CLASSIFICATION OF CRYPTOGAMIC COMMUNITIES IN THE MARITIME ANTARCTIC

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ABSTRACT. As a means of assessing the acceptability of an established subjectively generated classification of the bryophyte- and lichen-dominated communities of Signy Island, South Orkney Islands, in the maritime Antarctic, comparisons have been made with groupings derived from an objective approach using statistical procedures.

Three sites were selected in which most of the principal terricolous cryptogamic community types of the island were represented. Percentage cover of all species was recorded in quadrats of three sizes (100, 200 and 400 cm.^{2}) at a total of 240 sampling points. Qualitative notes were made at each sampling point describing the substratum and water regime. The data were then subjected to various statistical analyses.

i. Data from all the 400 cm.^{2} quadrats at each site were combined and subjected to normal association analysis. The classification generated is remarkably consistent with that produced subjectively. Groups of stands separated at $\chi^2 = 23 \cdot 00$ correspond very closely to what have been classed as associations in the subjective classification, while the sub-groups separated at $\chi^2 = 6 \cdot 64$ correspond to several of the sociations.

ii. From individual sites, data from each quadrat size were subjected to normal association analysis. The resulting classifications for each site are very similar for each quadrat size and, although the major divisions were usually made on different species, the quadrat groupings, separated at $\chi^2 = 3 \cdot 84$, are almost identical in each instance.

iii. Data from the three quadrat sizes at each site were subjected to inverse association analysis. The most informative dendrograms resulted from the data of the largest (400 cm.^{2}) quadrats. Most of the species combinations correspond satisfactorily to sociations of the subjective classification.

iv. The similarity of species composition and abundance among the largest sized quadrats at each site was determined by using a frequency-modulated homogeneity function, and the stands were subsequently grouped by a clustering method, average member linkage, to produce a dendrogram. Most major groupings are separated below a homogeneity (similarity) index of 50 per cent, signifying that each is a relatively discrete unit. These groups correspond closely to sociations recognized in the subjective classification. However, frequent interrelationships between the groups were evident when the values for similarity between each stand and the several major groups were plotted on maps of the sites.

v. Ordination by principal-components analysis of the major community groupings which had been produced by association analysis of the combined data from all sites revealed distinct floristic and environmental gradients. While each group of stands is associated with a particular habitat or soil type, floristic trends within each appear to be correlated mainly with moisture availability during the brief summer. This lends further evidence of continua within the vegetation.

It is concluded that the results of the various analyses strongly support the validity of the community groupings (associations, sociations) proposed in the subjective classification.

THE range of terrestrial plant communities occurring in the Antarctic is restricted, but habitats which are clear of ice and snow in summer are occupied by a simple type of cryptogam-dominated tundra vegetation. This is best developed in the maritime Antarctic, comprising the west coast of the Antarctic Peninsula and offshore islands, and various island groups on the Scotia Ridge (Holdgate, 1964). Within this region there is a wide variety of distinct communities comprising bryophytes and lichens, while the two native angiosperm species, *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv., are locally frequent in many coastal areas. Accordingly, two major floristic groupings were recognized by Gimingham and Smith (1970), namely an "Antarctic non-vascular cryptogam tundra formation" and an "Antarctic herb tundra formation".

The absence of any great complexity in this vegetation, either in physiognomy or in species diversity, provides a favourable context in which to carry out detailed examination of variation in community composition. Furthermore, recent developments in biological and environmental sciences in the Antarctic have led to a demand for an acceptable, comprehensive classification of vegetation for use in connection with terrestrial ecosystem studies, and with zoological, microbiological, pedological and other investigations.

