Vegetation change and vegetation type stability in the Cape of Good Hope Nature Reserve 1966 – 2010

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Abstract

Vegetation stability was investigated within the Cape of Good Hope Nature Reserve by incorporating three vegetation surveys spanning a 44 year time period. The goals of this study were to investigate changes in overall species diversity within the reserve, stability of community composition within and between sites, and which factors are influencing stability. A survey was conducted on 26 vegetation plots across the reserve. Data from this survey and two previous surveys was used to compare species diversity between time periods. Vegetation compositional similarity was also compared between sites. I tested for the effect of difference in vegetation age and soil type as predictors of vegetation groups. Results showed an overall decrease in species diversity. Analysis of vegetation groups showed that vegetation types are mostly stable as current vegetation can be predicted by groups based on 1966 data. Vegetation is influenced significantly by fire history and soil types.

Introduction

The high species diversity and complexity of fynbos has been studied extensively in terms of spatial patterns and disturbance regimes over the course of the last few decades (Privett et al. 2001). Unfortunately, these have mostly involved once-off or short term temporal studies due to practical constraints, and the dynamics of fynbos ecosystems have generally been poorly studied over a longer time-scale. Long-term vegetation change in fynbos as well as other vegetation types in South Africa is suspected to have taken place, but little exists in the way of data to support of reject this argument (Mentis 1989).

It is of great importance to study vegetation change on a temporal scale in order to determine vegetation stability over differing time periods (Mentis 1989). If unstable, is there a specific direction of change and if so what will the likely magnitude of change be over given time period? If directional, is this change due to a change in climatic conditions or other conditions such as disturbance regime? Particularly in the Cape Floral Region with such high diversity including species with very specific habitat requirements, such changes could cause species to disappear from some areas or become dominant in others as has been predicted by models incorporating climate change and its effect on the Fynbos Biome and selected species of Proteaceae (Midgley et al. 2003).

In the face of habitat loss from anthropogenic sources it is important to have an idea of how vegetation is likely to change in order to develop effective conservation strategies and management plans (Midgley et al. 2003). An area that is currently of conservation value could lose that value in future due to the effects of disturbance or global change if these effects make conditions unfavourable for survival of local species of conservation priority value. Alternatively, areas that currently have little biodiversity value could become important refugia for priority species or communities in future due to range shifts of rare species into such areas.

People are reliant on ecosystem services provided by natural vegetation, for example the provision of fresh water (van Wilgen et al. 1998). Knowledge of a directional change in a vegetation type could be beneficial as it may alter the abundance or quality of water supply in future. By studying temporal vegetation stability and identifying the drivers of change, this knowledge could be used to predict larger scale changes, both spatially and temporally.

The aim of this study is to improve our understanding of fynbos plant community dynamics through time by analysing three surveys of the same set of vegetation plots over a 44 year period. The biodiversity records from different time periods along with data for a number of environmental and disturbance variables can be used to investigate vegetation turnover in both space and time. My goal is to detect any changes in vegetation composition and to test for the affects of a set of potential drives of this change.

The vegetation of the Cape of Good Hope section of Table Mountain National Park (Cape of Good Hope Nature Reserve) has been studied over a number of decades, with permanent plots established and surveyed in 1966 (Taylor 1984a) and surveyed again in 1996 (Privett et al. 2001). Vegetation in the Reserve is highly dynamic with an average of nearly 40% species turnover at local sites over the 30 year period between 1966 and 1996. Thuiller et al. (2007), however, found that species presence and abundance were stable at the metacommunity (reserve) scale over that period. For example, *Leucadendron laureolum*, a common non-sprouting species, showed a high change in distribution within individual sites, but no overall change in abundance or frequency of occurrence across all sites (Privett et al. 2001).

Frequency and seasonal timing of fires varied greatly across the reserve and the fire regime was found to be at least partially responsible for fynbos composition. There was a negative relationship between post-fire vegetation age and species diversity at both times of vegetation surveying (Privett et al. 2001). Different species respond positively to different components of the fire regime, such as season of burning (Bond et al. 1984, Cowling 1987, le Maitre 1987, Midgley 1988), and growing conditions following a fire (Cowling 1987, le Maitre 1987). Although autumn has been shown to result in optimum seedling establishment and post-fire recovery, variation in season of burn and other aspects of fire regime is likely to be an important factor in sustaining high levels of plant diversity in the long-term within an area of fynbos (Cowling 1987).

In this study, I investigate the stability of the vegetation of the CGHNR over a 44 year period by performing a contemporary field survey of the permanent plots for comparison with the existing surveys from 1966 and 1996. In particular, my questions are:

1. Has species diversity in the CGHNR as a whole changed over the last 44 years?
2. Is community composition within local sites stable over time?
3. Does the compositional similarity between sites remain stable over time?
4. Is the compositional similarity between sites influenced by soil type, fire history or spatial distance?

Methods

Study site description

The vegetation of the Cape of Good Hope Nature Reserve consists primarily of Peninsula Sandstone fynbos and Hangklip Sand fynbos, with a narrow band of Cape Flats Dune Strandveld along the coastline (Mucina & Rutherford, 2006). Taylor (1984b) proposed a similar classification, identifying three broad vegetation types: Coast fynbos (containing four fynbos types), Inland fynbos (containing six fynbos types), and small areas of broad-leaved thicket of more subtropical affinity (containing two vegetation types). The fact that the Reserve contains a high species diversity and complexity, as well as permanent monitoring sites with previous data and detailed management records for the reserve since 1966, make this a most suitable location in which to conduct a study of temporal effects on fynbos vegetation.

Field data collection

Taylor (1984a) laid out 100 vegetation plots mostly in an evenly spaced grid pattern throughout the CGHNR. These plots were marked with cement poles in the south-western corner of each plot, and each plot was laid out 10 metres true North and 5 metres East of the marker to produce a plot of $50m^2$. The size of the plots was chosen by doing a preliminary study of how many species were likely to be recorded in 350 plots across the Peninsula of varying sizes, from $100m^2$ down to $20m^2$. Regression equations showed that a $50m^2$ plot was the most effective size in terms of both maximizing recorded diversity and minimizing surveying time. A rectangular plot also increases the environmental gradient within the plot compared to if it were square. Each plot was divided into 10 quadrats of 2x2.5m each to facilitate recording species abundances. A species list was recorded for all perennially identifiable species noting presence and abundance of individuals. Abundances were converted to a five-category system that corresponds to Acocks' (1975) system of abundance symbols. Annual or seasonally apparent species were recorded where seen for descriptive purposes. Photographs were taken for some but not all plots. Privett (2001) was able to relocate 81 of these plots and resurvey them using the same method as described by Taylor (1984). Since that time a few more have permanently been lost and at the time of the present survey only 67 had been relocated. The contemporary survey followed the same protocol as the two previous studies. Data was collected during August 2010 during which time 26 plots were surveyed. Species present were recorded for abundance of individuals and percentage cover within each quadrat. Photographs were taken of each plot and surroundings to compare with previous photos taken by Taylor (1969), Privett (2001) and other workers (SAEON archives).

Fire history and environmental data

Fire data was derived from SANParks fire history GIS database. Geographical distances between plots were obtained from GIS data. Soil types were deduced by overlaying plot localities on a soil map of the reserve (Smith-Bailie 1976).

Data Analysis

Because of the small sample number of plots surveyed during the August 2010 survey, data analysis was performed on data from the 26 plots surveyed in 2010, as well as on the full set of 81 plots for 1966 and 1996. The analyses were performed


Cape Point Vegetation Survey Sites

Fig 1. Study area and location of plots included in the vegetation survey. Plots estimated and located refer to the present time (2010).

(Map courtesy of Adam Wilson)

using the ade4, ape, labdsv, picante and vegan packages in the program R 2.10.1 (R development Core Team 2010).

Diversity and meta-community stability over time

Changes in species diversity across the reserve were assessed using species accumulation curves (Coleman et al. 1982). The species accumulation algorithm used a randomization procedure with 1000 permutations (Fig 2). The 81 plot datasets were used from the 1966 and 1996 survey, with the 26 plots incorporated from the 2010 survey. Results based on the same set of 26 plots for all three surveys were qualitatively the same. Temporal turnover in species composition was investigated by producing histograms of the proportion of turnover within all plots between 1966 and 1996, and between 1996 and 2010 (Figs 3 and 4). Two different methods of dissimilarity measure were used. Sorensen's coefficient was used to analyze presence/absence of species, while Bray-Curtis distance was used to analyze abundances of different species, allowing investigation of the effect of relative abundances of different species on the relationship between plots. The designdist function in the package vegan (Koleff et al. 2003, Legendre & Legendre 1998) was used to produce dissimilarity matrices for the data.

Classifying vegetation types

Vegetation can be classified into similar groups based on one or a selection of species common to a number of plots within the survey area. This is necessary in order to test stability of types of vegetation over time. It would be tedious and of limited value to attempt to analyse each plot in isolation as it is hard to make judgements as to how much change counts as a shift to a different type of vegetation. By grouping vegetation based on the presence or abundance of species within plots, it can be determined how many types of vegetation are present, as well as the distribution of these vegetation types throughout the area of study. Surveys from different points in time show whether there is change in species composition over time, and thus whether different vegetation types change in abundance or area of occurrence over time.

