Ordination by detrended correspondence analysis (DCA) of the vegetation of Swartboschkloof, Jonkershoek, Cape Province

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ABSTRACT

The data of a Braun-Blanquet vegetation classification was ordinated using detrended correspondence analysis (DCA). This was done at the Fynbos Biome intensive study site, Swartboschkloof, Jonkershoek, to investigate the factors determining the distribution of the plant communities. Superimposition of environmental data on the DCA ordination confirmed the indications of the Braun-Blanquet classification that the distribution of plant communities is most strongly correlated with soil geology and, to a lesser extent, with soil moisture status. The ordination also proved useful for examining the relationships between the transitional communities and the distribution of Swartboschkloof.

UITTREKSEL

Die gegewens van 'n Braun-Blanquetplantegroeiklassifikasie is georden deur gebruik te maak van neigingsverwydering-ooreenstemmings-analise (DCA). Dit is by die intensiewe studieterrein van die Fynbosbioom, Swartboschkloof, Jonkershoek, gedoen om die faktore wat die verspreiding van die plantgemeenskappe bepaal, te ondersoek. Deur die omgewingsdata op die DCA-ordening te plaas, is die aanduidings van die Braun-Blanquetklassifikasie bevestig dat die verspreiding van plantgemeenskappe die sterkste met grondgeologie en in 'n minder mate met grondvogstatus gekorreleer is. Dit blyk ook dat die ordening nuttig is om die verhoudings tussen oorgangsgemeenskappe en die bepaalde gemeenskappe van Swartboschkloof te ondersoek.

INTRODUCTION

Details of the physiography of the Swartboschkloof study site (Fynbos Biome Project) are given by Van der Merwe (1966), Werger, Kruger & Taylor (1972) and McDonald (1983, 1985). Werger et al. (1972) tested the Braun-Blanquet (B-B) method (Mueller-Dombois & Ellenberg 1975; Werger 1974) in the floristically rich vegetation of Swarboschkloof and classified the vegetation from 44 relevés. Eleven years later McDonald (1983 & 1985) re-surveyed Swartboschkloof more intensively and extensively (201 relevés) using the B-B phytosociological method with the objectives of re-classifying, mapping the vegetation and relating the plant communities to the environment.

Classification of the Swartboschkloof vegetation resulted in the description of 21 plant communities which were then mapped. The relationships between the plant communities and the environment were, however, not clear. The classification suggested that the plant communities are related to soil geology and soil moisture status, indicating a need for further data analysis using ordination.

Numerous ordination methods have been tested using simulated and field data, with the objective of establishing which method summarizes ecological data most effectively in 'low-dimensional space' (see Gauch 1982, for review of the literature). Detrended correspondence analysis (DCA) (Hill 1979) stands out as the most suitable ordination method for community analysis for very heterogeneous communities (Hill & Gauch 1980; Gauch 1982). Recent application of DCA includes studies in island vegetation of the Channel Islands off the coast of southern California (Westman 1983), in Tasmanian vegetation (Brown, Ratkowsky & Minchin 1984), in hazel

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scrub in northeast Ireland (Cooper 1984) and in savanna, forests, woodlands and grasslands in South Africa (Lubke, Morris, Theron & Van Rooyen 1983; Theron, Morris & Van Rooyen 1984; Whittaker, Morris & Goodman 1984; Deall 1985). The widespread trend towards the use of DCA in studies of vegetation, its robustness, low demands on computer-processing and its ease of output interpretation (Gauch 1982) were positive indications for application of DCA in analysing the Swartboschkloof vegetation data.

METHODS

Data were collected from 201 plots in the study area. One hundred of these were placed as close as possible to soil pits (Fry in prep.). In the fynbos vegetation 50 m^2 rectangular plots and in the forest vegetation 200 m^2 rectangular plots were used. In the fynbos samples, the long axes of the plots were aligned with the contour to avoid downslope variation. The forests are often narrow, so downslope orientation of the forest sample plots was necessary.

