy and Rydin, 1997).
1.4 Objectives

In the present study, I examine the effects of fragmentation on bryophyte diversity in renosterveld vegetation of South Africa’s west coast. The main objectives of the study are to;

- Document bryophyte species assemblages in remnant fragments of renosterveld vegetation.
- Investigate the effect of fragment size, isolation and heterogeneity on bryophyte diversity patterns in renosterveld.
- Determine the extent to which species composition of the fragments is nested.
- Evaluate the extent to which existing conservation measures are appropriate for the long-term survival of the bryophyte flora in this vegetation type.
CHAPTER 2: MATERIALS AND METHODS

2.1 The Study Area

Field studies were undertaken in January and February 2005 in the Swartland area approximately 100 km north of Cape Town (Fig.1). In this region, most renosterveld has been plowed for cereal cultivation, and remaining patches are located in agricultural lands. To facilitate comparison with other studies, sampling was undertaken in patches previously investigated for birds, (Cameron, 1999; Donaldson et al., 2002 & Harrison, 2003) and plant species especially geophytes (Cowling, 1990).

Figure 1 Map showing the location of 23 vegetation sites in the Swartland, Western Cape, South Africa. A circle shows patches with a number representing the site.
2.2 Data Collection

Although previous workers sampled up to 54 sites, time constraints in this study restricted the number of sites to 23. These were selected to cover the size range of fragments, and to a lesser extent to represent varying degrees of isolation. The size of the patches investigated ranged from 1000 to 1,018,400 m². In each case as much of the site as possible was covered on foot, a particular attempt was made to examine different microhabitats within sites. At each site, each species identifiable by eye was recorded but vouchers were collected for subsequent verification. Specimens of every species not identifiable in the field were collected for later identification.

In addition to species composition, the following were determined for each habitat patch:

1. Area. This was determined with the aid of the Geographical Information Systems (GIS) computer software Arc view 3.3 (ESRI, 2004). For small fragments not digitised on available GIS overlays, the boundaries were recorded using a hand-held Global Positioning System (GPS) device to estimate the area size. Any transformed areas within patches were excluded from the measurements.

2. Mean area of the nearest fragments was calculated (in m²) by measuring the area of the four nearest fragments whether these were sampled for this study or not.

3. Mean distance to the nearest fragments. This is the mean distance to the four nearest patches as determined in 2.

4. Distance to nearest large fragment. This is the distance (in m) to the nearest renosterveld fragment that was at least 16000 m² (this value was obtained as a measure from the graph of area/species accumulation curve). The distances were calculated in Arc View 3.3.

5. Landscape/patch heterogeneity. In each patch, the following habitat characteristics were visually assessed; soil type (sand, clay and silt), degree of rockiness (no rock, some rock and rocky), site aspect (presence of shrub cover, succulents, renosterbush, slope, hill, valley, flat, streams, north facing, south facing, west facing, east facing, tree/large shrub presence and cover), Surrounding vegetation (wheat field, eucalyptus, vine and aliens) and fragment size (very small, small, medium and large). Each one of these above variables were recorded.
from individual patches and given scores of 0, 1, 2 and 3. Variation in patch heterogeneity was based on the presence/absence of a variable in each patch/fragment (see details in Appendix 2) the scored variables obtained from each patch were summed up to give an overall measure of patch heterogeneity.

2.3 Statistical Analysis

To compare species richness among sites, species numbers were plotted against the sample size and number of individuals. The program EstimateS 7.5 (Colwell, 1997) was used to randomize the sample (500 times) in order to produce species accumulation curves which allowed an assessment of whether sampling effort was sufficient.

Since the interest of this study is explicitly on the species/area relationship for this system, regression analysis (Statistica 7.0, Stat Soft., 2004) was used to examine the effects of patch area on species numbers. A multiple regression approach, as implemented in Statistica 7.0 (Stat Soft., 2004) was used to examine the joint effects of all five variables simultaneously on species richness. Forward and Backward stepwise variable selection procedures were used, with F-to-enter set at 0.25 and F-to-remove set at 0.1. In addition, the partial regression plot (i.e. the influence of each variable when all others were held constant) for each variable on species numbers was examined. For all these analyses, area was log-transformed.