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With these objectives in mind, contributions towards a classification were made by Holdgate (1964) and Longton (1967), while between 1964 and 1967 one of the present authors (R.I.L.S.) carried out a thorough phytosociological analysis of the vegetation of Signy Island, South Orkney Islands (lat. 60°43′S., long. 45°38′W.), and of a number of other localities in the maritime Antarctic to lat. 68°S. in Marguerite Bay in the south of the west side of the Antarctic Peninsula. Arising from these studies, Gimingham and Smith (1970) published a scheme of classification for the terrestrial vegetation of the maritime Antarctic, while a more detailed classification of the Signy Island communities has been given by Smith (1972) and this is summarized in Table I. This was intended as a preliminary rather than a definitive scheme,

TABLE I. SUMMARY OF SUBJECTIVE CLASSIFICATION OF CRYPTOGAMIC VEGETATION ON SIGNY ISLAND INCLUDING ONLY THOSE COMMUNITIES REPRESENTED IN THE PRESENT SURVEY (CONDENSED FROM SMITH (1972))*

Antarctic non-vascular cryptogram tundra formation

1. Fruticose lichen and moss-cushion sub-formation
   a. *Andreaea–Usnea* association
      i. *Andreaea* sociation
      ii. *Andreaea*–lichen sociation
      iii. *Andreaea–Himantormia lugubris* sociation
   b. *Tortula–Grimmia antarctici* association
      i. *Tortula* sociation
      ii. *Grimmia antarctici* sociation
      iii. *Tortula–Grimmia antarctici* sociation
   c. *Pottia austro-georgica* association
      i. *Pottia austro-georgica* sociation

2. Moss-turf sub-formation
   Polytrichum alpestre–Chorisodontium aciphyllum association
      i. *Polytrichum alpestre*–lichen sociation
      ii. *Chorisodontium aciphyllum* sociation
      iii. *Chorisodontium aciphyllum*–lichen sociation
      iv. *Polytrichum alpestre–Chorisodontium aciphyllum*–lichen sociation

3. Moss-hummock sub-formation
   a. *Bryum algens–Drepanocladus uncinatus* association
      i. *Bryum algens* sociation
      ii. *Bryum algens–Drepanocladus uncinatus* sociation
      iii. *Bryum algens–Drepanocladus uncinatus–Tortula excelsa* sociation

4. Moss-carpet sub-formation
   a. *Calligeridium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* association
      i. *Drepanocladus uncinatus* sociation
      ii. *Calliergidium austro-stramineum–Calliergon sarmentosum* sociation
      iii. *Calliergon sarmentosum–Drepanocladus uncinatus* sociation
      iv. *Calliergidium austro-stramineum–Calliergon sarmentosum-Drepanocladus uncinatus* sociation

Where only the generic name is given two or more species are involved. *Calliergidium austro-stramineum* has been previously referred to by Smith (1972) as *Brachythecium* cf. *antarcticum*.

but already, with certain amendments, it appears to have served the needs of workers in other disciplines and other localities, as well as describing appropriately certain categories encountered in plant ecological studies. The classification referred to employs in the first place physiognomic criteria, and secondly, floristic criteria. Although based on detailed survey work, it is subjective in approach. Consequently, it was regarded as desirable to carry out a separate investigation using, so far as possible, an objective approach and statistical procedures, in order to generate an alternative classification or set of classifications with a view to checking, amending or rejecting the proposed general purpose scheme.

* Abbreviated definitions of categories used in subjective classification (from Smith, 1972).
Formation: unit based on major physiognomic criteria of which life form is the most important.
Sub-formation: unit based on the growth form of the predominant components of respective stands.
Association: unit based on floristic similarity between component stands and differentiated according to the high constancy of certain species.
Sociation: unit based on the dominance of one or more species within stands of an association.