Species cover-abundance estimates were made using the Braun-Blanquet scale. Structural data of the vegetation were collected as were site-related data such as landfacet, altitude, slope, aspect and geology. Cover of surface rocks, litter and projected canopy cover of the vegetation were estimated on a percentage scale at each sample site. Data on the soils were obtained from Fry (in prep.).

Since the data collected by Werger *et al.* (1972) are compatible with those of this study, they were added to the data set for further analysis (see below).

Classification

The data were arranged in a two-way species-bysamples matrix and sorted with the aid of the TABSORT



FIGURE 1.—Diagram of the Braun-Blanquet table of the Mountain Fynbos shrublands of Swartboschkloof (after McDonald 1983).

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computer program (Boucher 1977). After initial sequencing, it became clear that it would be necessary to separate the fynbos samples from the forest samples, to treat them in separate tables. This distinction reflects the two vegetation types recognized: Mesic Mountain Fynbos (*sensu* Moll, Campbell, Cowling, Bossi, Jarman & Boucher 1984) and Afromontane Forest (White 1978).

The Mountain Fynbos table diagrammatically represented in Figure 1 was systematically sorted to give 20 groups. Of these, 17 groups were characterized as specialized communities. Two of the three remaining groups consist of species with wide ecological tolerance but with certain differential species of the specialized communites absent. The third of the latter three groups represents the widespread species in the fynbos vegetation of Swartboschkloof.

A similar procedure was followed with the forest vegetation data (Figure 2). Sequencing of the species-bysamples matrix resulted in seven groups. Three of these groups (3, 5 and 6 in Figure 2) were distinguished as true remnant Afromontane Forest communities; Groups 1 and 2 are communities transitional between fynbos and forest vegetation and Groups 4 and 7 represent species transgressive between the fynbos/forest transitional communites and the Afromontane Forest communities.

Ordination

The computer program DECORANA (Hill 1979) was used to ordinate the data. A number of options are open to the user of DECORANA. For the purposes of this study the standard or default option was used. The program also allows data subsets to be extracted from the whole data matrix so that different parts of the matrix may be ordinated separately (Peet 1980). The results of the DCA presented here therefore have the following limitations:

(a) the standard or default option was used throughout for all parameters except number of samples;

(b) number of samples and samples selected varied according to each respective ordination; and

(c) DCA scores for Axes I and II only are presented because the eigenvalues for these axes were closest to unity (1) in all cases.

The evaluation of DCA here is not a comparison with other ordination methods to establish its effectiveness. Rather, it is an evaluation to see what information it may provide additional to that given by the classification (McDonald 1983 & 1985). The 'standard two-step procedure' (Gauch 1982) was followed in the analysis:

(a) Summary of community patterns

The three groups of fynbos shrublands, the azonal seep communities, the forest communities and the fynbos-forest ecotonal communities determined in the classification, were superimposed on the ordination using different symbols. Firstly, the full data set (McDonald 1983 & 1985) was analysed (Figure 3), then the forest data were removed and the residual data analysed (Figure 4). Thirdly, the data from the azonal seeps and the forests were excluded and the remaining data ordinated (Figure 5). In order to test for a 'disjunction' between the



Relevés

FIGURE 2.—Diagram of the Braun-Blanquet table of the forest vegetation of Swartboschkloof (after McDonald 1983). 1 and 2, transitional between fynbos and forest communities; 3, 5 and 6, true remnant Afromontane Forest communities; 4 and 7, transgressive species between fynbos/forest transitional communities and Afromontane Forest communities. A, *Hartogiella schinoides–Diospyros glabra*; B, *Diospyros glabra–Rapanea melanophloeos*.

