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A vegetation survey of the Cape of Good Hope Nature Reserve. I. The use of association-analysis and Braun-Blanquet methods*

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ABSTRACT

The survey aimed to establish broad vegetation units that could be mapped on an extensive scale in the Cape of Good Hope Nature Reserve at the southern tip of the Cape Peninsula. This paper compares the performance of two methods, association-analysis and the Braun-Blanquet method as developed by the Zürich-Montpellier School of Phytosociology. One hundred 50 m² sample plots, covering the whole Reserve, were placed systematically at grid intersections on the 1:18 000 topographical map, at 1 000-yard (914 m) intervals. Species lists, recording merely presence of all species with permanently recognizable aerial parts, were made for each plot.

The association-analysis resulted in a classification of 23 final groups of sample plots, of which only five groups showed high floristic and ecological homogeneity. Of the remainder, eight groups contained some anomalous, misplaced plots, and ten represented small, isolated fragments of natural units. The original data were then analysed using Braun-Blanquet methods to provide an independent classification for comparison with the former. The Braun-Blanquet communities were found to be more homogeneous in terms of previously defined habitat groupings and showed floristic relationships consistent with these groupings.

It is concluded that, with the type of sampling used, the synthetic phytosociological Braun-Blanquet method provides a more natural classification of plant communities of the Reserve than does the monothetic divisive association-analysis method.

INTRODUCTION

When Acocks (1975) first wrote his Veld types of South Africa in 1953, little was known of the ecology of the complex fynbos vegetation of the Capensis region (Taylor, 1978). Acocks was therefore unable to subdivide fynbos to the same extent as he did the vegetation of other parts of South Africa. Though there had been general descriptions of fynbos by Marloth (1908) and Adamson (1938) and a few quantitative studies like those of Wicht (1948) and Rycroft (1951), there was still scant information on the response of different types of fynbos to treatments like veldburning and grazing. To determine the effects of such treatments, experimental research was initiated locally but these isolated projects could not be satisfactorily compared with one another, or extrapolated to other areas, in the absence of a synoptic account of fynbos. To fulfil this need, it was decided in the early 1960's to conduct a primary survey of Cape Mountain Fynbos (Acocks's Veld Types 69 and 70) and, for this purpose, a suitable method had to be found. The survey of such a large area — some 37 000 km² in rugged mountain terrain — would have to be divided into components, and the method would have to be sufficiently formalized and uniform to allow valid comparison of data from each component. In seeking a method suitable for a major survey of this kind, a trial on a smaller area of fynbos was required.

The Cape of Good Hope Nature Reserve (Fig. 1) was chosen as the site for the trial, because its flora was comparatively well known (Adamson & Salter, 1950), and its area large enough (77 km²) and its vegetation sufficiently diverse to provide a representative sample of fynbos. The work was begun by the author in 1966 and presented as a thesis to the University of Cape Town (Taylor, 1969).

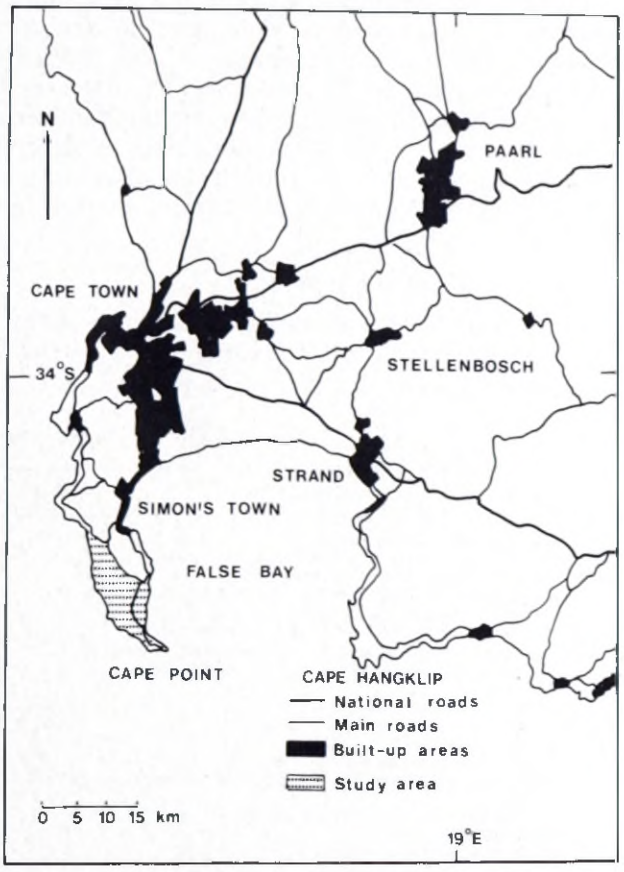


FIG 1.—Geographical location of the study area.

* Based on an M.Sc. thesis, University of Cape Town.

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The results of this trial, the first of its kind in fynbos, led to the adoption by many subsequent workers of the Braun-Blanquet phytosociological method which has proved eminently suitable for standard primary surveys of South African vegetation. This account compares the performance of two methods used in the trial.

METHODS

The aim of the survey of the Cape of Good Hope Nature Reserve was to establish broad vegetation units that could be mapped on an extensive scale. For this, a classification was needed. The first requirement was to test a method that could permit comparison of the vegetation of different areas. Before the development of the electronic computer, classifications based on statistical methods were unsuccessful (Blackman, 1935; Ashby, 1936). By 1966, however, statistical and computing techniques had been improved to provide practical methods that could be interpreted comparatively easily.