The computer programme Nested Temperature Calculator (Atmar and Patterson, 1993; The Field Museum, Version, 2004) was used to detect whether bryophyte assemblages in renosterveld fragments comprised nested subsets. A matrix of species presence and absence in each site was used as input. The extent of "unexpected" presences and absences was measured by the 'temperature' of the matrix (Atmar and Patterson, 1995). It ranges from $0^0$ to $100^0$, where $0^0$ is fully nested, i.e. where bryophyte assemblages, in small fragments, are perfect subsets of larger fragments.
CHAPTER 3: RESULTS

3.1 The Bryophyte Flora

From the 256 specimens collected in the 23 fragments, 72 bryophyte species were recorded (Table 4 Appendix 3). No species were recorded from all fragments. The commonest species, *Pseudocrossidium crinitum* and *Tortula atrovirens*, were recorded from nearly 80% of the investigated fragments; these two were also quite abundant in most fragments. Several other species (*Fissidens megalotis*, *Grimmia laevigata*, *Grimmia pulvinata* and *Trichostomum brachydontium*) were found at more than half the investigated sites. The rarest species, (*Acaulon recurvatum*, *Asterella marginata*, *Bartramia compacta*, *Brachymenium acuminatum*, *Bryum radiculosum*, *Chamaebryum pottioides*, *Didymodon australasiaceae*, *Funaria clavata*, *Orthotrichum diaphanum*, *O. incurvomarginatum*, *Pleuridium ecklonianum* and *Pleuridium nervosum*) were recorded in only one to two fragments.

Some new species or genera could not be placed in currently recognised species or genera due to short period of study. As this study represents only one climatic season, there may be quite an extensive element of undescribed biodiversity especially among ephemeral groups, which are not dealt within this study. However, current additional data collections indicate that new species (e.g. *Marchantia spp*, *Hornwort spp* and *Bryum spp*) are continually being identified in the process.

The results from EstimateS (Fig 2) show that sampling effort was probably sufficient as accumulation curves reached an asymptotic phase. Generally there was progressive increase in the number of species from smallest patches to the largest patches.

3.2. Species-Area Relationships

The regression analysis shows a significant relationship between fragment area and species numbers ($R^2 = 0.32; p = 0.0051$). However, visual inspection shows that three patches have anomalously high species numbers for their size (see Fig 3), and residuals analysis confirms that these are outliers. After excluding these, fragment size accounts for
almost three-quarters of the variation in species numbers among fragments. ($R^2 = 0.75, p << 0.001$) The outlier fragments are discussed in more detail below.

3.3 Multiple regression analyses:

Once all the data points indicating the sites were allowed to remain in the multiple regression model there was significant relationship (Table 2) below. However, the removal of the outliers significantly improved the predictivity power of the relationship between the fragment area, mean distance, distance to the nearest large patch and bryophyte species numbers (Table 3).

Bivariate plots of species numbers against the individual habitat variables showed that sites 1 and 5 had anomalously high species numbers in each case. These two plots were excluded from subsequent analyses.

With all three of the variable selection approaches, the stepwise multiple regression analysis retained only three of the five habitat variables (Table 3, Fig 4, 5 and 6) that together account for >70% of the variation in species numbers. The first variable to be entered in the forward model, and the one with the highest coefficient of determination (CD = 0.46), was patch area. The second variable to be entered was the mean distance to neighbouring patches, with an incremental increase of 0.12 in the CD, while the addition of distance to the nearest large patch increased CD by a further 0.09. Species numbers are positively associated with larger patches and negatively associated with increasing distance from neighbouring patches and from large patches.

The heterogeneity of the landscape is positively associated with species numbers ($R = 0.64; p = 0.001$) Fig 7 but this effect disappears when area is accounted for. This is because heterogeneity is positively associated with area.

3.4 Nested subsets

The analysis of nested subset patterns indicated that bryophyte assemblages in fragmented landscape exhibited a highly nested distribution ($T = 11.88^0, P < 0.001$), validating the probability inference made in the lower graph (Fig. 8) below, in which the
likelihood that observed structure was part of the simulated (i.e. randomised) scores is ~ 10^{-26}.

Table 1 Characteristics of the twenty-three West Coast renosterveld sites studied. Site numbers correspond to those indicated in Fig.1.