Erica hispidula–Diospyros glabra Shrublands and the *Erica hispidula–Restio sieberi* Shrublands, the data from the *D. glabra–Protea repens* Transitional Shrublands were excluded (Figure 6). Finally, the data from the Werger *et al.* (1972) survey were added to the above-mentioned full data set, with the objective of examining (a) the effect of additional data on the ordination and (b) the interpretation of the Werger *et al.* (1972) study in terms of the more recent classification (Figure 7).

(b) Comparison of community patterns with available environmental data to give an environmental interpretation of the ordination

The following environmental parameters were symbolically superimposed on the scatter plot representing

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FIGURE 3.—Ordination (DCA) of the whole data set from McDonald (1983) ◆, Afromontane Forest; ▽, azonal seep communities; ○, Erica hispidula-Restio sieberi Shrublands; ▲, Diospyros glabra-Protea repens Transitional Shrublands; ●, E. hispidula-Diospyros glabra Shrublands; □, Halleria elliptica-Cliffortia cuneata Shrubland; *, poor relevés. 1, Mesic Mountain Fynbos communities; 2-5, seep communities; 6, Halleria elliptica-Brabejum stellatifolium Short Forest; 7, boulder scree forests; 8, streambank forest.



FIGURE 4.-Ordination (DCA) of the data from the Mountain Fynbos (McDonald 1983) to demonstrate the relationships between the azonal seeps and fynbos; data from the Afromontane Forest communities are ex-cluded. \circ , Erica hispidula-Restio sieberi Shrublands; 🔺 , Diospyros glabra-Protea repens Transitional Shrublands; •, Erica hispidula-Diospyros glabra Shrublands; □, Halleria elliptica-Cliffortia cuneata Shrubland; ∇ , seep commu-nities. 1, Mesic Mountain Fynbos communities; 2-5, seep communities. G, Myrsine africana-Cliffortia dentata Shrubland. One releve is omitted from cluster 4 in this diagram.



FIGURE 5.—Ordination (DCA) of the Mountain Fynbos data only; azonal seep and forest vegetation data are excluded. ○, Erica hispidula-Restio sieberi Shrublands; ▲, Diospyros glabra-Protea repens Transitional Shrublands; ●, Erica hispidula-Diospyros glabra Shrublands. G, Myrsine africana-Cliffortia dentata Shrubland with 29 & 30 denoting two relevés representing this community (see text). E/F, a cluster of relevés from the closely related Rhus angustifolia-Myrsine africana and Myrsine africana-Olea europaea subsp. africana Shrubland communities. (Note: the communities represented by the symbols G and E/F fall within the Erica hispidula-Diospyros glabra Shrublands, hence the use of the symbol ●.)



FIGURE 6.—Ordination (DCA) of the Mountain Fynbos data, excluding data from the transitional fynbos communities reveals the disjunction between the *Erica hispidula–Diospyros glabra* Shrublands, ○, and the *Erica hispidula–Restio sieberi* Shrublands, ○. The open squares, □, represent the Halleria elliptica—Cliffortia cuneata Shrubland, indicating its affinity to the *E. hispidula–R. sieberi* Shrublands.

the ordination of the augmented data set: altitude, aspect, slope, geology, soil form, soil series, percentage cover of rocks and relative moistness or dryness of each sample site. Only soil geology and soil moisture showed positive correlation with plant community distribution (Figure 8). Results for the other environmental parameters are therefore not presented.



FIGURE 7.—Ordination (DCA) of the whole data set (McDonald 1983) augmented with data from Werger et al. (1972). ◆, Afromontane Forest; ▽, seep communities; ○, Erica hispidula-Restio sieberi Shrublands; ▲, Diospyros glabra-Protea repens Transitional Shrublands; ●, Erica hispidula-Diospyros glabra Shrublands; ■, Halleria elliptica-Cliffortia cuneata Shrubland; *, poor relevés; ■, Werger et al. (1972) relevés.