Species presences and abundances may be tied to certain vegetation groups, and so a change in occurrence of a vegetation type can allow inferences to be made about changes in associated species' demographics.

Taylor (1966) used an association analysis method of clustering plots into different vegetation types depending on species common to different plots (Williams &

Lambert 1959). This works well in a situation in which different vegetation types are temporally and spatially discrete, with well-defined boundaries separating them across which at least species typical of these units are not present. This is true for the broader vegetation types defined by Acocks (1975), these being mountain fynbos and coastal thicket. However, within the fynbos category there are a number of factors influencing species composition. High diversity as well as high spatial and temporal species turnover between sites experiencing the same conditions mean that not all characteristic species will necessarily be present in a small plot. A number of species are tolerant of a wide variety of conditions but may for example be dependant on fire for recruitment and senesce after a few years following a fire (Cowling 1987). Association analysis using such species may group plots that have burnt recently but which may otherwise be rather different in terms of the rest of the vegetation present.

Distance based methods, which incorporate all species present within a site, should provide a better basis on which to cluster sites into similar vegetation types because more of the information of what makes up the vegetation of the site can be incorporated, and so analysis is less dependant on the effect of individual species. These distances are based on either presence and absence or abundance data. Sorenson's coefficient method was employed by Privett (2001) to analyze changes in floristic composition between his survey and Taylor's survey. Taylor (1984a) had used Association analysis and Braun-Blanquet to try to group plots into groups o similar vegetation types. A potential problem of presence/absence data is the equal weighting of all species irrespective of abundance. Incorporating abundance downweights the influence of rare species. However, many different methods have been developed for assessing species turnover (Koleff et al. 2003) which can lead to ambiguities in assessments incorporating multiple studies using different methods, or a single study using a single method, which may not be the most appropriate method in the particular case.

In this study I employ both the Sorensen's coefficient, which measures turnover between plots based on the presence or absence of species, and Bray-Curtis distance, which is analogous to Sorensen's coefficient but weights the importance of species by their relative abundance.

Distance measures are used to generate matrices of the distances between plots which are in turn used as a basis by which to cluster plots into vegetation types. Unfortunately, generating a cluster diagram from a distance matrix involves unavoidable distortion of the distance between plots because not all plots in one cluster share exactly the same distances to plots in other clusters.

Different methods of clustering plots using matrix data with Sorensen's and Bray-Curtis distances were investigated for the degree of distortion involved in clustering plots. Cophenetic plots can be used to investigate the degree of distortion generated by a clustering algorithm. These plots are produced by comparing the original matrix of distance between plots with a matrix obtained by reading the distances off the cluster diagram. By assessing the correlation coefficients for cophenetic plots produced using each method it was found that the "average" method produced the least distortion of the data for both dissimilarity measures (see Appendix 2).

Cluster diagrams were drawn using this method with Sorensen's coefficients and Bray-Curtis distances to illustrate relationships between different plots at all three time periods. The 1966 data was used to cluster plots into eight vegetation groups based on a cut-off level of similarity which would produce this number of groups from the data. More than eight groups led to a number of single plot groups which is not very useful for analysis, while less than eight produces groups will result in underestimating levels of change in vegetation types. Plots were drawn using the 1996 and 2010 clustering data but colour-coded with 1966 vegetation groupings to illustrate stability of these groups (Figs 7 and 8). The 26 plots from all three time periods were also combined into a single large cluster diagram of 78 plots for each dissimilarity method to see whether the same plots will group together at different times (Fig 9).

Graphs of dissimilarity data were also plotted for 1966 vegetation distances against 1996 vegetation distances in one graph and 1996 against 2010 data in the second. This was done for both Sorensen's coefficient and Bray-Curtis distances (Figs 5 and 6).

Testing vegetation type stability through time, and the influence of soil type, spatial distance and fire history

The effect of fire history was analysed by noting vegetation age (years since last fire) for each plot at each time of survey. Vegetation age difference was plotted against vegetation dissimilarity data for each survey for Bray-Curtis distance and Sorensen's coefficient methods (Figs 10 and 11). Histograms of relative plot ages were drawn to show the spread of different aged vegetation in the reserve at the different survey times (Fig 12).

Spatial distance was plotted against vegetation dissimilarity for 1966 and 1996 for all 81 plots surveyed at these times, in order to investigate whether geographical separation has an effect on vegetation (Figs 13 and 14).

In order to statistically determine similarity in spatial turnover between plots and plot groupings at different times, Mantel tests (Mantel 1967), and a Multi Response Permutation Procedure of Within- versus Among-Group Dissimilarities (MRPP) (McCune & Grace 2002) were performed on the distance matrices. A Mantel test determines the probability of correspondence between two data matrices by randomly swapping values within them. A high z-statistic relative to the null distribution of generated values indicates that the data sets are correlated to the point that random swapping of values will decrease correspondence between data sets. A MRPP test determines whether average within-group dissimilarity of plots is lower than between different groups, which can be seen by expected and observed delta (average distance) values. Performing a Meandist test (van Sickle 1997) on the data shows the average within-group dissimilarity as well as that between each group as a data matrix. This shows which grouping variables, if any, are responsible for the resulting vegetation groups.

A Mantel test was performed separately on the Bray-Curtis distance and Sorensen's coefficient matrix data between different time periods. This was to assess the level of correspondence in terms of vegetation difference at one time from the difference at the time of the preceding survey. Mantel tests were also performed on vegetation dissimilarity data as predicted by vegetation age at the time, and subsequently as predicted by geographical distance between plots. A table is drawn up with the z-statistic and p-value from each test (Table 1).

MRPP tests were performed on three predictors of vegetation groupings in terms of Bray-Curtis distance and Sorensen's coefficient. These were the 1966 vegetation type groups, vegetation age at time of each survey, and basic soil types. Table 2 shows the observed versus expected delta value for each test, as well as p value.

Results

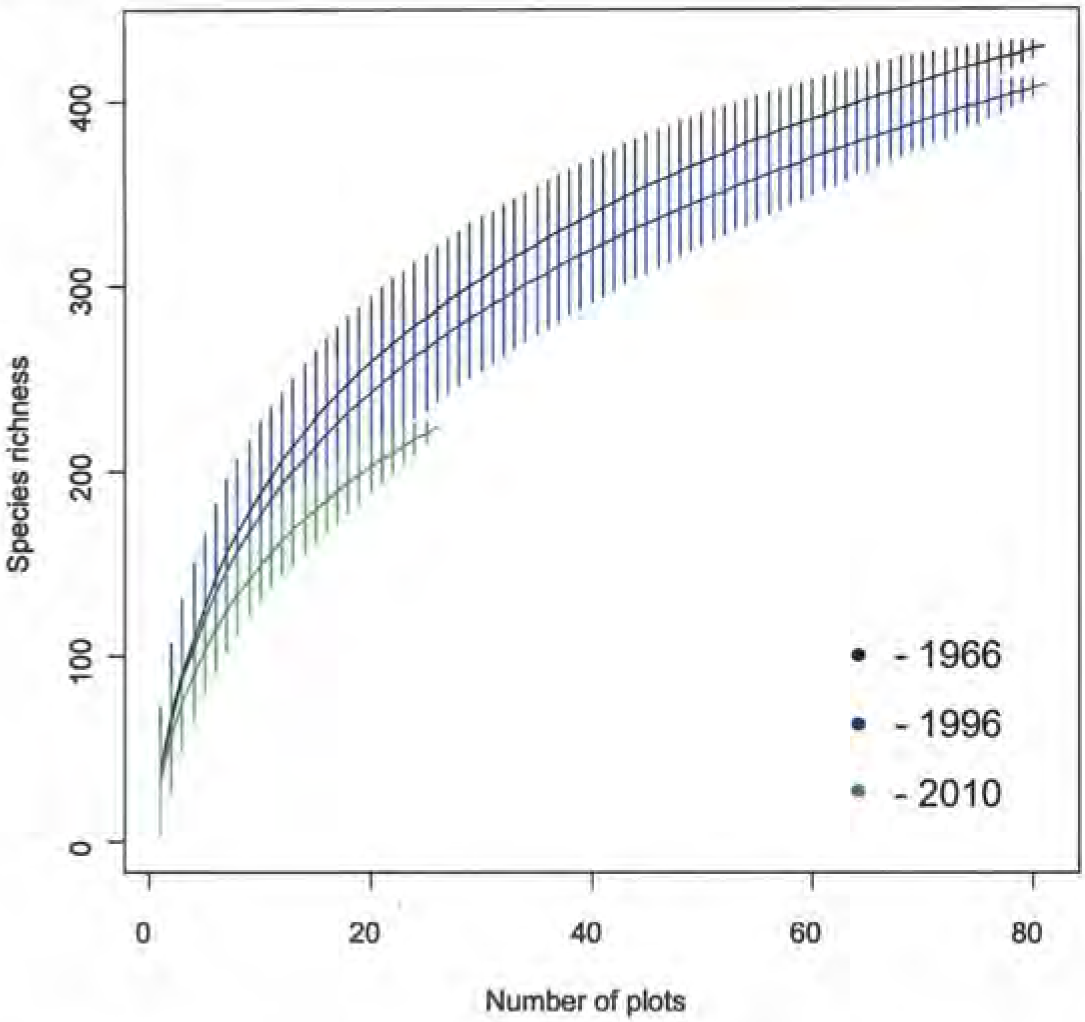


Fig 2. Species accumulation curve for plots from all three surveys

Diversity and metacommunity stability over time

The species accumulation curves of all three surveys (Fig 2) showed a decline in predicted species richness across all plots from 1966 to 1996, and an even greater decline from 1996 to 2010. This was not taking into account if species were present in the surrounding area but only those which were recorded in plots. Although fewer plots were surveyed in 2010, when a species accumulation curve was produced for only the plots surveyed during all three time periods the same trend was observed. After the 26th plot in 1966 there were 290 species predicted, while in 1996 there were 270 and in 2010 only 220 species were predicted. That equates to almost a 25% decrease in species richness.