<table>
<thead>
<tr>
<th>Site</th>
<th>Area of patch (m²)</th>
<th>Species number</th>
<th>Mean area of nearest four patches (m²)</th>
<th>Distance to nearest large patch (m)</th>
<th>Mean distance to the nearest four patches (m)</th>
<th>Landscape heterogeneity scores</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>232200</td>
<td>38</td>
<td>20495.39</td>
<td>2208.14</td>
<td>194.713</td>
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<td>56000</td>
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</tr>
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<td>3479.69</td>
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<td>58789.04</td>
<td>3320.31</td>
<td>548.59</td>
<td>15.00</td>
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</tbody>
</table>
Figure 2 Species accumulation curve for bryophyte species from the entire fragmented renosterveld landscape.

Figure 3 The relationship between the number of bryophyte species and Ln fragment area in a fragmented renosterveld landscape. When three outliers were excluded (R = 0.86; p << 0.001) was highly significant.
Table 2: Stepwise regression results on the environmental variables

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>R</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.564</td>
<td>9.77</td>
<td>0.0051</td>
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<td>Mean distance to neighbours</td>
<td>206.151</td>
<td>0.597</td>
<td>11.65</td>
<td>0.0026</td>
</tr>
<tr>
<td>Distance to the nearest large patch</td>
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<td>0.285</td>
<td>1.855</td>
<td>0.188</td>
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</tbody>
</table>

Table 3: Stepwise regression results on the environmental variables

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>R</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fragment area</td>
<td>1.597</td>
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<td>16</td>
<td>0.00070</td>
</tr>
<tr>
<td>Mean distance to neighbours</td>
<td>189.837</td>
<td>0.675</td>
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<td>Distance to the nearest large patch</td>
<td>0.000858</td>
<td>0.6095</td>
<td>5.88</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Figure 4: Partial residual plot for Ln Area.

Correlation: $r = .81453$
Figure 5 Partial residual plot for mean distance to the four neighbouring patch.

Figure 6 Partial residual plot for distance to nearest large patch.
Correlation: $r = 0.63768$

Figure 7 Relationship between bryophyte species numbers and landscape heterogeneity.

Figure 8 Nestedness distributions of 72 species of bryophyte in 23 fragments in West Coast renosterveld. Species richness declines with size fragments. The temperature of the system is $11.89^0$ and the probability that this could be due to chance is $10^{-26}$. The boundary line delimited the unexpectedness, above it the absence and below it the presence.
CHAPTER 4: GENERAL DISCUSSION

The current study shows that bryophyte diversity in remnants of renosterveld is strongly affected by patch (fragment) area, habitat heterogeneity and various measures of isolation. The results of this study revealed that species numbers are positively associated with increasing patch size and negatively associated with increasing distance from neighbouring patches and from large patches. As expected fragment area showed a strong effect on plant diversity. Kemper (1999) reports that, there was no significant linear relationship between fragment size and species diversity in the system he studied. However, a majority of studies on fragmentation show negative influence on species diversity (e.g. Bond et al., 1988; Saunders and Hobbs, 1992).

The decline in species living in original habitat seems to be related to the proportion of original habitat lost. This effect of fragmentation on species area relationship and various measures of isolation as a result of agriculture in this vegetation reduces the size of habitat patches. At the same time creating barriers between fragments, this in turn affects diversity of bryophytes. The smaller the patch becomes, the less the number of bryophyte species. This decrease in species diversity is as a result of reduced space for expansion and limited microhabitat in such resulting small patches. However, this may vary depending on the degree of fragmentation.

Fragmentation leads to habitat loss, and this has a significant impact on the bryophyte species distribution and diversity. The more land lost, the more microhabitats for species are lost in the region, and in turn the fewer the chances for the bryophyte species to get a suitable habitat. Hence bryophytes species become vulnerable to extinction. In the case of renosterveld, in the south there are still many fragments. But most of the land to the west of this vegetation type has been affected by disturbance regimes and lots of land has been lost through cultivation with few remaining fragments. It is not easy to reverse this situation. However, where possible, bryophytes do extend their territories through recolonisation. This is evident from the open areas of renosterveld. For example at the edge of the renosterveld patches around farm settlements and in old fields which have not been ploughed for a period of time.
As earlier mentioned from the results, certain outliers were removed as they had anomalously high number of species. The removal of outliers improved significantly the predictive power of the relationship between the variables and species numbers. The anomalous numbers may be attributed to the following factors:

1. There were traces of ephemerals/annual shuttle species which were still present or surviving during the sampling period in such patches. Some of these were sampled earlier than the remaining patches, at the end of the wetter season.

2. Secondly, there were many suitable habitats which were present in those particular patches and also the nature of the surrounding landscapes was a contributing factor.