RESULTS AND DISCUSSION

Classification of the Mesic Mountain Fynbos

The diagrammatic table representing the Mesic Mountain Fynbos communities (Figure 1) was subdivided into three main sections; each section represents a group of communities. The first group (top left of diagram, Figure 1) is the *Erica hispidula–Diospyros glabra* Shrublands. These shrublands occur on soils of granite or colluvial derivation in the mid-central part of the study area. Included in this group are the essentially azonal 'seep' communities which are only included here for convenience of table sorting.

The second group (centre of diagram, Figure 1), the *Diospyros glabra-Protea repens* Transitional Shrublands is found on the ecotone between the above-mentioned first group and the third group (right-hand side of Figure 1). The third group is the *Erica hispidula-Restio sieberi* Shrublands associated with shallow sandstonederived soils above 750 m elevation.

From an applied research and management viewpoint it was necessary to know which of the above groups represented groups of easily identifiable communities. As mentioned, the classification indicated the existence of two distinct fynbos community groups and one transitional group, but there was doubt as to whether it could clearly define the relationships of these groups to each other.

The classification of the fynbos vegetation (apart from the azonal seep communities) also pointed to a strong relationship between the pattern of community distribution and soil parent material at Swartboschkloof. No other environmental factors appeared to be as strongly correlated with fynbos community distribution as soil geology. However, the possibility that one or more other factors such as availability of water, soil-water retention, slope, altitude and so on, also markedly affect community distribution could not be ruled out.

Classification of the remnant Afromontane Forest

The classification of the forest vegetation (Figure 2) shows that the two communities transitional between fynbos and forest are found on colluvial soils. *Brabejum stellatifolium* (wild almond) and the fern *Blechnum australe* are two species common to the transition communities and the forests along the perennial streams. This community can in turn be separated from the *Diospyros glabra-Rapanea melanophloeos* Tall Forest by the presence of water-loving species such as *Cunonia capensis* and *Ilex mitis*. Both granite and sandstone boulders are found in the streambeds. However, percentage rock cover in the streambeds is 30 % less on average than on the sandstone boulder screes where the *D. glabra-R*.



FIGURE 8.—Ordination (DCA) of the whole data set (McDonald 1983) with soil geology symbolically superimposed on the scatter of points. Sandstone-derived soil, ●; colluvial soil, ♡; granite-derived soil, ■.

melanophloeos Tall Forest and the *R. melanophloeos*-*Heeria argentea* Short Forest are found. The latter two communites are very similar; they are separated by the respective absence and presence of *H. argentea*.

Floristic similarity of the two communities constituting the remnant Afromontane Forest in Swartboschkloof indicated the need for further testing of the forest data as well, to establish whether the separation of this vegetation into three communities is justified.

Ordination

(a) Summary of community patterns

In the first analysis, the whole data set of the Swartboschkloof vegetation was analysed using DECORANA and the results plotted in a scatter diagram (Figure 3).

The separation of the Afromontane Forest (\blacklozenge) from the Mountain Fynbos is immediately apparent; this indicates the difference between these two vegetation types. The seep communities (\bigtriangledown), although part of the fynbos, are distinctly separate and are also not linked to each other.

If the forest vegetation is considered first (Figure 3), it is seen that there are three clusters of points. The first (cluster 6) represents the *Halleria elliptica-Brabejum stellatifolium* Short Forest which, although it is more forest-like, is transitional between fynbos and forest. Cluster 7 represents the forests on the boulder screes. This group of samples was split into two communities in the classification, based on presence and absence of *Heeria argentea*. It is therefore significant that the ordination clusters these samples together. Cluster 8 represents the streambank forest which is distinct from the boulder scree forests.

The fynbos vegetation is more complex than the forest vegetation and boundaries are not clear-cut, except for those of the seep communities (clusters 2, 3, 4 & 5) as noted above (Figure 3).