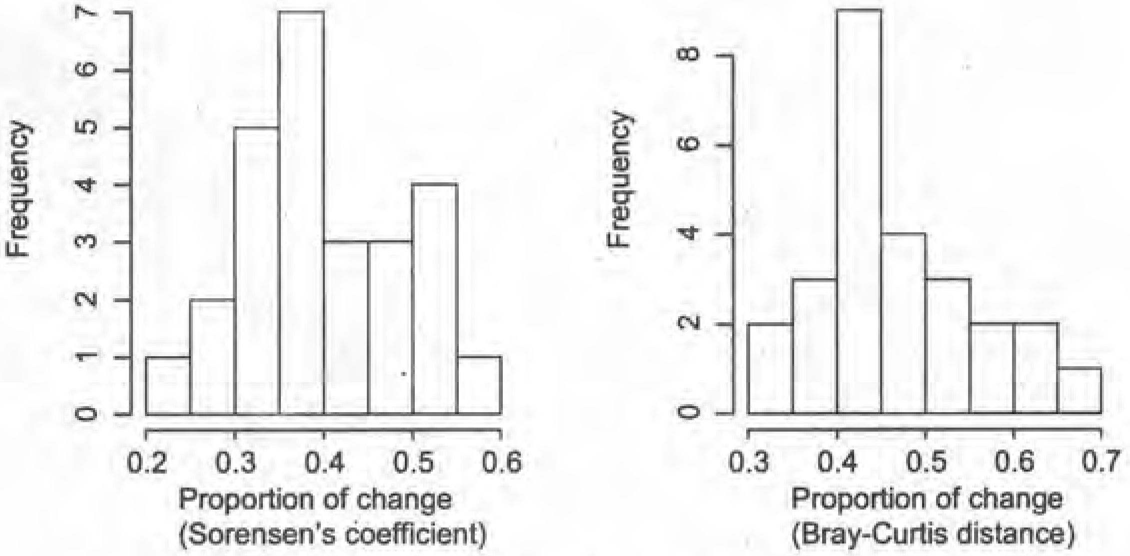


Fig 3. Histogram of turnover within 26 plots between 1966 and 1996 using two different dissimilarity measures

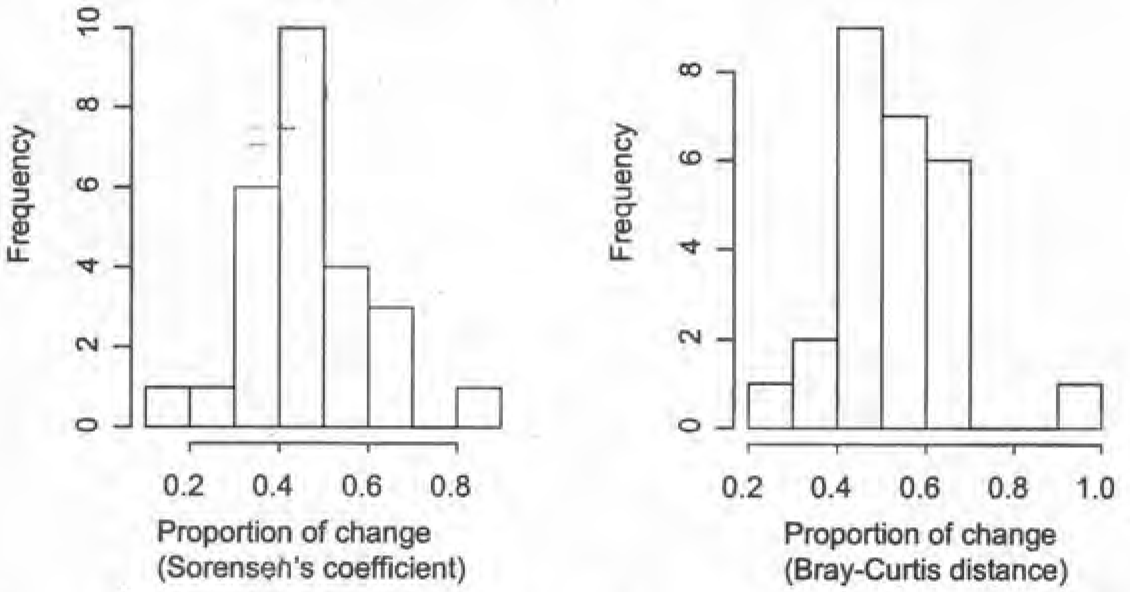
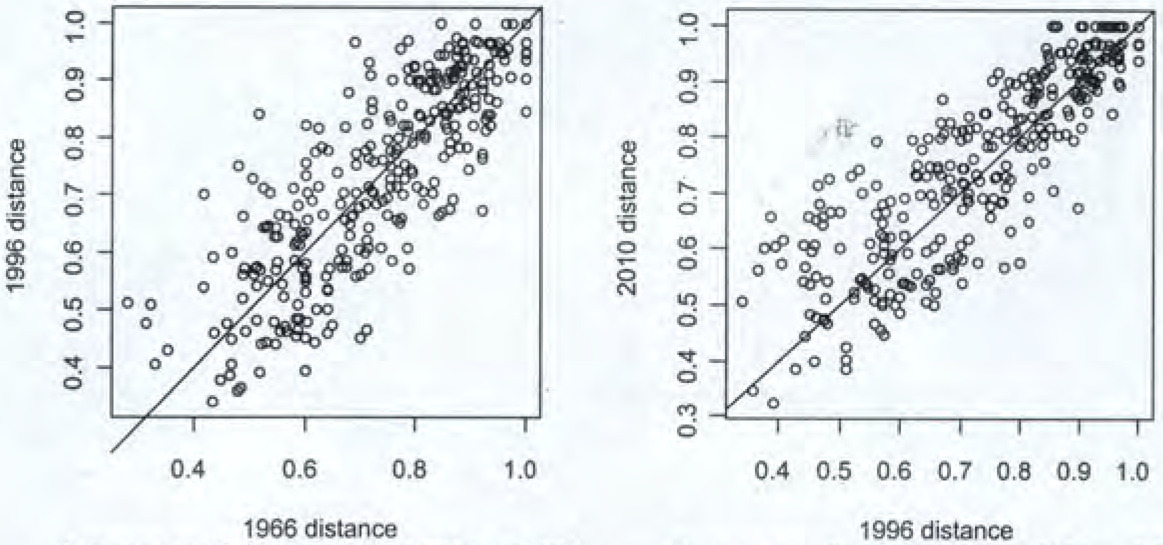


Fig 4. Histogram of turnover within 26 plots between 1996 and 2010 using two different dissimilarity measures

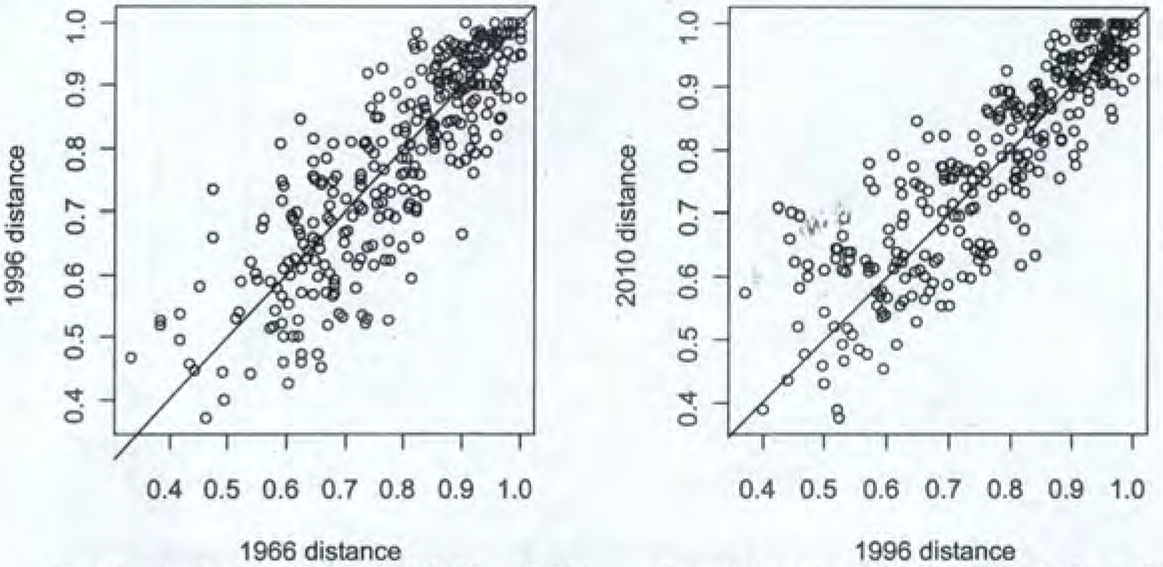
The histograms of species turnover using the two methods (Figs 3 and 4) showed the highest frequency of plots to have a turnover of around the 0.4 region during both time comparisons. However, between 1996 and 2010 the frequencies of turnover were more spread out but also higher than in the period 1966 to 1996. There was shown to be a higher frequency of high turnover in plots between 1966 and 1996 using the Bray-Curtis distance method (0.4-0.45) as opposed to the Sorensen's coefficient method (0.3-0.35). The lower and upper limit of turnover is higher in Bray-Curtis than in Sorensen's coefficient.