Association-analysis (Williams & Lambert, 1959; 1960) appeared to be one suitable method. It had given promising results on small areas of relatively simple vegetation in Britain, by recording presence of all species on small quadrats closely and systematically spaced in a grid pattern. It would be physically impossible to follow an identical procedure in the large area of complex fynbos. Nevertheless, it was thought that the method might be adaptable by using larger plots spaced a kilometre or more apart, and it was decided to use the method, thus adapted, in the trial on the Reserve.

After the association-analysis results were interpreted, the original data were used in another analysis applying the technique of the Zürich-Montpellier School of Phytosociology, here referred to as the Braun-Blanquet method (Braun-Blanquet, 1932; Becking, 1957; Whittaker, 1962; Küchler, 1967; Werger, 1974), to provide an independent classification for comparison with that obtained by association-analysis.

Sampling and recording procedures

To provide a reference framework before sampling commenced, habitat categories were classified, on physiographic/physiognomic criteria, in the system shown in Table 1.

For the statistical analysis, sample plots were placed systematically in a grid pattern over the whole area, following the objective procedure of Williams & Lambert (1959).

In a pilot enumeration conducted to determine the best size and spacing of plots, twenty plots, each 10 m × 10 m, were placed at random intersections of the grids on the 1: 18 000 map of the Cape Peninsula. Each plot was subdivided into ten sub-plots, each 2 m × 5 m. Separate lists for each sub-plot were made of the permanently recognizable species (discussed below), and the cumulative number of species occurring in each successive sub-plot was calculated. Regression equations for plot sizes of 20 m^2, 50 m^2 and 100 m^2 were derived and, by extrapolation, the number of species which one could expect to record in 350 plots of these sizes, was calculated. (About 350 intersections of the grid on the above-mentioned map occur in natural vegetation on the Cape Peninsula.)

The results showed that, using plots of 100 m^2, 734 species could be expected to occur in the samples. If the plot size were reduced to 50 m^2 one could expect to record 624 species, whereas if the plot size were further reduced to 20 m^2 the expected number of species would be 469. Therefore, a 50% reduction in plot size would result in only a 15% expected reduction in species present. This did not mean that the survey could be completed in half the time, however, since location and laying out of plots, and the recording of observational data, took equally long in both cases. Therefore, with further reduction in plot size the time saved becomes less and less. The use of a 20 m^2 plot would effect very little further saving in time while the expected number of species would be reduced by 36%.

To check these calculations, the mean number of additional species actually found in the ten sub-plots (1, 2, 3 ..... 10), was determined. The results agreed closely with the expected figures calculated theoretically.

Since rectangular plots are likely to cover greater variations in pattern, and to include a greater number of species than square plots (Brown, 1954;

TABLE 1. – Habitat categories and equivalent vegetation units

	Habitat categories	Vegetation units*
1.	Sites exposed to recurrent fires	**FYNBOS**
1.1	Marine sands and coastal Table Mountain Sandstone soils	***Coast Fynbos***
1.1.1	well-drained marine sands of the coastal shelf	(Coast-shelf Fynbos)
1.1.2	well-drained aeolian dunes of marine origin (including inland dunes)	Dune Mixed Fynbos Degrading to Dry Sandflats and *Metalasia–Passerina* Communities
1.1.3	poorly-drained coastal flats of marine origin	(Coast Marsh Sedgeland)
1.1.4	well-drained cliffs and ledges of the rocky sandstone coast	Rocky Coast Fynbos (including *Coleonema* Fynbos)
1.2	Acid sands derived from inland Table Mountain Sandstone soils	***Inland Fynbos***
1.2.1	well-drained rocky hills, mountains and lower sandy slopes	Upland Mixed Fynbos including Western Hillveld, Dry Hillveld, Mountain Fynbos and *Metalasia–Passerina* Fynbos; degrading to Dry Sandflats Community
1.2.2	well-drained ferricrete slopes	Tall Fynbos (including *Protea lepidocarpodendron* Community)
1.2.3	well-drained steep, rocky, northerly slope	(*Protea nitida* Woodland)
1.2.4	drained level plateaux	Plateau Fynbos
1.2.5	seasonally inundated flats on the plateau	Tussock Marsh Community
1.2.6	permanently moist seepage steps demarcating the terraced flats of the plateau	Seepage Fynbos
2.	Sites protected from recurrent fires, occurring on	**BROAD-LEAVED THICKET**
2.1	dunes of marine origin	*Sideroxylon* Thicket
2.2	slopes and screes of sandstone origin	*Maurocenia–Chionanthus* Thicket