The community represented by 'cluster' 3 is characterized in the classification on the basis of one sample (192). This is unsatisfactory but the ordination shows that it has close affinity to the seep community represented by cluster 5. In Swartboschkloof this community is very localized but seeps with similar species composition have been noted in other parts of the Hottentots-Holland Mountains.

The intergrading of the Mesic Mountain Fynbos communities shown by the classification is borne out by the ordination (Figure 3, cluster 1). There is a more or less continuous scatter of points along Axis I which are then spread vertically by Axis II. By superimposing the three groups of fynbos communities defined in the classification, (McDonald 1983, 1985) the 'continuum' nature of the fynbos shrublands is demonstrated. The open circles (O) represent the Erica hispidula-Restio sieberi Shrublands; the shaded triangles (\blacktriangle) represent the *Diospyros* glabra-Protea repens Transitional Shrublands and the shaded circles (\bigcirc) represent the *E*. hispidula–D. glabra Shrublands. The open squares (D) represent one of the ecotonal communities, the Halleria elliptica-Cliffortia cuneata Shrubland transitional between fynbos and forest. Asterisks (*) denote poor samples. The difficulty

experienced in defining clear-cut community boundaries in the classification of the Mesic Mountain Fynbos is thus explained by the 'continuum' apparent in the ordination.

To investigate the relationship of the azonal seep communities (\bigtriangledown) to the fynbos communities, the forest data were excluded. The analysis (Figure 4) shows that seep communities 5 and 4 are close together on Axis I but widely separated on Axis II and although seep community 3 is unique it is closer to 5 on Axis II. At the same time, seep community 2 is close to 3 on Axis I yet close to 4 on Axis II. Community 2 is also more closely allied to the fynbos communities. Interpretation of this pattern with respect to the environment is discussed below.

The relationship of the fynbos vegetation groups to one another was investigated by removing the forest and seep data. The scatter of points in Figure 5 is more spread out along both Axes I and II because the limiting effect of the seep and forest data on the ordination is absent. This ordination does not differ significantly from the analysis in which the data for the fynbos and seep communities are included. The fynbos 'continuum' is still obvious but in addition the ordination has separated two clusters of samples from the main scatter of points. The first cluster (G in Figure 5) is a cluster of four relevés representing the Myrsine africana-Cliffortia dentata Shrubland. There were some doubts when classifying the vegetation as to whether releves 29 & 30 (see Figure 5) actually represented this community. In the classification the decision was made to retain these two releves as representing this community. The ordination vindicated this decision by clustering the four releves of the above-mentioned community, including releves 29 & 30, together.

The second cluster (E/F in Figure 5) consists of relevés from two communities (the *Rhus angustifolia– Myrsine africana* Shrubland and the *Myrsine africana— Olea europaea* subsp. *africana* Shrubland) closely related in the classification. This may be interpreted in two ways: (1) that, based on the floristic composition, the classification has made finer distinction between relevés than that achieved by DCA; or (2) that the ordination has clustered these relevés on the basis of some factor or factors not obvious in the classification.

Checking of the higher axes of DCA did not reveal any further reason for the differences observed between the clasification and the first two dimensions of DCA. The disjunction between the *Erica hispidula–Diospyros* glabra and *E.hispidula–Restio sieberi* Shrublands can be demonstrated if the data of the seeps, forests and transitional fynbos communities are excluded, and the remaining data ordinated (Figure 6). Since the intergrading transitional communities have been omitted, the disjunction between the two above-mentioned fynbos groups is not real. However, the ordination serves to show the relationship of these two groups to each other without the modifying effect of the data from the ecotonal communities.

The inclusion of data from Werger *et al.* (1972) (solid black squares in Figure 7) caused more definite clustering in the ordination; compare Figures 3 & 7 (augmented data set). It shows that sampling in the Werger *et al.*

study was more selective, particularly in that no samples were taken towards the 'lower' end of the fynbos gradient (DCA Axis I: 275–400 in Figure 7).