This aim necessitated detailed analysis of limited areas rather than widespread survey. The work was carried out in February 1966 on Signy Island (Fig. 1), where there is a wide range of environmental conditions producing a diversity of habitats in the ice-free areas and good representation of the two formations already mentioned. A detailed account of the climate, topography, soils and available habitats of Signy Island in relation to the vegetation has been provided by Smith (1972). Three study areas of not less than 1,000 m.[2] each were selected. The criteria for selection were: first, each study area should contain as wide a range of variation in community composition as possible and that, taking all three together, most of the variation to be observed throughout the island should be included and, secondly, each of the study areas should have some elements in common with the others. The choice of sites naturally depended upon subjective selection, but thereafter the methods employed were designed to minimize personal judgement in arriving at a classification.

Study Areas

Site 1 (Thulla Point)

The largest of the three sites lay east-north-east of Thulla Point on the west coast of the island. It extended in a north–south direction from near sea-level up a steep north-west-facing slope which reached a peak at about 55 m. a.s.l. before dipping gently towards a small lake. To include as much floristic variation as possible, a further 60 m. of rising ground on the south side of the lake was incorporated (see Fig. 3a). At the time of sampling the site was interrupted about mid-way up the scarp slope by a late-lying deep bank of snow, about 25 m. wide, while an extensive snow bank extended for approximately 100 m. from a little beyond the crest of the hill to the north shore of the lake. The area sampled was approximately 85 m. by 200 m., and quadrats were located at 14 m. intervals along seven transects each 14 m. apart.

This site possessed the widest range of edaphic and moisture regimes of all the sites and consequently the greatest diversity of community types including all the major cryptogamic associations, with the exception of saxicolous communities, occurring on Signy Island. The lower, gently sloping area at the northern end was permanently wet and dissected by numerous small melt streams. At the eastern side these flowed over mildly acidic quartz-mica-schist debris (pH 5·0–6·0), while to the centre and west they flowed over marble debris (pH 6·5–7·5). A little higher the substratum both below and above the snow bank consisted of dry marble outcrops and debris and occasional base-rich flushes (pH 7·5–8·2). Above this was a deep moss peat bank (pH 4·0–4·5) which extended over the crest of the hill and ended abruptly as an eroded face about 1·5 m. deep on its south side. A small knoll, occupied by a breeding colony of giant petrels (*Macronectes giganteus*), protruded through the most exposed part of this moss bank. The second patch of late-lying snow extended from the eroded face of the bank to the lake, beyond which the site was exposed and more sparsely vegetated with a substratum of the dry gravelly schist debris (pH 5·0–5·5) and scattered boulders.

Site 2 (Tern Cove)

This site had the least floristic variation of the three study areas and was situated a little to the west of the Tern Cove in the north-east of the island. Its long axis lay approximately north–south, commencing at the north end a little below the brow of a low hill (*c.* 25 m. a.s.l.) (see Fig. 6a). The gentle but windswept slope of the fairly dry quartz-mica-schist debris and scattered rocks in the upper part gave way to a shallow moss peat bank occurring on the well-drained stony ground. The slope terminated in a level area of drainage channels traversing the central area of the site; after a slight rise again over dry schistose soil and rocks, the ground levelled off on a wet terrace below several rock outcrops. Since there was no marble in the vicinity, calcicolous communities of flush and dry habitats were lacking and the range of pH was considerably less than at the other sites, varying from about 4·0 in the moss peat to 5·5 in the swamp communities, with intermediate values recorded for the dry schistose soils.

The site measured approximately 15 m. by 120 m. and data were recorded from quadrats located at 7 m. intervals along four transects spaced 5 m. apart.