* Vegetation units in parentheses are not mentioned in this text

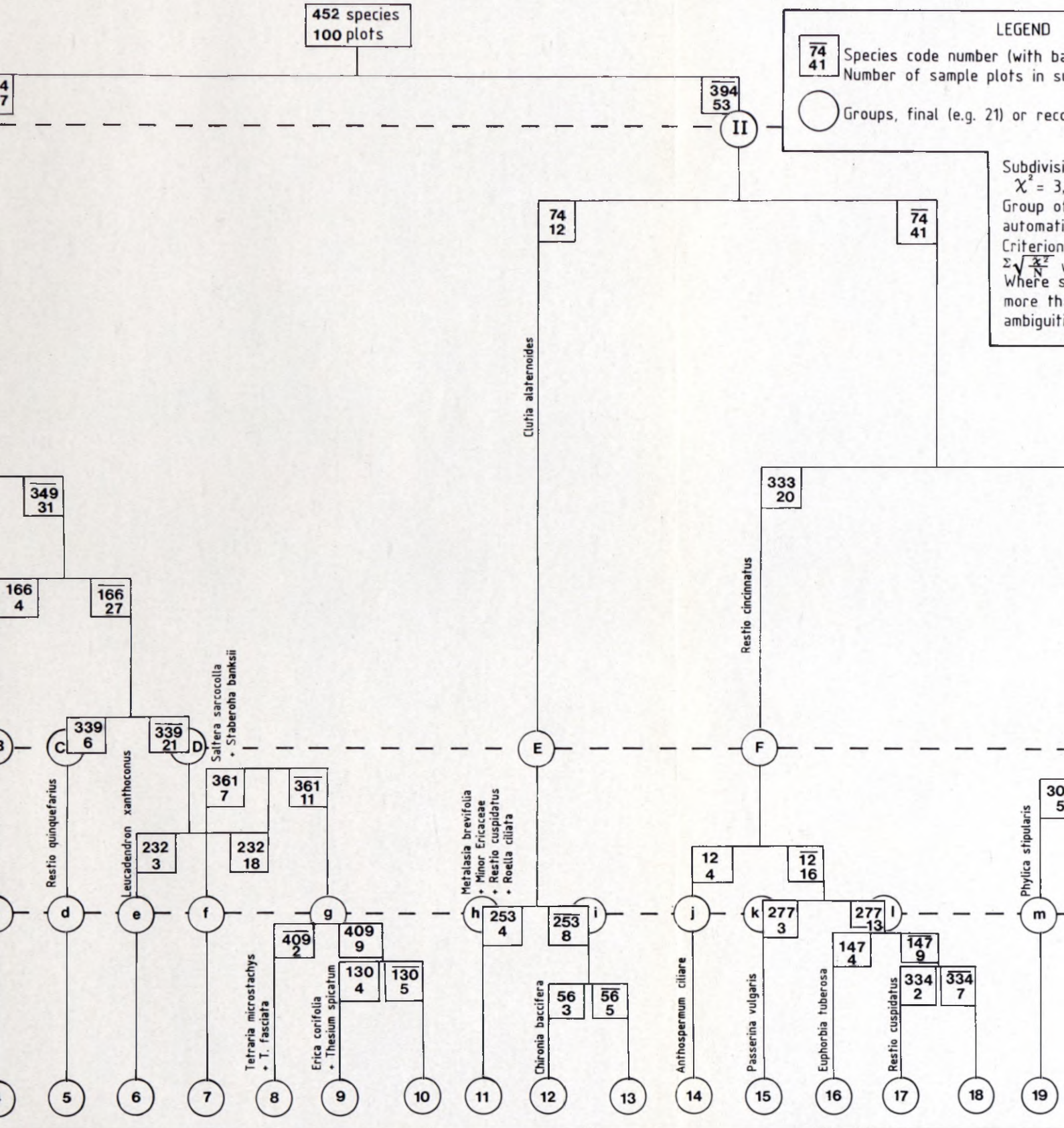


FIG 2.—Association-analysis hierarchy of the Cape of Good Hope Nature Reserve.

Cain & Castro, 1959; Greig-Smith, 1964; Kershaw, 1964) it was decided to use a rectangular plot of 5 m × 10 m as being the most efficient size. The examples given by Werger (1972) confirm that a plot of 50 m^2 is usually adequate for sampling fynbos.

Therefore, the sample plots on the Cape of Good Hope Nature Reserve were placed systematically at intersections of the grids on the 1:18 000 topographical map, at 1 000 yd (914 m) intervals. One plot, in the middle of an extensive thicket of the alien *Acacia cyclops,* was discarded. Three specially chosen summit samples were added, giving 100 plots for the Reserve.

After locating the plot positions in the field by pacing distances from fixed points scaled on the map, each plot was laid out with the long side facing true north-south.

Species lists were made for each sample plot. Since annuals and geophytes appearing temporarily at different seasons would obscure differences between species lists made at different times of year, lists for the computer analysis included only those species with permanently recognizable aerial parts. Plants appearing seasonally were noted for descriptive purposes. A supplementary list was made of additional species characteristic of the community but occurring only outside the plot. These 'surround lists' facilitated subsequent interpretation of the plot data, but were not used in the association-analysis.

Whereas plants were positively identified to species wherever possible, some species-complexes had to be amalgamated, either because they could not be specifically identified in the field or because their taxonomy had been inadequately worked out. Examples are certain minor genera of the Ericaceae and some members of the Mesembryanthemaceae. Alien species, the subject of a separate study, were excluded from the association-analysis. An assessment of abundance using Acocks's (1975) symbols was made for each species on each plot. This was another valuable aid in interpreting the data, though not needed for the association-analysis.

Post-burn 'age', based as far as possible on the branching of Proteaceous shrubs described by Hall (1959), was recorded, and descriptive notes on dominance (if any), prevalent life-form, average height and crown cover, and evident successional trends, were made on each plot to help to identify the groups revealed by association-analysis.

The following habitat data were recorded at each sampling site: altitude, aspect and degree of slope; percentage cover of stones of various size classes on a five-point scale; and soil moisture also estimated on a five-point scale (Taylor, 1969). Notes were made on soil texture, soil colour, amount of humus, and geological formation. A black-and-white photograph was taken of the vegetation of each plot.

The field enumeration of the 100 samples was done in 45 days during the period January to November 1966. I was accompanied in the field by one assistant who laid out the plots and helped with the collection of environmental data.