Sorensen coefficient, z stat=190.6841, p<0.001

Sorensen coefficient, z stat=196.6191, p<0.001

Fig 5. Graphs showing change in plot distances between surveys, using Sorensen's coefficient dissimilarity. Mantel test results below each graph.



Bray-Curtis distance, z stat=212.0536, p<0.001

Bray-Curtis distance, z stat=214.0569, p<0.001

Fig 6. Graphs showing change in plot distances between surveys, using Bray-Curtis distance dissimilarity. Mantel test results below each graph.

Distances between plots over the 30 year time period do not change drastically from the first survey to the second, although there is still a level of variability as seen in deviation from the diagonal line (Figs 5 and 6). They do correspond significantly according to the Mantel test (p<0.001).

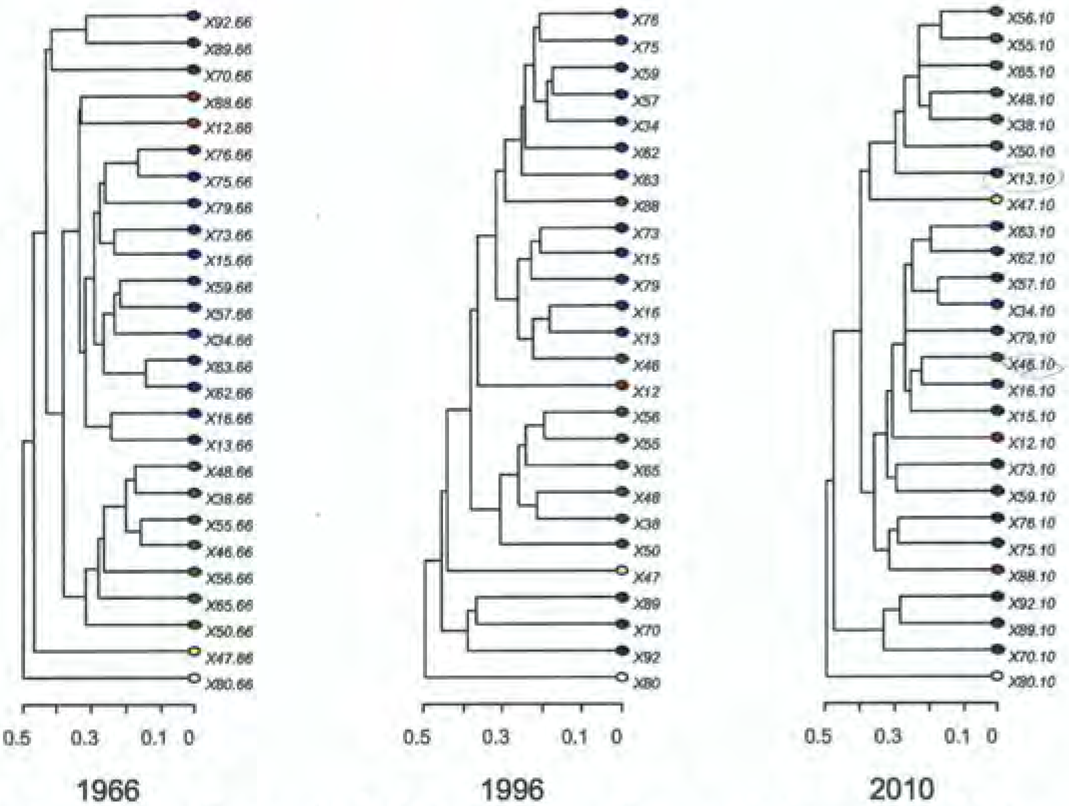


Fig 7. Cluster diagram of plots for three time periods grouped into vegetation types using Sorensen coefficient. Colour coding in all diagrams indicates vegetation type inferred from 1966 cluster analysis.

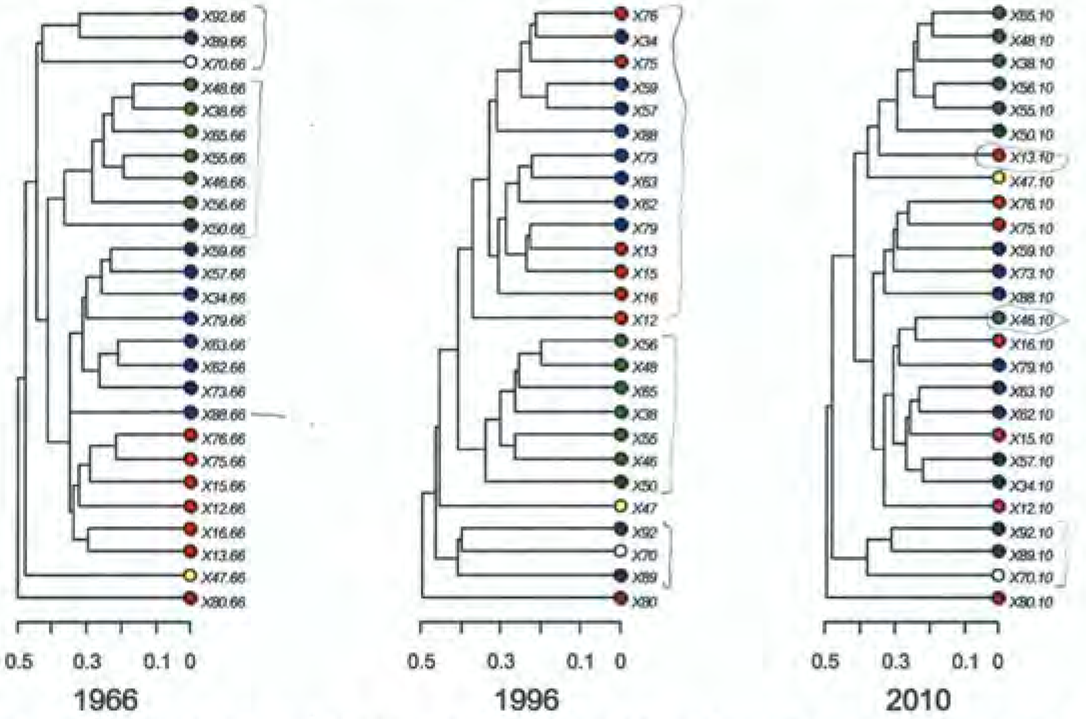


Fig 8. Cluster diagram of plots for three time periods grouped into vegetation types using Bray-Curtis coefficient. Colour coding in all diagrams indicates vegetation type inferred from 1966 cluster analysis.

Vegetation type classification and stability through time

Cluster diagrams (Figs 7 and 8) grouped vegetation into eight types. Plot 80 is coastal scrub, which supports its placement away from all other plots. The largest groups using either method are light green, representing damp restioid fynbos (see Fig 15), while blue and red represent drier rocky fynbos (see Fig 16). The latter two groups are less well defined or conserved through time. The light green group appears to be the most conserved of the large groups, while red and blue are generally conserved with respect to the other vegetation types, but there is considerable mixing between them over time. That most of the red group of the Bray-Curtis distance data is included in the blue group using Sorénsen's coefficient suggests that species compositions associated with both groups are similar and it is more the dominance of certain species in some of these plots that cause a bigger divide within this group under Bray-Curtis distance. Plots 70, 89 and 92, although classified as two groups on the cluster diagrams, are well conserved as a group in both 1996 and 2010 (see Fig 17). Plot 47 is an anomalous plot not grouping anywhere near any other plot in 1966 or 1996 but in 2010 it is close to the light green group. The same trend is observed with this plot using both clustering methods. Plot 46, however, was well nested within the light green group in 1966 but in 2010 is found within the blue and red group. Plot 50 is grouped in Bray-Curtis distance on its own but always groups closer with the light green group than any other group.

Figure 9 shows that all plots from different surveys cluster very well within 1966 vegetation groups for Sorensen's coefficient, while red and blue groups are mixed for Bray-Curtis distance. Other than that, plots are generally closer to their past vegetation state or other plots within their vegetation group than plots from other groups even after 30 or 44 years.

Influence of fire history on compositional similarity between sites

Vegetation dissimilarity plotted against difference in vegetation age for the 26 plots in all surveys (Figs 10 and 11) shows a general pattern of clustering towards the top left corner of the graph, showing that while similar aged plots may be relatively similar or very different, plots that differ greatly in age will tend to be more different. This is shown to be significant except in 1966 for Sorensen's coefficient method using Mantel tests (Table 1). When a Mantel test is performed on the whole data set of 81 plots the significance increases. However, a Mantel test is not an appropriate statistic to use because the relationship in the data is not linear.