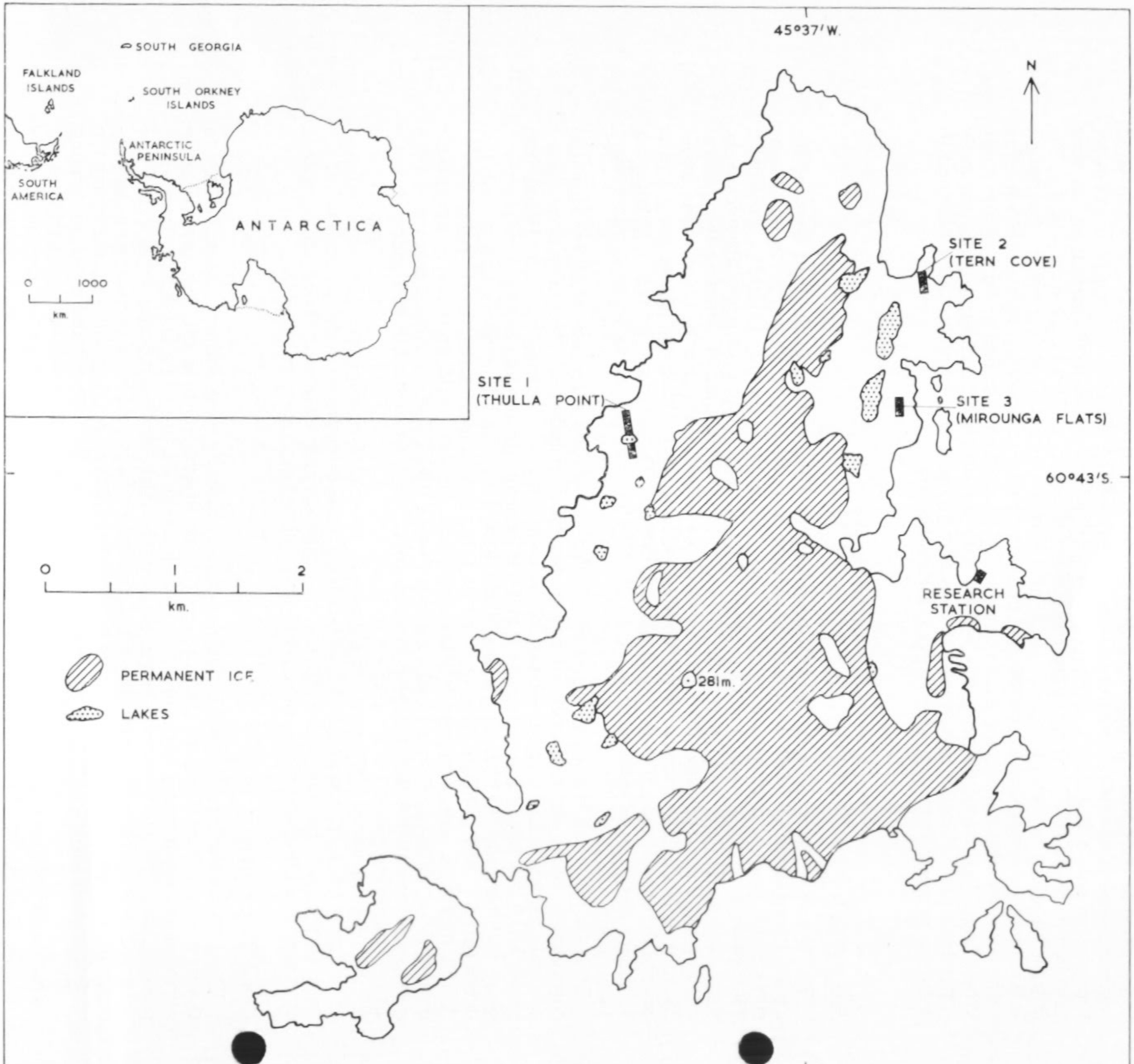


Fig. 1. Signy Island, South Orkney Islands, showing location of study areas. The inset shows the South Orkney Islands in relation to Antarctica.