The association-analysis method

The use of interspecific associations for classifying vegetation was pioneered by Goodall (1953) who examined presence-or-absence data from random quadrats. Based on his work, Williams & Lambert (1959 & 1960) developed the methods of 'normal association-analysis', 'inverse analysis' (Williams & Lambert, 1961) and 'nodal analysis' (Lambert & Williams, 1962). Differences between association-analysis and Goodall's method are discussed by Taylor (1969). By 1966, association-analysis had been used to classify vegetation in South Africa by Van der Walt (1962), Grunow (1965), Roberts (1966), Downing (1966) and Miller (1966). All these were done in the floristically poorer karroid grassveld and bushveld vegetation.

Fynbos, by contrast, has a much richer flora occurring in rugged terrain with many intergrading habitats — conditions that were thought to differ sufficiently to justify testing the method for its applicability to this particular vegetation type.

Because time and suitable modifications to computer programmes were lacking, the present study was confined to normal analysis. The criterion used for subdivision was the highest $\sqrt{\frac{\chi^2}{N}}$ aggregate which Williams & Lambert (1959; 1960) considered to result in the most efficient subdivision. Subdivision continued until no individual χ^2 value equalled or exceeded 3,84 (corresponding to $p \leq 0.05$). The relevant class was then designated a 'final group'. Since a group must exceed seven quadrats before this value can be attained, any group containing less then eight quadrats was automatically declared a final group. Where subdivision occurred on more than one species, the species occurring first in alphabetical sequence was used (though the ambiguities, prefixed by +, are also shown in Fig. 2).

Out of the total of 452 species that occurred on the plots, the highest number per plot was 83, the lowest 5, and the average 38, 26. Computation was done in 1968 on an ICT 1900 computer using the Fortran programme for association-analysis (AANAL).

The Braun-Blanquet method

Association-analysis is a monothetic, divisive method in which successive subdivisions of the sample set take place on the presence or absence of a single species each time. The Braun-Blanquet method, in contrast, is a polythetic agglomerative method, using the joint occurrence of more than one species to characterize each community. Because of this basic difference in the treatment of data, the Braun-Blanquet method commended itself as an independent test of the relative merits and demerits of association-analysis as compared with the Braun-Blanquet method. The original data were therefore re-examined to determine whether a community classification that showed better correlation with environmental factors could be obtained.

The Braun-Blanquet method had been successfully used by Continental phytosociologists for over half a century but had in the past been poorly

received by workers not trained in Europe. This was largely due to the fact that earlier published work contained no precise English description of the actual method of synthesis which was consequently misunderstood and severely critized. Braun-Blanquet's techniques have since been revised and comprehensively described in English, amongst others by Becking (1957), Küchler (1967), Mueller-Dombois & Ellenberg (1974), and Werger (1974). After the results of the present study showed the success of the method, it has been increasingly applied in South Africa in diverse types of vegetation including Transvaal woodlands and grasslands (Coetzee, 1974a, 1975; Coetzee *et al.*, 1976; Van der Meulen, 1979; Bredenkamp & Theron, 1978, 1980), forests and bogs of the Drakensberg (Van Zinderen Bakker Jr, 1973; Van Zinderen Bakker Sr & Werger, 1974), karroid vegetation and grassland in the Orange Free State and northern Cape (Werger, 1973; Leistner & Werger, 1973; Werger & Coetzee, 1977; Werger, 1980), aquatic vegetation in Zululand (Musil, Grunow & Bornman, 1973) and in Cape fynbos (Werger, Kruger & Taylor, 1972; Boucher & Jarman, 1977; McKenzie, Moll & Campbell, 1977; Van der Merwe, 1977; Boucher, 1978; Glyphis, Moll & Campbell, 1978; Laidler *et al.*, 1978).

The application of the Braun-Blanquet technique in the present study deviated from standard practice. In the first place, from the phytosociologist's viewpoint the original data were faulty because sampling was systematic so that transitions between communities were also sampled. The data were also incomplete, because cover-abundance estimates for the species in each plot were not available; the coded data, assembled for association-analysis, were given only in the form of presence-or-absence. In addition, all species were not included in the tables. To do so, when working in such a rich flora, was beyond the scope of the trial: it would have greatly increased the complexity of the tables, and at that time no mechanical sorting apparatus (cf. Müller *et al.*, 1972) and no computer programmes to assist in sorting tabulated data were available. Therefore, the construction of the tables also differed from normal practice.

Instead of a single 'raw table' that included all plots, each plot was first assigned to the most appropriate of three broad habitat/vegetation types that had been erected from knowledge and experience gained in the original survey. Doubtful plots were placed in more than one type to establish where they fitted best. Species to differentiate each type were chosen partly with the help of a Species Constancy Table (Taylor, 1969) which showed the percentage occurrence of each of the 452 species in each of the 23 association-analysis groups. All positive dividing species of the plots selected, and other species that experience suggested might be of character value, were also included. Surround occurrences of the species selected, were included in the tables. The three raw tables were then manipulated in the usual way until 'blocks' of plots, or noda, represented by differential species, emerged. The plots within these noda were subjected to a Peculiarity Index test (Hall, 1965; Taylor, 1969) to determine whether they were appropriately placed. A Sneath's Modulus test (Sneath, 1962; Hall, 1968; Taylor, 1969) and a Fidelity Factor developed by Taylor (1969) were used to determine which species were most characteristic of the units already distinguished, and thereby to assess the efficiency of the species already chosen. The improved arrangements resulting from these tests were depicted in the three Final Tables (see Table 3).