3. Some of the anomalous patches were sampled along with a very experienced collector (Prof. T. Hedderson). Thus it is possible that many rarer species were not found in patches that he did not visit.

Fragment area is an effective measure of species diversity; and this study shows that bryophyte species' numbers increased significantly with increasing patch area. At least, large patches have representative species. The results confirm the general validity of species-area relationships, and this has been shown before for other plant communities (e.g. Ouborg, 1993; Grashef-Bokdam, 1997; Honnay et al., 1999; Bruun, 2000; Krauss et al., 2003). Although some large fragments at some point were seen to accommodate few species, these few irregularities in the number of species appeared to have come as a result of mixed factors such as, the shape of fragment, limited microhabitats within a patch and sampling errors. The number of species that a habitat is expected to hold after a period of isolation is usually considered to be strongly area-dependant (Cox et al., 2003). The increase in number of bryophyte species can be attributed to the role of the patch size in metapopulation dynamics. The number of diaspores produced by a population in a patch may be directly dependent on population size which will in turn depend on the patch size. Large habitat patches will be a ‘target area’ for dispersing diaspores and will receive more of the diaspores than a smaller area. In addition, large fragments do not only support a higher original number of species, but are also characterised by a lower rate of subsequent extinction. This is presumably because they have more physical space or due to the spatial pattern of the vegetation, degree of rockiness and a greater resource base that can sustain a larger diversity of species or populations.
Contrary to the predictions of the increase in the number of species, in relation to the mean area of neighbouring patches, we could not find any effect of mean area of neighbouring patches on bryophyte species diversity. Without knowing the nature of these patches it is not feasible to say with any certainty why this relationship does not hold. However, we may speculate that, this is perhaps because there are fewer chances for species to find suitable microhabitats or landing on suitable patch in the surrounding areas.

Although fragment area has a greater influence on species diversity, the landscape heterogeneity (habitat heterogeneity) within the patch, all else being equal, is also shown to increase species numbers. Increasing habitat heterogeneity tends to increase the bryophyte species numbers, but due to close correlation with habitat area this effect was eliminated in multiple regressions. The increase in diversity of species is due to the provision of essential resource requirements. It is of greater importance than the landscape parameters in ensuring a species’ persistence within a fragment (Simberloff and Abele, 1982). The more heterogeneous the patch, the more the number of species in a habitat patch. The diversity will be higher in habitats with more ecological niches (MacArthur et al., 1962) or in a landscape with more habitats (Wiens, 1995). Thus vegetation changes such as those driven by secondary succession can directly affect the biodiversity of the system. Therefore, increasing heterogeneity or patchiness leads to an increase in biotic diversity.

Distance between habitat fragments, is shown to be another important key parameter for species distribution and diversity, especially to species with short distance dispersal ranges. The isolation effect on plant species are mainly found for plant species with low dispersal abilities. Stepwise regression results obtained show that the mean distances to the neighbouring patch were highly associated with the number of species. The number of species decreased with an increase in mean distance. Patches that are closer and surrounds the patch under investigation tend to show greater similarity in species richness and diversity to the patches under investigation. At the same time, they tend to have more or less the same number of species. This is accounted for by the ability of bryophyte diaspores to disperse between the patches. Large diaspores size will travel short distance in relation to small size diaspores which will travel long distances. Studies have shown
that the high variance of the mean distance indicate that the patches are aggregated together and are subsets of habitats lying close to each other, and may favour the spread of species, where as their spread between habitats will be less for greater distance.

Distance to the nearest large fragment was found to have a negative significant effect on bryophyte plant species diversity. While studies of species groups have generally shown no or weak isolation effects (Ouborg, 1993; Köchy and Rydin, 1997; Honnay et al., 1999; Bruun, 2000). There is a decrease in the number of species with increasing distance to the nearest patch. The longer distance created between patches, as a result of fragmentation, the less the dispersal of diaspores and ability of at least some species to tolerate or utilise the habitat matrix. The ability of species to colonize a fragment depends to some extent on the distance of the fragment from other areas of native habitats (Saunders et al., 1991). The longer the distance between habitats, the less the chances for the species to reach others patches, with an exception of spores with high dispersal ability, which travel longer distances.

Although edge effects were not formally measured, it was observed that edges of habitats were rich in bryophyte species. Although the distance between fragments and surrounding agriculture field is shorter, there are high chances that those spores which land in agricultural fields, die at the early stage of their development. This is because of the continuous cultivation of the fields.