Site 3 (Mirounga Flats)

This site was situated about 150 m. west of Mirounga Flats and about 1 km. south of site 2. Like site 1, it included both marble and quartz-mica-schist rocks and soils which supported a fairly wide range of community types, although the moss peat banks, prominent in the two other sites, were absent. The long axis was almost north–south, commencing at the north end in a wet basin, at about 15 m. a.s.l., through which several small streams from surrounding knolls were directed. The ground sloped gently to the south but rose sharply by about 2 m. on to a dry flat-topped knoll of predominantly marble rock and debris which diagonally traversed the central part of the site. Beyond this boundary between wet and dry ground there was a fairly abrupt transition to schist, although pockets of mixed marble and schist debris occurred in both areas. The base status of wet ground adjacent to the marble outcrop was considerably higher than that where the water flowed over the more acid schist and the range of pH was similar to that of site 1.

The site measured approximately 12 m. by 85 m. and data were recorded at 5 m. intervals along four transects spaced 4 m. apart.

METHODS

Data collection

The plant communities of the study areas were systematically sampled using quadrats arranged according to a rectangular grid. The longer axis of the grid was orientated so as to encounter as much as possible of the visible variations in floristic composition. The size and shape of the grid, and distances between stands (quadrats), varied to a limited degree between study areas to allow for local features of topography and extent of vegetation cover, as described above. 100 quadrats were recorded at site 1, 70 in each of the others, and these were numbered consecutively:

1–100 Site 1, Thulla Point
101–170 Site 2, Tern Cove
171–240 Site 3, Mirounga Flats.

To allow for consideration of the effects of sample size on the outcome of statistical procedures of classification and ordination, each 20 cm. by 20 cm. quadrat was subdivided into 100 cm.^{2} (10 cm. by 10 cm.), 200 cm.^{2} (10 cm. by 20 cm.) and 400 cm.^{2} (20 cm. by 20 cm.), thus providing three sample sizes at each sampling point. The largest quadrat size of 20 cm. by 20 cm. proved to be adequate for the relatively small number of species occurring in the cryptogamic communities under investigation (Smith, 1972).

At every recording point, lists were made of all species contained in the samples of each size, thus providing presence/absence data. For certain of the proposed analyses, however, it was necessary also to have quantitative data. Cover was regarded as the most appropriate quantitative measure and, in the relatively small sample areas employed, it was not difficult to estimate by eye to the nearest 5 per cent. Thus percentage cover was recorded for every species and was repeated for each sample size. From the 240 quadrats (400 cm.^{2} size) the total number of species included 29 mosses, seven liverworts, 29 lichens and two algae. Several species of crustose lichen were grouped in the appropriate genus since their identification was not possible in the field.

It was, unfortunately, not possible to undertake a quantitative investigation of habitat factors at each sampling point. However, notes were made describing the topography, substratum and, as far as possible, water supply at each point, these qualitative data being indicated on a map of each site (e.g. Figs. 3a and 6a).

Data exploration

Normal association analysis. Since the aim was to generate classifications, a widely used statistical method of classifying presence/absence data was employed, viz. association analysis (Williams and Lambert, 1959, 1960). A computer program was employed using $(\chi^2/N)^{\frac{1}{2}}$ as the test of association between species, on the basis of their occurrence in quadrats. Dendrograms were drawn up, placing the successive divisions of sample groups at levels determined by the highest χ^2 value shown by the species responsible for the division, for positive or negative association with any other species in the particular group of samples under test.

This normal association analysis was applied to the combined data from all study areas (240 quadrats) using the largest sample size.* It was also carried out for each sample size in each study area separately. The resulting dendrograms were terminated arbitrarily at levels beyond which ecological interpretation would appear to be difficult or impossible.

By this means, stands were classified into groups. Representation of each group was entered on maps of the study areas, and the distributions were compared with those of habitat factors in so far as information was available. The floristic composition of each group of samples was also examined and compared with the groups (sociations) recognized in the initial subjective classification.