RESULTS AND DISCUSSION

Association-analysis

The analysis resulted in a classification containing 23 final groups of sample plots (Fig. 2). Because of the low sampling density, all final groups contained seven or less plots; subdivision was therefore automatically terminated before a common level of heterogeneity was reached. The mapped final groups (Taylor, 1969, Map 2) did not yield entities that fitted the pattern of environmental variation satisfactorily. The final groups were therefore recombined and mapped at successively higher levels of association.

In some association-analysis studies in South African vegetation (e.g. Grunow, 1965; Downing, 1966) mapping of the first division made an ecologically interpretable pattern by separating the wetter from the drier sites. In the present study this was not the case. The first ten groups characterized by presence of *Struthiola ciliata,* for instance, contained not only the Inland Fynbos of rocky hills and mountains (category 1.2.1 of Table 1) but also the communities of the moist flats of the central plateau (Group 5) and communities transitional to Coastal Fynbos found on wind-blown sand (Group 4). In the same way, the major right-hand leg of the hierarchy shown in Fig. 2 characterized by absence of *Struthiola ciliata,* contained the remainder of hill and mountain vegetation, and the major portion of the moist flats and coastal communities. Therefore, no fusion of groups based solely on level of association could give a satisfactory interpretation of the hierarchy. The same phenomenon, that several closely related communities were widely separated and consequently obscured in the association-analysis hierarchy, was reported by Coetzee (1974b) for the Central Bankenveld of the Transvaal. In a recent comparable study of kwongan vegetation, an Australian counterpart of fynbos, Hnatiuk & Hopkins (1981) tried but soon discarded a monothetic divisive classification of site data, because it produced very heterogeneous results.

To interpret the association-analysis hierarchy, the composition of each final group was described and evaluated in detail and the habitat characteristics of each plot in each group tabulated in a summary of plot characteristics (Taylor, 1969). The variation in ecological and floristic content within each group was then summarized (Table 2) and the homogeneity of groups assessed both subjectively and by means of a Homogeneity Index (Taylor, 1969). The final groups did not, in general, combine

TABLE 2. — Summary of group characteristics

ECOLOGICAL					FLORISTIC						HOMOGENEITY			Habitat and vegeta
Stoniness			Soil moist-ure index	Sub-stratum	No. of plots in group	No. of spp. in group	No. of species in plots				Index	Subjective assessment		
ass	Percentage													
Max.	Min.	Max.					Min.	Max.	Mean	Range		Ecol.	Flor.	
5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
5	0*	18	1	T	6	145	53	83	69	30	25	High	High	Western hills and escarpment bearing recent p **Western Hillveld** rich in species.
0	0	0	1,3	T	4	126	44	74	64	30	10	High	Med.	Sandy flats along western escarpment; Weste **Tussock Marsh** elements.
5	3	80	1	T	6	159	23	75	57	52	6	Low	Low	Dry hill slopes and ridges with outcropping be impregnated; depauperate or atypical Weste
0	0	0	1	T	4	107	39	48	45	9	9	Med.	Med.	Patches of deep sand on coastal shelf or inlan with added coastal elements.
3	0	15	1-3	T	6	107	32	57	42	25	16	Med.	High	Poorly drained flats with **Plateau Fynbos**; plo bears Restionaceous **Upland Mixed Fynbos.**
5	40	49	1-5	T	3	88	39	49	45	10	15	Med.	High	High, cool, eastern slopes, mostly with iron-in unburnt **Mountain Fynbos** with **Dry Hillveld**
4	7	60	1	T	7	108	31	51	46	20	19	High	High	Warm, dry, rocky hills bearing homogeneous
0	0	0	1	T	2	60	35	36	35	1	18	Low	Med.	Heterogeneous dry-habitat ecotones; transiti or **Upland Mixed Fynbos.**
3	0	15	1	T	4	70	33	42	37	9	19	High	High	Dry, rocky ridges or sheetrock; depauperate
4	0	40	1	T	5	79	26	41	36	15	21	High	Med.	Dry, mainly rocky ridges with coarse, white s **Plateau Fynbos** or **Upland Mixed Fynbos.**
5	0	43	1	T+M	4	135	46	65	53	19	5	Low	Low	Either rocky hills with depauperate **Western** with **Dune Mixed Fynbos.**
4	5	60	1,2	T	3	99	44	60	51	16	13	Med.	High	Cool boulder-slopes or summits; **Mountain F Thicket** elements where protected from fire.
5	0	77	1	T+M	5	99	15	36	26	21	3	Low	Low	Heterogeneous: rocky summits and slopes; dune; vegetation correspondingly varied.
3	0	37	1-2	T	4	92	34	42	38	8	7	Low	Low	Gentle sandy slopes with Restionaceous **Upla** plot 51 on rock outcrop with depauperate D
5	0	6	1,3	T	3	76	27	45	34	18	8	Med.	Med.	Sandy coastal plain with **Dry Sandflats Comm** bedrock with atypical **Tussock Marsh/Uplan**
0	0	0	2-4	T	4	65	24	34	30	10	11	High	Med.	Moist flats with Restionaceous **Tussock Marsh**
5	0	5	1,2	T	2	46	28	35	32	7	37	Med.	High	Boundary between rocky hills and moist flats elements of both **Upland Mixed Fynbos** and
0	0	0	3,4	T	7	61	18	24	21	6	3	Med.	Med.	Moist flats with simple or complex **Tussock M Seepage Fynbos.**
3	0	6	1	T	5	99	24	50	32	26	8	Med.	High	Inland dunes, sandy slopes or coastal terraces *Metalasia-Passerina* **Fynbos.**
0	0	0	1,2	M	5	70	14	36	24	22	11	High	High	Stabilized littoral dunes with woody *Siderox*
3	30	55	1	T	3	37	7	24	16	17	8	High	Med.	Rocky littoral with semi-succulent variety of
0	0	0	3,4	T	3	40	14	22	19	8	5	Med.	Med.	Moist flats with simple or complex **Tussock M Seepage Fynbos.**
3	0	20	1-5	T+M	5	47	5	13	11	8	0	Low	Low	Completely heterogeneous as to both habitat