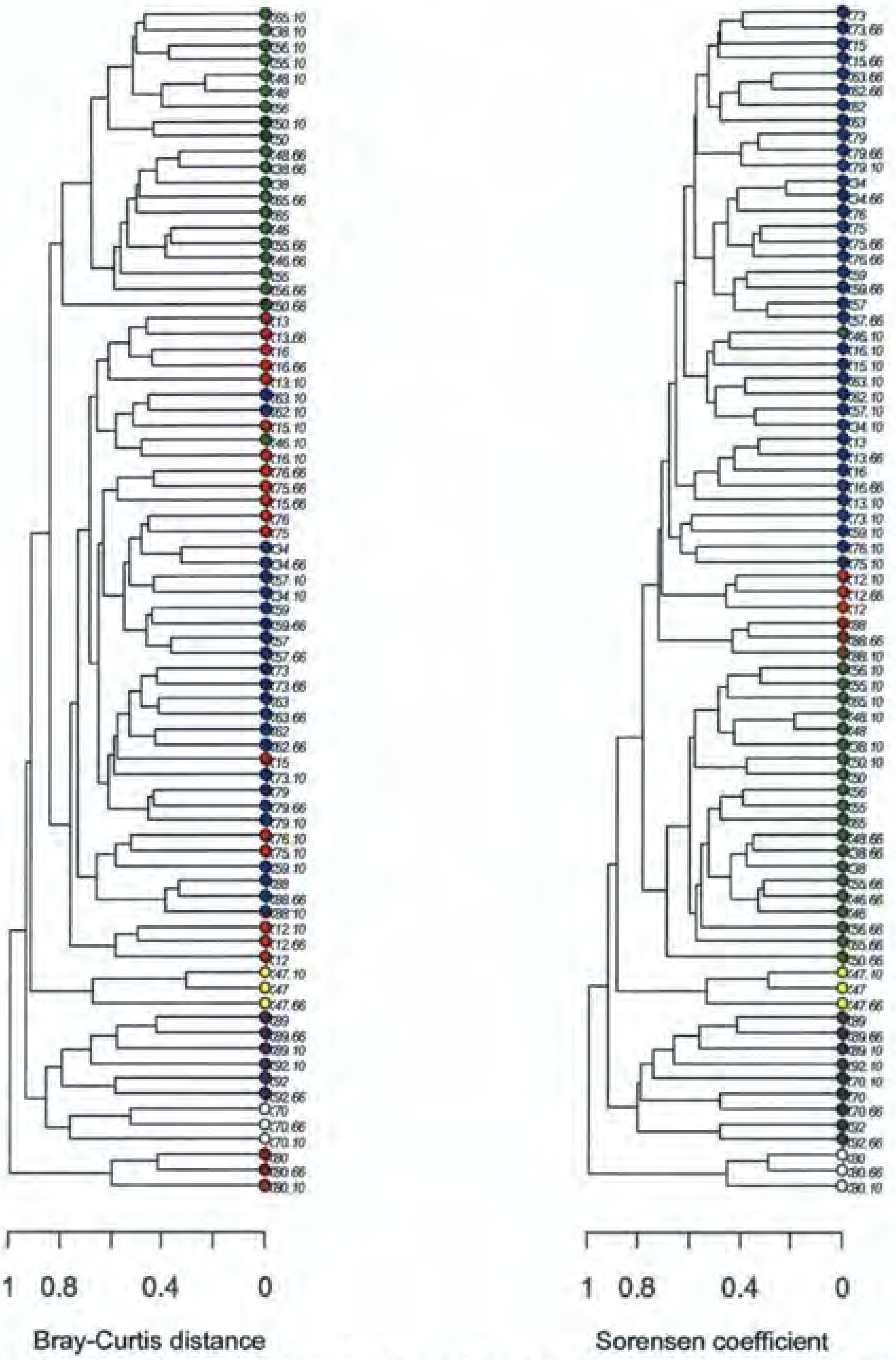


Fig 9. Cluster diagram of plots from three time periods in one cluster grouped into vegetation types using two methods. Colour coding in all diagrams indicates vegetation type inferred from 1966 cluster analysis.

Histograms of vegetation age of plots for each survey (Fig 12) show that within the 26 plots surveyed during all time periods, there was higher heterogeneity in plot age during the 1966 survey. In 1996 there were almost no plots older than 10 years, while in 2010 the majority of plots were less than five years old, with a smaller peak just younger than 20 years.

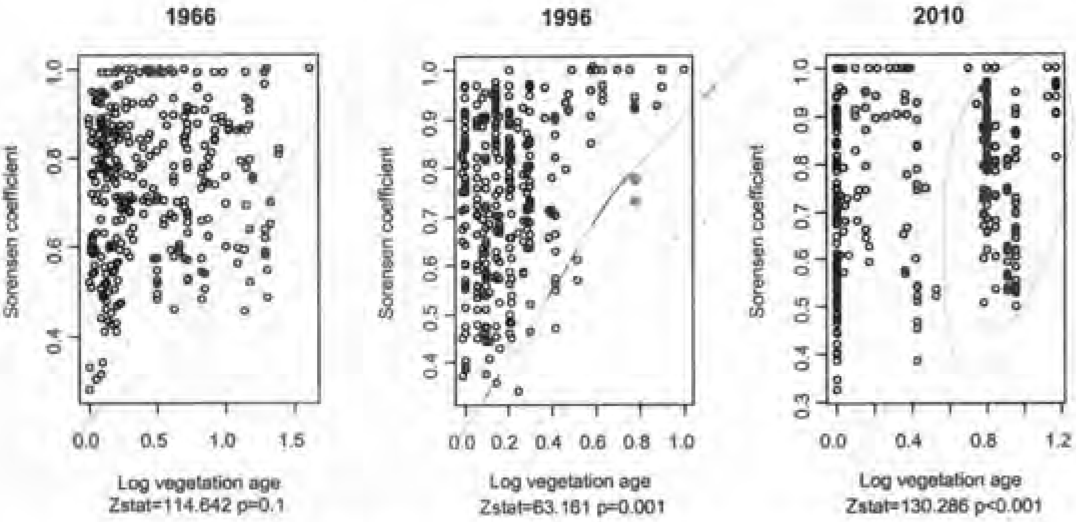


Fig 10. Graphs showing change in vegetation composition (using Sorensen's coefficient dissimilarity) relative to change in vegetation age in each survey. Mantel test results below each graph.

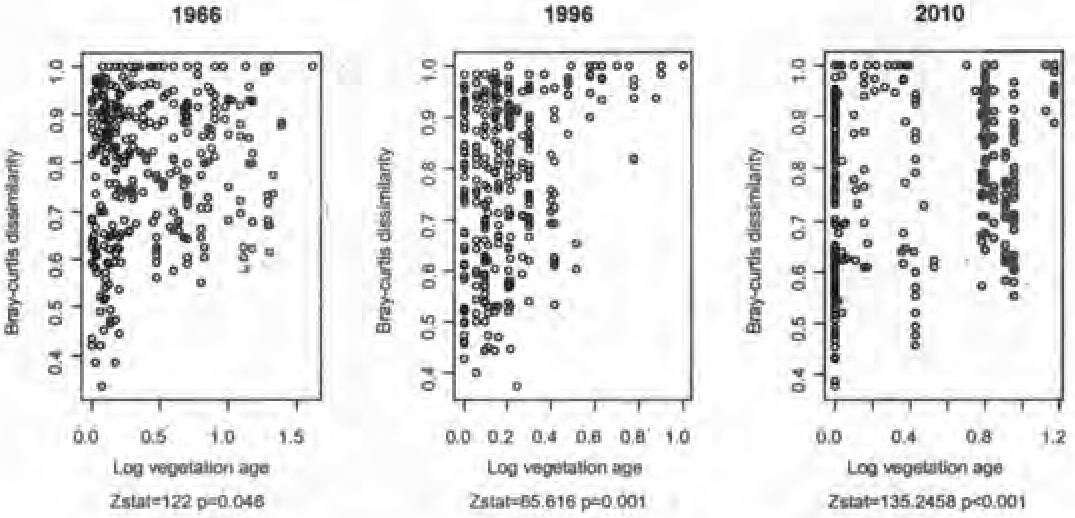


Fig 11. Graphs showing change in vegetation composition (using Bray-Curtis distance) relative to change in vegetation age in each survey. Mantel test results below each graph.

Influence of geographical distance on compositional similarity between sites

Plots of vegetation dissimilarity against geographical distance between plots (Figs 13 and 14) show a similar trend to that of vegetation age. Plots close together may be relatively similar or very different in terms of vegetation, while plots further away are less similar. Mantel tests based on 26 plots from all surveys did not show a significant trend. Tests based on all 81 plots from both 1966 and 1996 were significant with p<0.001 using either distance measure.