Bryophyte species assemblages in renosterveld vegetation display a nested distribution among the sites; this suggests that prior to fragmentation of the landscape the species pool had a heterogeneous distribution, possibly owing to the high environmental diversity and the complex biogeographic history of this type of vegetation. Habitat fragmentation has influenced local extinction and colonisation processes which have in turn resulted in a nested arrangement of diversity among sites. Therefore, a change from a random to a non-random distribution of bryophyte species in the landscape studied may have been influenced by Habitat fragmentation. Nestedness is common in nature (Wright et al., 1998) however, the level of nestedness we report among renosterveld fragments (T = 11.88° P < 0.001) is notably higher than that reported in other fragmentation studies.
Fragments/islands at different distances from a source of colonists could produce a nested set of species (Patterson and Atmar, 1986). It is worthy to note that, good dispersers would be found in all communities, even the most isolated and depauperate, while the least dispersive species would be found only on the closest (presumably most diverse fragments). Distance effects on nestedness should be strongest in islands or fragments with wide variation in isolation distances, colonised by species with a range of dispersal abilities comparable to the range of distances provided by the fragments.

Fragment area potentially at some point seems to complicate the picture. Most renosterveld (set of coherent fragments) have different sizes of fragments, and even the more dispersive species will be absent from the nearby islands if they are sufficiently small, while less dispersive species may persist almost indefinitely on large far islands that they happen to reach, breaking the distance nested pattern. Distance and area may also enhance one another in their effects on nestedness if the islands closer to the source tend to be bigger.

Nestedness in this type of vegetation can result from different needs for area by different species. Species with large area requirements will only be found on large islands, while species that can survive even on smallest islands are likely to be found everywhere. Consistence with this mechanism, we found that nestedness is positively associated with the disparity in size between the largest and smallest islands sampled. On this note, area effect on nestedness should be strongest in fragments with wide variation in area, colonised by species with wide variation in area requirements.

The decline in species diversity and abundance has most commonly been linked to the size of the remnants and their degree of isolation (e.g. MacArthur and Wilson, 1967; Diamond, 1976; Simberloff, 1976; Terborgh, 1976). The smaller a fragment is, the greater the chances are that a population will be viable while the greater the isolation the less likely it is that migrants will bolster unsustainable populations (sensu the ‘rescue effect’ of Brown and Kodric –Brown, 1977; Soulé et al., 1988). If the declines are area dependant, the disappearance of species from a series of fragments will often follow a ‘nested’ pattern with smaller fragments containing a subset of species occupying larger reserves (Patterson and Atmar, 1986; Patterson, 1987).
Bryophyte flora recorded, and as shown by the results of the analysis, were highly consistent with this proposed nested system, with species exhibiting a more or less orderly absence from fragments as a function of decreasing area. The absence of a species within fragments is often considered to depend on a number of factors including individual spore size, spatial requirements, population densities, dispersal abilities, degree of specialisation and chance (McNab, 1963; Laurance, 1990; Redford and Robinson, 1991; Bright, 1993; Chiarello, 1999; Nupp and Swihart, 2000). Patterns of nestedness can provide some insight into the species that are most vulnerable to the fragmentation process.

In accordance with previous conservation measures, it is possible to establish a system that conserves at least 10% of renosterveld in these areas, a conservation goal recommended by the IUCN (World Conservation Unit) (McNeely, 1993). The conservation of bryophyte of this vegetation has not been the focus of research, but for long-term survival of the bryophyte of this vegetation, it may be suggested that existing measure of this vegetation seem appropriate as this is the only remaining option. However, the remaining land is not enough to preserve all bryophytes of this vegetation. Since bryophytes are cosmopolitan with wide distributional range, areas covering large geographical range would be an appropriate strategy for conservation. In addition, remnants should be surveyed using cost–effective techniques (Margules and Austin, 1991) in order to stratify remnant vegetation into meaningful categories and identify specific localities of rare and endemic species. More to this, particular attention should be given to threats, especially the potential for clearing flatter land on the larger remnants in the west and where possible the fragments which are not included in the managed areas should be the focus. The priority areas for inclusion in the system should be identified on the basis of irreplaceability (presence of unique attributes) and on actual and potential threats. This can be achieved by liaising with the private landowners to ensure that the remaining remnants are managed sympathetically.
5. CONCLUSIONS

In conclusion, bryophyte plant species have been recorded, well documented and are abundant in western renosterveld. Except the mean area of neighbouring patches, which showed no effect on diversity of species, other remaining parameters (habitat area, mean distance to the nearest patch, distance to the nearest large patch, and landscape heterogeneity) are all predictors explaining bryophyte community diversity. The results stress the point that habitat area and increasing habitat heterogeneity have a significant effect and are most important determinants of plant diversity. However, continuous utilization of this vegetation type by human activities which results into habitat fragmentation is a threat and leads to decline in bryophyte diversity.