tion of estimate-symbols, see Taylor (1969)
Sandstone soils; M = transported sands of marine origin
Homogeneity Index values, see Taylor (1969)
t

into a classification that accorded closely with the ecological patterns in the Reserve. Only groups 1, 7, 16, 20 and 21 showed high floristic and ecological homogeneity. Groups 2, 4, 6, 10, 12, 18, 19 and 22 contained some anomalous misplaced plots, whereas the remaining ten groups represented small, isolated fragments of natural units. All groups except the five first mentioned could not be readily interpreted in terms of habitat factors because each group included samples of vegetation with different ecological characteristics. In order to obtain a classification that accorded with habitat, these final groups could not be combined by simply raising the level of heterogeneity; instead, their constituent plots had to be regrouped selectively on extrinsic characters of the habitat. This introduced a subjective element.

Fynbos has long been considered a vegetation having few discernible clear-cut communities. Although some fynbos species do show great ecological tolerance, most species have an optimum habitat in which they are more common than in others. If a finer measure of abundance had been used, a closer correspondence with habitat might have been obtained. In association-analysis, however, the only record of abundance is the crude 'present' or 'absent' rating, resulting in great loss of information. When fairly large sample plots are used, as in the present study, a species is likely to be recorded as present irrespective of whether it is abundant or occasional, so the optimum habitat of tolerant species will not be revealed by this technique. Many of the dividing species responsible for forming the hierarchy in this study appeared to be tolerant or wide-ranging species. Since this could explain the scattering of ecological units among the final groups, the autecological characteristics of the dividing species were closely examined (Taylor, 1969). It was found that, of the 32 dividing species of the hierarchy, only 11 were restricted to specialized habitats. The remaining 21 possessed wide ecological amplitudes, therefore having little or no character value for natural vegetation units. Dividing species, by definition, effect the most efficient subdivision of sets of plots. In the present study, those subsets that do not represent recognizable plant communities, may reflect the response of the vegetation to factors such as fire or grazing. (All plots in Group 2, for instance, had been burnt less than six years before the survey.) Analysis of variance and other tests failed, however, to reveal a simple correlation.

In a monothetic, divisive method like association-analysis, the final groups are determined solely by presence or absence of a small set of dividing species. No account is taken of the finer degrees of abundance of different species, which might constitute important differences between stands; nor of other species that might help to characterize the groups.

If natural vegetation units were discrete, with no transitions between them, the final groups of an association-analysis should theoretically reflect these natural units exactly. If transitions occur, they will be composed of tolerant species common to the intergrading units. Where tolerant species act as dividing species in an association-analysis, transitional plots will fall into different groups in which a dividing species is present in the one group and absent from the other. If presence-or-absence of these tolerant dividing species differentiates between heterogeneous subsets at a high level of $\sqrt{\frac{\chi^2}{N}}$, the transitional groups will be widely separated in the hierarchy. The greater the degree of intergradation between vegetation units and the greater the number of tolerant dividing species (especially at high levels of χ^2) the greater will be the fragmentation of legitimate communities into uninterpretable groups situated far apart in the hierarchy.

This would seem to explain some anomalies of the present association-analysis hierarchy. Fynbos communities in general intergrade freely. Many of the dividing species on the Cape of Good Hope Nature Reserve were shown to have wide ecological amplitude; many of the final groups include transitions and anomalous heterogeneous variations of natural units widely separated in the hierarchy.

However, this does not mean that natural units do not exist. There are indeed natural units characterized by assemblages of 'faithful' species (as shown later) but if the 'faithful' species are not dividing species, the natural units will not be revealed in an association-analysis.

Anomalous groups may arise not only from transitions between natural units but also from variations within them, provided the dividing species for these groups are sensitive to the factors causing the variations. It was shown, for instance, that *Leucadendron xanthoconus,* a wide-ranging dividing species, seemed to be a 'stray' in Plot 67 rather than a true indicator of its habitat, thus placing Plot 67 in the 'wrong' group. Again, *Struthiola ciliata, Roella ciliata* and others are sensitive to fire, being abundant in recently burnt stands but only occasional in long-unburnt stands. Such species will occur in all plots in recently burnt stands, but will be absent from some plots in unburnt stands; the latter plots will be relegated to a second group, often widely separated from the first, although both groups represent basically the same community. In addition, the second group may contain plots representing transitions between this community and another in which the dividing species are missing for reasons other than fire, so that this second group will comprise a mixture of natural units.

On examining the manner of regeneration of dividing species it appeared that many of those which regenerate from seed, e.g. the three mentioned in the preceding paragraph, were poor character species for the groups which they differentiate, whereas most of those which regenerate from coppice or sprouts were good character species for the groups which they differentiate. Seed-regenerating species are more sensitive to fire history of the vegetation than sprouting plants, being more abundant or rarer in often-burnt veld depending on their regeneration behaviour and the frequency of fires. Abundance of sprouting plants is much less affected by fire. Other factors that could

affect the abundance of dividing species, and therefore the grouping of plots, without radically altering the community, might be the intensity and rotation of grazing, the depredations of baboons, the influence of man, and local changes in habitat occasioned by biotic factors or small climatic variations, e.g. blown sand or desiccation of seepages.