(b) Environmental interpretation

The habitat data collected at each site were superimposed on the ordination to test which factors were influencing the distribution of the plant communities. The interaction of environmental factors is complex and it is difficult to isolate one factor that has an overriding effect on vegetation pattern. No meaningful conclusions could be drawn when slope, aspect, altitude and percentage rock cover were superimposed on the ordination. This is attributed to the grossness of these factors; the vegetation is apparently sensitive to more specific habitat factors. The data for the soils of Swartboschkloof are not comprehensive (M. Fry pers. comm.) therefore parameters such as soil pH, percentage organic C, available N and P, particle-size distribution and soil-water retention properties could not be applied to the ordination to investigate their effects. The lack of these data prevented conclusive quantitative testing of the hypothesis that available soil moisture is one of the major determinants of vegetation patterns in Swartboschkloof. The ordination of the augmented data set gives the clearest definition of the environmental gradients. The moisture gradient is more or less at right-angles to the gradient associated with the soil parent material (Figure 8).

If the ordination of the fynbos is considered separately, there is a clear diagonal gradient from shallow sandstone-derived soils (left) to colluvial and granite-derived soils (right) on Axis I. This corresponds well with the pattern of fynbos community distribution: the *Erica* hispidula-Restio sieberi Shrublands and the Diospyros glabra-Protea repens Transitional Shrublands are associated with sandstone-derived soils whereas the *Erica* hispidula-Diospyros glabra Shrublands are found on colluvial or granite-derived soils. The hypothesis that soil parent material is a major determinant of fynbos community distribution in Swartboschkloof is therefore upheld.

Owing to the azonality of seeps and their dependence on phreatic water, it is not easy to relate their occurrence to soil geology. Correlation exists between seeps 2, 3 & 5 (Fig. 8) and sandstone-derived soils. Seep 4 is associated with colluvial soils in a bottomland situation, which could account for its remote displacement from the other seep communities in the ordination. With the forest communities it is found that the *Halleria elliptica-Brabejum stellatifolium* Forest and the *Rapanea melanophloeos-Cunonia capensis* Forest both occur on colluvial soils. They are, however, not close together in the ordination. This separation is attributed to differences in the water regime: the former community is found along drier seasonal drainage lines and the latter along moist perennial streams.

The forests on the sandstone boulder screes are thought to be associated with the irregular nature of the substrate. It would be difficult to prove that they owe their existence to the presence of sandstone rather than granite boulders, as one may be tempted to conclude from the ordination.

CONCLUSIONS

The detrended correspondence analysis has proved useful in that it has enhanced understanding of the relationships of the plant communities in Swartboschkloof. The ordination did not give much more information than was already known from critically analysing the classification, but it portrayed the communities in 'ecological space' of low dimensions which was helpful when relating communities or groups of communities to each other. An additional advantage of using DCA is that it effectively conveys information to researchers who are familiar with ordination techniques but unfamiliar with the Braun-Blanquet approach.

The clear distinction between Mountain Fynbos and Afromontane Forest was shown together with the position of the communities transitional between these two vegetation types. It was also possible to clearly demonstrate the 'continuum' nature of the fynbos vegetation. However, the distinct difference between the Erica hispidula-Diospyros glabra Shrublands and the E. hispidula-Restio sieberi Shrublands could be shown by removing the transitional fynbos communities, the seep communities and the forest communities from the data set. In the ordination the affinity of the seep communities to the fynbos is evident but their uniqueness stands out.

The unfortunate lack of soil data prevented an in-depth study of the effects of important soil parameters such as pH, organic carbon, available N and P, and soil moisture. However, the relative wetness-dryness assessment of sample sites gave sufficient information to show that soil moisture plays a secondary role in determining plant community distribution patterns. Application of the soil parent material data to the ordination supports the hypothesis that soil geology plays the major part in determining the distribution of the plant communities, particularly of the Mountain Fynbos, in Swartboschkloof.

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