It is clearly noted that small fragments are likely to continue to lose species as a result of a variety of processes. Small fragments still appear relatively intact in terms of maintaining plant species diversity and biological attribute representation and must therefore not be neglected. Fragmentation of these areas has been recent and long term persistence of these and smaller patches are questionable in the absence of intensive management.

The anthropogenic habitats located throughout the landscape, represent a large gradient of transformation and these habitats have different effects on species dynamics and biodiversity. Habitat fragmentation does not act directly on the species assemblages or groups. It is the changes in environmental conditions that act on species (specifically on each population) in an independent manner. So the change in the number of species of each group in a given area is the cumulative result of specific events. In conservation perspective, the largest and richest renosterveld fragment is not sufficient to preserve bryophyte of this landscape. The maintenance of a set of renosterveld fragments extensively distributed in proximity to agricultural fields appears to be an appropriate strategy for maintaining plant diversity of the renosterveld vegetation.

The vegetation has high biodiversity and for a long time has been affected by fragmentation; hence there is a significant need to prevent the decline of this biological diversity. The fragments 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. Where formal reserves are not feasible, every effort must be made to demonstrate and sensitise the benefits to farm-scale economies of retaining and managing fragments, especially the large ones, since on farm conservation is seen to be the only option. Furthermore, these remnants provide reservoirs of biodiversity for restoring natural pastures should environmental change or economic factors result in cropping becoming unsustainable. Therefore, not only the fragments are the only option for conserving renosterveld and what is there-in, they may have direct economic value in the future. The challenge today for researchers is to demonstrate the benefits to the farmers of what services that will be offered in the end by these fragmented ecosystems. Assuming that the actual size of the fragments will be retained, regular records of occurrence and abundance will determine the long-term patterns of persistence of categorise of bryophytes in the vegetation. Further studies, especially the effect of fragment area and measures of isolation at the genetic level within and among populations should be the next focus to ensure effective conservation or restoration activities.
REFERENCES


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- 37 -


Scott, J., 1986. The effects of grazing on the alpha diversity of the west coast renosterveld at the farm Eensaamheid. unpublished student project, Department of Botany, University of Cape Town.


7. APPENDICES

Appendix 1

Photos: The photos shown on the hard cover of this thesis are some representations of the species found in West Coast renosterveld.

The *Grimmia laevigata* is at the centre of the hard cover on rock substratum.

The remaining photos are for *Bryum argenteum* on lower left and *Tortula muralis* on the lower right hand of the *Grimmia laevigata* photo.

Appendix 2

Different habitat classification measurements that were used in understanding landscape heterogeneity are clearly shown. Variables of the landscape were visually selected from each fragment visited and each recorded variable were given score of (0, 1, 2 and 3).

1. Soil type (Sand = 1, Clay = 1, Silt = 1, Sand + Clay = 2, Sand + Clay + Silt = 3).
2. Rockiness (no rock = 0, some rock = 1, rocky = 2).
3. Site aspect (presence of shrub cover = 2, Succulents = 2, Renosterbush = 2, Slope = 2, Hill = 2, Flat = 2, Valley = 2, Trees/large shrub presence and cover = 2, North facing = 1, South facing = 1, West facing = 1, East facing = 1).
4. Surrounding vegetation (Wheat field = 0, Eucalyptus = 1 Vine = 1 Aliens = 1).
5. Fragment size (Very small = 0, Small = 1, Medium = 2, Large = 3).
Appendix 3

Table 4 Representation of presence-absence of a species recorded and number of habitat occupied from twenty-three sites of West Coast Renosterveld Vegetation, Swartland, South Africa.

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<tr>
<th>Taxon</th>
<th>Site</th>
<th>Number of habitat occupied</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Acaulon recurvatum</td>
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<td>1</td>
</tr>
<tr>
<td>Acaulon spp</td>
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<td>1</td>
</tr>
<tr>
<td>Anacolia breutelii</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Archidium spp 1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Archidium spp 2</td>
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