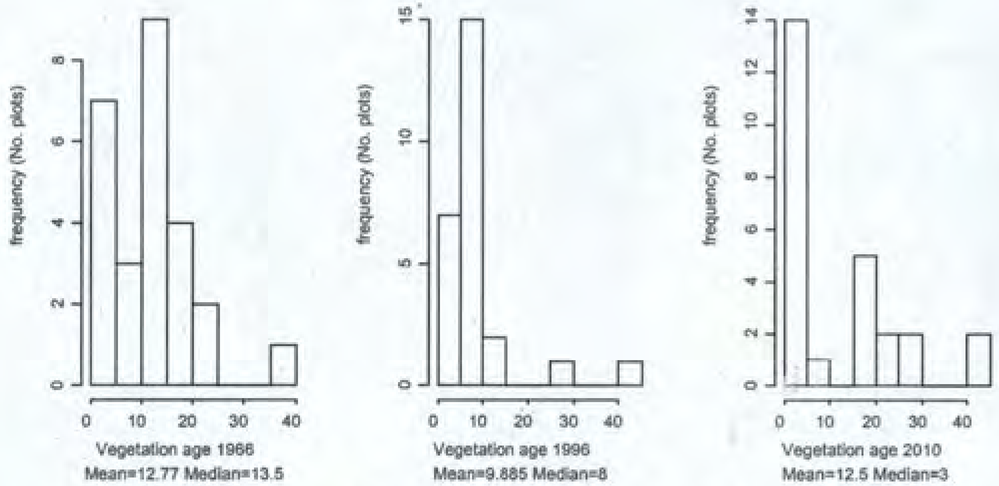


Fig 12. Histograms of vegetation age of plots at time of each survey. Mean and median plot age below each graph.

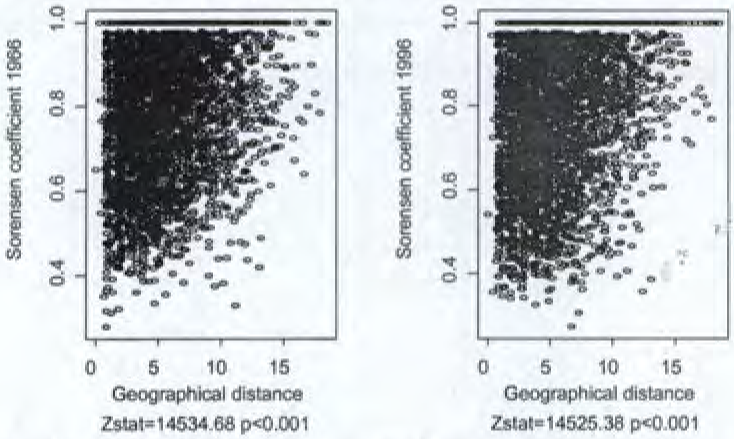


Fig 13. Graph showing vegetation dissimilarity between plots (using Sorensen's coefficient) relative to geographic separation. Mantel test results below each graph.

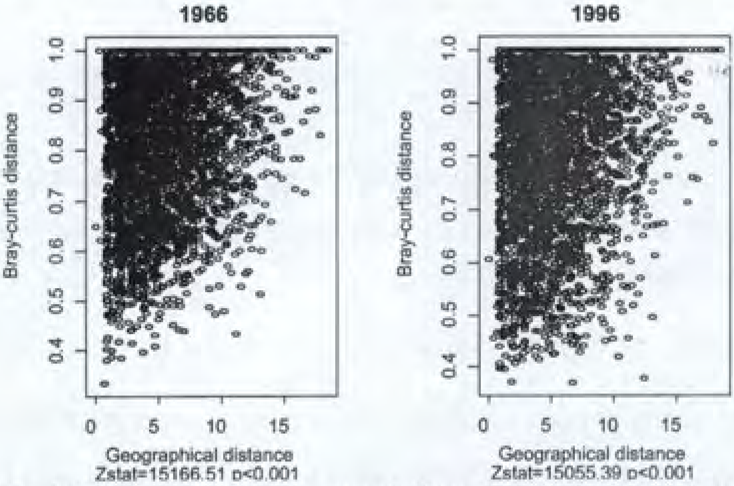


Fig 14. Graph showing vegetation dissimilarity between plots (using Bray-Curtis distance) relative to geographic separation. Mantel test results below each graph.

Results from MRPP tests for significance of predictor variables

Vegetation groups from 1966 were a significant predictor of vegetation groupings using data from both 1996 and 2010 according to MRPP analysis for both distance methods. Vegetation age is also a significant predictor of plot similarity using both distance methods for either time period. Soil types were found to be a significant predictor of vegetation groupings with all cases having $p<0.05$ except for the 1996 data using Sorensen's coefficient. The Meandist analysis revealed that two soil types, apedal sandy soils and multiple-dominant soil series' including soils of wetter conditions, caused plots to be more similar within their groups than between groups. The plots within the sandy soil group were mostly of the large red and blue group of vegetation, and the other soil group included the distribution of plots of the green vegetation group. Soil types therefore account for the distribution of dominant vegetation types in the reserve.

Table 1. Mantel test results comparing vegetation dissimilarity matrices to vegetation age and geographical distance between plots. Geographical distance is also compared with difference in vegetation age.

Response variable			Z-	P-	
Distance metric & year		Predictor	statistic	value	N
Bray-Curtis	1966	Difference in veg age in 1966	122.00	<0.05	26
Bray-Curtis	1996	Difference in veg age in 1996	65.62	<0.01	26
Bray-Curtis	2010	Difference in veg age in 2010	135.25	<0.001	26
Sorensen	1966	Difference in veg age in 1966	114.64	NS	26
Sorensen	1996	Difference in veg age in 1996	63.16	<0.01	26
Sorensen	2010	Difference in veg age in 2010	130.29	<0.001	26
Bray-Curtis	1966	Difference in veg age in 1966	1290.33	<0.01	81
Bray-Curtis	1996	Difference in veg age in 1996	814.67	<0.001	81
Sorensen	1966	Difference in veg age in 1966	1231.39	<0.05	81
Sorensen	1996	Difference in veg age in 1996	791.06	<0.001	81
Bray-Curtis	1966	Geographical distance	1260.49	NS	26
Bray-Curtis	1996	Geographical distance	1241.8	NS	26
Bray-Curtis	2010	Geographical distance	1273.55	NS	26
Sorensen	1966	Geographical distance	1184.81	NS	26
Sorensen	1996	Geographical distance	1179.04	NS	26
Sorensen	2010	Geographical distance	1227.86	NS	26
Bray-Curtis	1966	Geographical distance	15166.51	<0.01	81
Bray-Curtis	1996	Geographical distance	15055.39	<0.001	81
Sorensen	1966	Geographical distance	14534.68	<0.001	81
Sorensen	1996	Geographical distance	14525.38	<0.001	81
Difference in vegetation age	1966	Geographical distance	9243.53	<0.01	81
Difference in vegetation age	1996	Geographical distance	5964.27	<0.01	81
Difference in vegetation age	1966	Geographical distance	864.76	<0.001	26
Difference in vegetation age	1996	Geographical distance	406.19	NS	26
Difference in vegetation age	2010	Geographical distance	859.22	<0.01	26

Distance metric refers to the measure used to produce a dissimilarity matrix for the vegetation data collected during the year noted in each row. Difference in vegetation age as predictor refers to age difference between each plot at the time given. Rows in grey denote non-significant predictors of vegetation data. N is the number of plots included in analysis ie. 81 = All plots surveyed in 1966 and 1996; 26 = All plots surveyed in all three surveys.

Table 2. MRPP analysis using 1966 vegetation groupings, vegetation age and soil type to predict vegetation groupings .

Response variable			Delta			
Distance metric & year		**Predictor**	**Obs**	**Exp**	**P**	**N**
Bray-Curtis	1966	Bray-Curtis group 1966	0.5889	0.7974	0.001	26
Bray-Curtis	1996	Bray-Curtis group 1966	0.619	0.7918	0.001	26
Bray-Curtis	2010	Bray-Curtis group 1966	0.6198	0.8023	0.001	26
Sorensen	1966	Sorensen's group 1966	0.5578	0.7488	0.001	26
Sorensen	1996	Sorensen's group 1966	0.5652	0.7505	0.001	26
Sorensen	2010	Sorensen's group 1966	0.5698	0.7706	0.001	26
Bray-Curtis	1966	Bray-Curtis group 1966	0.7154	0.8236	0.001	81
Bray-Curtis	1996	Bray-Curtis group 1966	0.7141	0.8151	0.001	81
Sorensen	1966	Sorensen's group 1966	0.6684	0.7866	0.001	81
Sorensen	1996	Sorensen's group 1966	0.6696	0.7819	0.001	81
Bray-Curtis	1966	Difference in veg age in 1966	0.7425	0.7974	<0.005	26
Bray-Curtis	1996	Difference in veg age in 1996	0.7183	0.7918	<0.005	26
Bray-Curtis	2010	Difference in veg age in 2010	0.7477	0.8023	<0.05	26
Sorensen	1966	Difference in veg age in 1966	0.6868	0.7488	<0.005	26
Sorensen	1996	Difference in veg age in 1996	0.6716	0.7505	0.001	26
Sorensen	2010	Difference in veg age in 2010	0.7477	0.8023	<0.01	26
Bray-Curtis	1966	Difference in veg age in 1966	0.7805	0.8236	0.001	81
Bray-Curtis	1996	Difference in veg age in 1996	0.7798	0.8151	0.001	81
Sorensen	1966	Difference in veg age in 1966	0.7443	0.7866	0.001	81
Sorensen	1996	Difference in veg age in 1996	0.7424	0.7819	0.001	81
Bray-Curtis	1966	Soil type	0.7705	0.7974	<0.05	26
Bray-Curtis	1996	Soil type	0.7574	0.7918	<0.05	26
Bray-Curtis	2010	Soil type	0.7628	0.8023	<0.05	26
Sorensen	1966	Soil type	0.7195	0.7488	<0.05	26
Sorensen	1996	Soil type	0.7259	0.7505	NS	26
Sorensen	2010	Soil type	0.7628	0.8023	<0.05	26
Bray-Curtis	1966	Soil type	0.8147	0.8236	<0.05	81
Bray-Curtis	1996	Soil type	0.8015	0.8151	0.01	81
Sorensen	1966	Soil type	0.7767	0.7866	<0.05	81
Sorensen	1996	Soil type	0.7697	0.7819	<0.05	81

Distance metric refers to the measure used to produce a dissimilarity matrix for vegetation data collected during the year noted in each row. Predictor Bray-Curtis/Sorensen's groups are vegetation types as defined by 1966 data; difference in vegetation age is between all relevant plots at that time. Rows in grey denote non-significant predictors of vegetation data. N is the number of plots included in analysis ie. 81 = All plots surveyed in 1966 and 1996; 26 = All plots surveyed in all three surveys.