Another cause of misclassified plots is the human factor, i.e. the accuracy of the field worker in recording data. This factor is independent of the method of data capture, but where mere presence or absence of a single species is of prime importance, its effect on the results will be much more serious than where several degrees of abundance, or alternatively a group of species, are used to characterize a vegetation unit. The effect is enhanced where, as at Cape Point, some of the key species — the dividing species in association-analysis — are inconspicuous or difficult to identify at certain stages or seasons. Normally, the human factor is not regarded as a serious source of error if the field worker is trained and observant. However, the rich fynbos flora contains many closely related plants often difficult to distinguish in the field, and the systematic positions of some taxa are still uncertain. The danger of inaccuracies resulting from misidentifications will therefore be greater than in simpler, better known floras.

Braun-Blanquet

The three Final Tables represent three broad vegetation types that can be identified in the original habitat classification (Table 1) as follows: (1) the Coast Fynbos and Broad-leaved Scrub (categories 1.1 and 2); (2) the Inland Fynbos of the moist flats (categories 1.2.5 and 1.2.6); and (3) the Inland Fynbos of well-drained slopes (categories 1.2.1 and 1.2.2). These tables (one of which, Table 3, is reproduced here as an example) show the noda or communities that were synthesized objectively and emerged naturally from the data matrix by the Braun-Blanquet method of manipulation. The objectivity of the method is borne out by an example: some refinements to Table 3 were effected by a colleague (M.J.A. Werger) who at that time had never seen the vegetation or the habitat, and this resulted in the subdivision of Community 2 into two floristically defined sub-communities that showed clear differences in structural and habitat features.

Each community, floristically defined by a group of differential species, could be satisfactorily interpreted in terms of habitat, as shown in Table 3 by the reference to the original habitat classification. There are, of course, transitional situations in any classification of vegetation where habitats intergrade, and this effect is enhanced where sampling has been rigidly systematic. Despite this, the tables revealed the existence of reasonably discrete communities and the floristic relationships between them.

On the other hand, the tables showed that most of the communities comprised a miscellany of association-analysis final groups, and conversely, that most final groups were scattered among a number of communities (see Table 3). Thus, either the association-analysis groups or the Braun-Blanquet communities do not accurately reflect the ecological patterns on the Reserve. Detailed examination and statistical tests have shown many of the association-analysis groups to be heterogeneous in terms of habitat — and indeed in floristics also, except for the dividing species. The Braun-Blanquet communities were found to be more homogeneous in terms of previously defined habitat groupings, and showed floristic relationships consistent with these groupings.

CONCLUSIONS

The advantage of association-analysis is that it produces a rapid, objective classification of units that can be mapped. However, in a monothetic, divisive system some plots are bound to be misplaced and this effect is enhanced if the occurrence of the dividing species depends on factors other than the habitat, as often appears to be the case in this study. Therefore, if the classification cannot be related to habitat without lengthy and complicated re-interpretation by someone with a detailed knowledge of the ecology of the area, the prime advantage of association-analysis is nullified and the map based upon it will be equally subjective. Indeed, if the original, crude 'block map' is transformed merely by rounding the outlines, the position of boundaries — especially where distances between points are large as in the present case — will be much less accurate than where the map is redrawn from an orthodox descriptive survey. On the other hand, if boundaries are interpolated by field re-examination, as much 'subjectivity' is employed as in orthodox mapping.

In association-analysis, where the path of subdivision depends solely upon the presence or absence of a single dividing species at each stage, the size, location and number of samples are crucial factors in determining the classification that results. In some instances, the plot size used in this survey appears too large to reflect a single vegetation unit; in others, it may be too small to represent the stand adequately where the flora is rich, the vegetation pattern coarse and the plot density low. The systematic location of plots makes for the inclusion of many transitional stands and, with the sampling technique used, the number of plots (representing 0,006% of the area of the Reserve) is too small to provide a picture of communities that can be accurately mapped. If stratified by major landscape features, the use of 100 plots would have been more efficient while subjectivity would have been minimized.

The present association-analysis is unusual in that the number of attributes (species) exceeds the number of individuals (samples). This has two disadvantages. Firstly, the effect of misplacement of a few plots owing to chance or to 'degree of absence' (absence in the plot through reduced abundance in the stand) will be relatively great. Secondly, because of the low number of constituent plots, final groups are terminated not by the limiting level of

TABLE 3. — Final synthesis table for moist flats

lysis Final Group No.	23	22	18	18	22	16	18	5	16	18	16	18	18	18	5	22	16	17	5	5	17	2	5	5	15	23	23
	32	58	50	49	18	6	11	17	7	56	22	38	65	48	55	83	78	46	35	64	37	13	16	79	14	29	47
y	1.2.6				1.2.5																						