Fig 15. Plot 56, example of moist restioid fynbos of sandy flats.

Fig 16. Plot 57, dry rocky fynbos with shallow soils and low vegetation.

Fig 17. Plot 92, Mature tall fynbos with some thicket elements.

Discussion

Change in reserve level species diversity over the last 44 years

There was found to have been an overall decrease of almost 25% in observable species diversity during the 44 years of study. There are a number of potential factors that may have contributed to this decline. Changes to the disturbance regime could include a change in fire frequency and intensity. The effect of grazing pressure from large mammal herbivores in the reserve could also be affecting diversity. Global change factors including changes in climatic conditions, or the impacts of alien species could also have influenced the changes observed. The number of species recorded in the survey also depends on the ability of the botanist conducting the survey to correctly identify all species that are present, and this is dependant on both their knowledge and well as time spent on each plot in the field.

Fire

Fire regime could have been responsible in part for the observed change in species diversity. In 1966 there was greater heterogeneity in vegetation age with most plots being relatively young in 1996 and 2010. This could be the result of the use of block burning as a management tool for maintaining biodiversity by preventing senescence and build-up of woody biomass in fynbos. While the reserve is now effectively a single management unit, in the past when it was still divided into a number of separately managed farms, fires would have been controlled and likely prevented from burning over boundaries as easily as they do today. The decrease in vegetation age heterogeneity since 1966 means that species typical of older vegetation may not yet have become established in the vegetation of many plots, even though vegetation should be at its peak in terms of species richness around this age (Hoffman et al. 1987). However, *Cassine maritima* and *Cussonia thyrsiflora* were the only species present in 1966 but absent in 1996, which are unlikely to be present in young fynbos, as they are typical of thicket or mature fynbos communities.

Fire occurrence may be too frequent to allow for slower growing species to reach sexual maturity (Cowling 1987). While most plots did not burn more than twice between 1966 and 1996, many have burnt as much as three times between 1996 and 2010. This frequency of fire may not allow sufficient time between each fire when slow maturing species could build up a seed bank, and so populations will likely decline over successive fire events until they disappear.

In terms of species traits, there was a proportionally higher decrease in seeders than resprouters between 1966 and 1996. ref ?? or analysis ? This could be a sign of too frequent fires, as this would prevent seeder species from building up a sufficient seed bank between fires. This could also be due to fires occurring during unfavourable seasons for seedling establishment. Autumn is considered to be the optimal season for a fire to take place (Midgley, 1988) as it is just before the onset of winter rainfall and cool conditions which allow for the establishment of seedlings before summer drought. If a fire occurs at a different time of year, fire-initiated seeds will either germinate while it is still dry if during summer or if not will more likely succumb to predation, or else will not have sufficient time to establish if during winter or spring (Bond et al. 1984). This will provide resprouting species with a competitive advantage. The historical fire record shows that fires occurred during all seasons in different plots between 1966 and 1996 (Privett. 2001).

Grazing and alien species

A potential impact at present that could be contributing to the decline in species richness is that of grazing by large mammal herbivores including Eland, Bontebok and Mountain Zebra. These species could be having a negative impact on the vegetation either by overgrazing palatable species or by trampling and causing increased disturbance. However, stock grazing also took place when the land was still divided up into private farms (Taylor 1984b) and so one would think that grazing pressure would have decreased since formation of the reserve. However, trait data of species growth forms showed a far higher proportional loss of herbaceous species from the reserve than any other growth form between 1966 and 1996. All other growth forms experienced species losses proportional to the relative abundances of these growth forms in 1966. Bontebok and Mountain Zebra prefer young veld that has recently burnt, and overstocking of these mammals resulted in shrub cover being replaced by grassy vegetation following small fires in Bontebok National Park (Kraaij & Novellie 2010). Diversity of grass species, however, was not negatively affected. A decrease in herbaceous species may, therefore be an indirect result of high browsing pressure, as the habitats of these species may have been degraded by grazing of grasses following fire.

Invasive alien plants were introduced intentionally or unintentionally prior to the formation of the reserve, and only relatively recently has alien vegetation been brought under control as it is today throughout most of the reserve. However, species richness should not have decreased by so much since 1996 if alien plants were a major impact on vegetation species richness.

Climate

Climate change or at least unfavourable weather conditions may have had an impact on certain species such as those with specific habitat requirements (Midgley et al. 2003). Although the last few years have been favourable in terms of winter rainfall to sustain damper habitats during the drier summer, 2010 experienced an unusually dry winter. Even at the time of surveying in August, which is historically the wettest month of the year, the ground in many wetland habitats was dry. Some species may have already succumbed to the conditions. Dry winters are not that uncommon, and all species in the reserve have likely survived worse conditions in the past.

Observer bias and quality of the present survey

Due to the high species diversity even within the confines of the CGHNR as well as uncertainties in taxonomic classification both now and in the past, it is almost impossible for any individual to identify all taxa to species level. However, in spite of this, at least in the 2010 survey, Ross Turner was able to identify almost all flora to species level, with the exception of a few groups such as Poaceae, Cyperaceae and the genus *Thesium*. Fortunately there are specialists of these groups currently at the University of Cape Town, as well as the facilities at the Bolus herbarium. This allowed the identification of most species of these groups with the exception of a few species not in flower at the time, which would only count for a few species at most and so would not have had a significant impact on number of species recorded.

Some habitats were poorly sampled in the 2010 field data collection, including coastal scrub, of which only plot 80 is representative. However, the same trend of decreasing species richness was noted when the species accumulation curve was drawn for all time periods but only incorporating the 26 plots in the 2010 survey.

From personal observation however it appeared that at least some of the species previously recorded within plots but now absent from any of them are still present in the immediate surroundings. This would likely lessen the extent of the decrease in diversity but probably not so far as to cancel out the decrease in species richness as noticed in the curve. Increasing plot size may have decreased the extent of species decline between surveys, although the plot size needs to remain standard since the first survey.

Stability of community composition within and between sites over time

Fynbos and Coastal Thicket vegetation contain few common species and so are well separated in terms of both dissimilarity measures. Coastal thicket is not well represented in the most recent survey and so is not discussed in detail, although it was found to cluster well during both previous surveys of 81 plots. Within Fynbos, three broad vegetation types can be differentiated as is shown by the cluster diagrams (Figs 7, 8 & 9). However, there are plots containing anomalous Fynbos habitats that do not cluster into a particular group, or that are not stable within a group between surveys.

All plots did experience at least some level of turnover both in presence of species as well as abundances. However, plots still cluster significantly within the same or similar groupings in 1996 and 2010 as they did in 1966.

Large vegetation groups as defined by dissimilarity distances

The light green coded group representing damp restioid type fynbos vegetation (Fig 15) was particularly stable across the whole time period and with both Bray-Curtis distance and Sorensen's coefficient methods. Abundant restio cover is a specific feature of the vegetation recorded in all plots in this group. However, the same is not true of the plots within the red and blue groups, as there is no dominant cover of any particular group of plants. This could be the reason for the lack of stability in their grouping over time since 1966 using Bray-Curtis distance (Fig 16). The purple group and plot 70 have not burnt often during this whole time and so lack of fire and resulting state of senescence may be responsible for their similarity as is the case at least in 2010 (Fig 17).

Plots of anomalous and unstable vegetation

Of interest is plot 47, which did not appear particularly unique during surveying, although in the 2010 survey did cluster loosely with the damp restioid fynbos group. Even during previous surveys, the species recorded do not appear much different from what was found in many plots that group within the damp restiod Fynbos type. It was however in an unusual geographical position, within a wetland situated in a slight dip on a sandstone ridge. On most sides was rocky but the location of the plot was in deep dark peaty soil, and the vegetation was much more lush and tall than almost any other plot of that age that had been surveyed during the present time.

In some places Fynbos types end abruptly, such as the edge of a seepage area where there is a well-defined discontinuity. An example of this was on the edge of plot 50 and plot 46 where most of the plot fell within damp restioid fynbos but one or two quadrats on one end of the plot contained species associated with well-drained habitat. In other areas the point of discontinuity between different vegetation types was less obvious, such as in plot 79 which was relatively rocky but with species from both wetter and well drained habitats recorded throughout the plot. Plot 13 was mature vegetation with signs of senescence, but also contained species of both moist and dry Fynbos.

In both cases, the mix of species associated with different vegetation types will lead to plots not clustering well with either fynbos type during successive surveys, thus causing potential confusion in trying to delimit long-term vegetation types. Bray-Curtis distance would be a better means of analyzing an area where species typical of one vegetation type are rarer than those of another, because they do not do as well on the edge of their range.

Influence of fire history on compositional similarity between plots

Vegetation types show a degree of similarity in age while the most different plots in terms of age are among the most different in terms of vegetation. However, as there has been a change in fire regime over the period of vegetation survey, vegetation groups could be expected to show changes associated with vegetation age if fire histoy does significantly affect vegetation groups.

Thicket and the mature fynbos of plots 70, 89 and 92 are similarly old at present as none have burnt in recent years. The moist restioid Fynbos of the green group all burnt during the most recent fire and so were all of the same age during the 2010 survey. However, plots in both of these groups were not all the same age during previous surveys when they also clustered as well.

From the 2010 data, one of the vegetation clusters from the blue and red groups included mostly young plots while the second was mostly older plots. This suggests that stability of groups within drier fynbos vegetation are determined by fire history, which would account for the movement of plots between groups between surveys. The other vegetation types may not be determined to the same extent by fire. Because the majority of plots contain dry Fynbos, this may account for the significance of fire in predicting vegetation groupings where this was found. Hoffman et al. (1987) found that species richness changed with vegetation age, and so my finding supports this argument.

Although the old vegetation plots (70, 89 and 92) all contain species dependant on fire, including non-sprouting members of the Proteaceae and Ericaceae, established thicket vegetation does not burn and in fact excludes fire. Fire frequency and intensity will also differ within fynbos types depending on conditions of the habitat, in particular rainfall variation (Wilson et al. 2010). Therefore, different vegetation types will affect the fire regime.

Influence of spatial distance on compositional similarity between plots

Spatial distance between plots shows a similar effect to that of age difference between plots, in that closer plots are likely to be either similar or different, while plots further away are never as similar in terms of vegetation composition. This was only significant though when incorporating all 81 plots. The reason for different vegetation composition of sites in close proximity is due to high habitat heterogeneity within the reserve (Personal observation). An example is on the central plateau area where numerous rocky outcrop ridges cut across otherwise sandy damp flats. These ridges are very different to the surrounding sandy flats in terms of habitat and resulting vegetation composition, and so adjacent plots on damp flats cluster together while adjacent plots in different habitats cluster far apart. Plots separated by greatest spatial distance will be those plots in the northern and southern extremes of the reserve. Those at the southern extreme will be more exposed to strong winds coming off the sea, while plots in the northern part of the reserve are mostly further from the coast and closer to the northern hills and mountains which provide protection to some degree from exposure and experience higher orographic rainfall.

However, geographical distance is more likely to be autocorrelated with the effect of fire regime on composition similarity between plots. Plots closer together are more likely to be a similar age than plots far away because a fire will usually burn all or most plots in a specific area at the same time. Difference in vegetation age was also found to be a stronger predictor of compositional similarity between plots. It was found that there is a significant correlation between spatial distance and age difference between plots, but not a directional relationship.

Spatial distance would certainly have an effect on the fire regime due to the landscape features across the reserve. Plots in the south of the reserve will likely burn less frequently as they are surrounded on three sides by the sea (Privett et al. 2001), while plots in the north are surrounded by land on all sides from which fires can spread.

Influence of soil types on compositional similarity between plots

Soil type showed an overall significant effect of predicting vegetation groupings in any of the datasets, specifically those two types associated with thin rocky sandstone soils and damp sandy flats respectively. The former corresponds with the distribution of the largest fynbos group, that of drier fynbos of rocky slopes. The latter soil type corresponds with the distribution of damp restioid fynbos as grouped as light green on the cluster diagrams (figs 7 and 8). As these are the dominant vegetation types in terms of representation within the plots, soil types provide a reasonably good means of identifying the distribution of these vegetation types within the reserves and up to a point where associated species are more likely to be encountered. Soil types associated with coastal areas would also likely correspond well with coastal vegetation within the reserve, but unfortunately very few plots were sampled within this vegetation type, thus reducing statistical power. Soil types were found van Wilgen & Kruger (1985) to correlate with different vegetation types along a gradient.

Influence of distance method employed on compositional similarity between plots

These measures differ the most when there is a large difference in abundance of individuals in some species relative to others within a plot, and are most similar when abundances are equal. Sorensen's Coefficient and Bray-Curtis Distance will affect the outcome of analysis differently depending on vegetation state. Young vegetation contains many different species in varying abundances. These plots would likely exhibit the greatest difference in analysis between Bray-Curtis distance and Sorensen's Coefficient. As vegetation gets older and fewer plants take up the area of the plot, the abundances of different species will become closer to each other and so the difference between methods used will decrease.

While older fynbos or thicket with few large plants in a plot may show the least difference in grouping between methods, the blue and red group which consist in part of young vegetation with high species richness show relatively large differences in association between Bray-Curtis distance and Sorensen's Coefficient. Bray-Curtis distance makes it easier to note changes in grouping since 1966 due to this method having clustered these plots into two similar sized groups rather than a single group. However, the fact that Sorensen's coefficient produces a large blue group while Bray-Curtis produces a red and blue group shows that this vegetation type has many common species. Abundances of certain species differ between plots of the two groups, which appear to be affected by vegetation age and thus fire history.

Conclusion

Within the Cape of Good Hope Nature Reserve there has been a decline in species richness within plots relative to 1996 and 1966. There are a number of factors that could have contributed to this trend. However, the available data points to a combination of grazing pressure and altered fire regime as having the greatest impact. Climate change may also be a contributing factor, or at least will be in future. While there has been turnover in vegetation composition within plots during the last 44 years, plots still generally cluster within the same groups with 1996 and 2010 data as they do with 1966 data of vegetation composition. Fires have become more frequent and the majority of plots are younger than in the past. Vegetation age was found to be a significant predictor of vegetation groupings when involving all 81 plots. Soil types are also significant predictors of distribution of vegetation types.

Overall, it appears that vegetation types at Cape Point are determined primarily by soil type and environmental conditions and secondarily by the impact of fire regime.

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Appendices

Appendix 1. Environmental data (Soil type and vegetation age) for all plots in 1966 and 1996 surveys.

Plot #	Soil	Age_66	Age_96	Age_2010
1	1	8	10	10
2	1	5	10	10
3	1	7	10	10
4	5	18	10	24
8	1	3	10	3
9	1	3	10	24
10	1	2	10	24
12	1	3	10	3
13	6	5	10	24
14	1	3	8	5
15	5	3	10	3
16	4	3	10	3
17	6	3	10	3
18	3	3	10	24
19	4	17	10	3
21	4	15	10	3
22	1	20	10	3
23	1	15	10	24
24	11	4	10	24
25	6	30	5	19
27	1	19	10	3
28	6	21	10	3
29	1	10	10	24
30	1	18	10	24
31	11	11	10	24
34	1	13	5	3
36	1	14	10	3
37	6	25	8	3
38	1	12	10	3
39	1	21	10	24
40	1	11	10	24
42	2	1	4	18
44	1	7	5	8
45	1	9	5	3
46	1	15	8	3
47	6	18	8	3
48	11	10	7	3
49	11	18	7	3
50	11	8	7	3
54	1	14	17	3
55	1	14	8	3
56	11	14	8	3
57	1	21	7	3
58	11	19	7	3
59	1	15	4	18
60	1	40	40	40
61	11	7	5	8
62	1	19	8	8
63	1	19	8	3
64	6	14	8	3
65	6	15	7	3
66	1	16	13	27
67	1	20	13	18
68	1	3	5	8
70	6	2	5	19
71	1	12	7	21
72	1	25	13	27
73	1	12	13	27
74	1	20	40	40
75	1	1	5	21
76	6	1	5	19
78	6	5	4	18
79	1	20	13	27
80	1	40	40	40
81	4	17	40	29
82	1	1	5	19
83	6	10	5	19
84	3	10	5	19
86	6	2	5	19
87	1	1	5	19
88	1	10	5	19
89	6	15	30	44
90	4	30	40	40
91	5	20	5	29
92	1	24	5	19
94	5	17	4	18
95	1	20	40	40
97	1	40	40	40
98	1	20	4	40
99	1	1	40	40
100	1	2	40	40

Soils are scored according to Soil Map of the Cape Peninsula (Smith-Bailie et al. 1976) and age is in years since last fire.

Appendix 2. Similarity between original distance matrices using Bray-Curtis and Sorensen's coefficient and distorted data using each method for producing cluster diagrams.

Distance method	Bray-Curtis distance		Sorensen's coefficient	
	1966	1996	1966	1996
Ward	0.2698	0.267	0.3358	0.2679
Single	0.5881	0.5713	0.6088	0.6377
Complete	0.4014	0.514	0.4557	0.5271
Average	0.7484	0.7585	0.7383	0.7856
Mcquitty	0.7107	0.5986	0.5428	0.6614

"Average" method produces least distortion and so similarites are shown in black, while other inferior methods are shown in grey.