sus	x	x	x	x																							
riscoides	x	o	x	o																							
osa	x	x	o	x	x	o																					
incta	o	x	o																								
a	x	o	o																						x		
	o		o	o																							
	o	o	o		o	o			x	x	x	x	o	x	x	x	x										
				x	o	o	o	x	x	x	x	o	x	o	x	x	x	o										T
ata						x	x	o	o		o	x	o	o	x	o		o				x					
ia subsp. *tenuifolia*					x		x	x	x	o							o								x	o	
sessilis					x	x	x	x	x																		
ia					x	x	o	x															o				
										o	x		x		o				x								
noides	o	x	x	x		o	o	x	x	x	x	o	x	x	o	x	o	o	o			x		x	o		
n nudum				o	x	x	o		x	o	x		x	x	o		x		x	x	x	x	x		x	x	
tacea			x		x	x	x	x	x	x	x	o	x	x	o	x	x	x	x	x	x	x	x	x			
		x	o		x	x	x	x	x	o	o	x	x	x	x	x	x	x	x	x	x		x		x	x	
			o	x	x	x	x	x	x	x	o	x	x	o	x	x	o	x	x	x	o	o	x		o		
rvifolia		x	x		o	x	x	x	x	o	x		x	x	x	x	x	o	x		x		x	x	o	x	
			o	x	x	x	x	x	x	o	x	x	x	x	x	x	o	x	x	x		x		x			
s			x		x	x	x	x	x	o	x	x	x	x	x		x	x	x	x	x		x	x	x	x	
ascosa				x	x	x		x	x	x	o		x			x	x		o	x	x		x	x		o	
					x	x	x	o	x	o	x	o	x	x	x		x		x	x		o	x	x	o		
			x		x			x		x	x	x	x	x	x	o	x	x	o		x				o		
achya					x		x			o												x	x		x	x	
		x	x			x		x	x	x	o		o	x	o		o		o						o		
	o	x	x			x	o	x					o			x					o						
																	x	o		x				x			
rpyllifolia	x																x							x			
a						x					x													x			

(1) Seepage Fynbos

(2a)

(2b)

(2) Tussock Marsh Community

(3) Simpler Tussock Marsh assemblages and transitions

Anom-alous plots

20
15
10
5

32	58	50	49	18	6	11	17	7	56	22	38	65	48	55	83	78	46	35	64	37	13	16	79	14	29	47

in plot
in plot surround

heterogeneity (usually highest single $\chi^2 \leq 3{,}84$) but by the limiting number of seven plots. Their individual χ^2 values therefore equal or exceed 3,84 but have not been determined. Consequently, while the final groups are not equally heterogeneous, their variation is not known; some might be capable of many further subdivisions, others of none, before reaching the limiting level. These drawbacks could to some extent be relieved by adopting the techniques of Crawford & Wishart (1968), who used a rapid agglomerative method after the initial divisive process, to check for any misclassifications.

The authors of association-analysis claim it to be a very useful tool in primary survey (Williams & Lambert, 1959). The aim of primary survey is not to elucidate minor factors causing community variation but to expose major habitat discontinuities reflected in major vegetational changes. It appears that association-analysis, as applied in this survey, makes a premature attempt at the former without accomplishing the latter. It has, perforce, produced a detailed and clear-cut classification which does not represent nature.

Association-analysis has two major drawbacks: the nature of the method, involving a rigid series of successive subdivisions on a single species each time, and the location of the plots on an equally rigid grid pattern. The adverse effect of misclassifications, poor sampling strategy and other drawbacks discussed above could be minimized by using an agglomerative method and a stratified location of plots.

The Braun-Blanquet method is agglomerative and polythetic. It starts from individual plots and combines units that are most similar, fusing groups at successively higher levels of the parameter used. In this way, a picture is obtained of the degree of similarity rather than the amount of difference between units. Moreover, as pointed out by Coetzee & Werger (1975), agglomerative classifications are regarded as more stable and as having higher extrapolative value when applied to regions outside the study area, than divisive classifications.

In the present study, when the Braun-Blanquet method was used in an independent assessment of the association-analysis, despite the drawbacks inherent in the data, the communities were found to be better correlated with habitats than either the final or recombined association-analysis groups. One must conclude that, with the type of sampling used, the synthetic phytosociological Braun-Blanquet method provides a more natural classification of communities of the Cape of Good Hope Nature Reserve than does the monothetic, divisive association-analysis method.

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UITTREKSEL

Met die opname is gepoog om breë plantegroeieenhede wat op 'n ekstensiewe skaal karteerbaar is, in die Kaap die Goeie Hoop Natuurreservaat op die suidelike punt van die Kaapse Skiereiland, tot stand te bring. Hierdie referaat vergelyk die doeltreffendheid van twee metodes, naamlik assosiasie-analise en die Braun-Blanquet metode soos deur die Zürich-Montpellier denkwyse van fitososiologie ontwerp. Eenhonderd 50 m² proefpersele wat die hele Reservaat bedek, was sistematies op ruitnet kruispunte op die 1: 18 000 topografiese kaart met intervalle van 1 000 tree (914 m) geplaas. Spesieslyste, waar die aanwesigheid van alle spesies met permanent herkenbare bogrondse dele in ag geneem is, was vir elke proefperseel aangeteken.

Drie-en-twintig finale groepe proefpersele waarvan net vyf tekens van floristiese en ekologiese homogeniteit getoon het, was vanuit die assosiasie-analise klassifikasie gekry. Van die oorblywende proefpersele is daar agt groepe met enkele onreëlmatige persele en tien groepe wat klein geïsoleerde brokstukke van natuurlike eenhede verteenwoordig. Die oorspronklike data was geanaliseer volgens die Braun-Blanquet metode om 'n onafhanklike klassifikasie daar te stel wat met die assosiasie-analise metode, vergelyk kan word. Die Braun-Blanquet gemeenskappe was meer homogeen wat vooraf gedefineerde omgewingsgroepe betref, en het floristiese verwantskappe wat verenigbaar is met die habitatsgroeperings getoon.

Die gevolgtrekking is dat die sintetiese fitososiologiese Braun-Blanquet metode gee 'n meer natuurlike klassifikasie van plantgemeenskappe van die Reservaat as die monotetiese verdelings assosiasie-analise metode met die tipe monsterneming in ag geneem.

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