Agglomerative classification. Since association analysis is a monothetic approach to classification, an opportunity provided by the kindness of Dr. A. V. Hall, Bolus Herbarium, University of Cape Town, was taken to classify the same data by means of a polythetic centroid-based agglomerative technique. This analysis involved the grouping of stands on the basis of a measure of floristic similarity among samples (either presence/absence or percentage cover data) calculated using the frequency-modulated relative homogeneity function (Hall, 1967) together with a clustering method, average member linkage (Hall, 1969), in order to form a dendrogram (Hall, 1970). This technique of classification is amenable to the use of both presence/absence and abundance data. However, the processing of presence/absence (0–1) data tends to produce an oversimplified classification and for this reason analysis of such data, for each of the three sample sizes, was restricted to one study area (site 2). For each site the more meaningful percentage cover data (0–100) for the largest sample size (400 cm.²) were also analysed.

The major groupings derived from the dendrograms based on cover data were then systematically evaluated to show trends within each grouping and interrelationships between groupings, as described by Hall (1970). Those quadrats within a particular group which are linked at a high level of homogeneity or similarity constitute the core from which the average number or centroid is determined by averaging the data. This represents a community and the similarity of each community within a site is independently compared relative to each stand with regard to species composition and abundance. The similarity values for each community are then plotted on separate maps of the site to produce a series of resemblance maps.

Inverse association analysis. As a further test of the validity of some of the groups of species recognized in the subjective classification, inverse association analysis (Williams and Lambert, 1961) was carried out on the presence/absence data from each sample size, for each study area separately. The grouping of species was terminated at the 1 per cent level ($\chi^2 = 6 \cdot 64$).

Ordination using principal-components analysis. Although classification was the main objective rather than a full study of variation in community composition, ordination was also carried out in order to provide some indication of major trends of variation and their possible ecological significance. For this purpose, the main groups of stands obtained at $\chi^2_{max.} = 23 \cdot 0$ from the normal association analysis of the bulked samples (400 cm.² quadrat size) from all study areas were independently subjected to principal-components analysis of matrices of Orloci's similarity coefficient (Austin and Orloci, 1966; Orloci, 1966) using the presence/absence data. Diagrams were drawn of the relative positions of stands in relation to the first two axes of variation extracted; use of the third axis appeared to add little information which could be readily interpreted. The first and second components account for between 14 and 30 per cent and between 12 and 14 per cent of the total variation, respectively. These ordinations of the stands were used for superimposing cover values of important species. Any resulting trends of variation were interpreted as far as possible in the light of knowledge of the autecology of the species concerned and, where possible, of information on the habitat in which the samples were situated.

* Although there were certain differences in the results from the three sample sizes, these were not of major importance. The largest sample size (400 cm.²), comprising the greatest information content, was chosen for association analysis of bulked data from all study areas.

Subjective community analysis. After examination of the species composition and cover abundance, each stand was subjectively ascribed to an appropriate association and sociation according to the system of classification proposed by Gimingham and Smith (1970) and Smith (1972) (see Table I). Each association was then denoted by a code letter and the sociations within these by a number (see Table II). By applying the same system of coding to the relevant groups produced by the objective analyses, the groupings derived from each could then be plotted on maps of each site and compared directly.

Results

Normal association analysis

Analysis of combined site data

The results of the association analysis of the combined data from the three sites are illustrated in the dendrogram in Fig. 2. This reveals four major groups separated at $\chi^2_{\text{max.}} = 58 \cdot 0$ with the first division being made on the presence or absence of *Andreaea* spp. Disregarding the three stands separated by the presence of *Pottia austro-georgica*, these four groups represent all the principal terricolous cryptogamic vegetation types on Signy Island, i.e. those communities dominated by calcifuge species of *Andreaea* and fruticose lichens (89 quadrats) typical of dry stony exposed ground; those dominated by calcicolous mosses, particularly *Bryum algens*, *Grimmia antarctici* and species of *Tortula* (35 quadrats) typical of dry basic soils; those dominated by the tall turf-forming mosses *Chorisodontium aciphyllum* and *Polytrichum alpestre* (30 quadrats) which develop acid peat banks on well-drained slopes; and those dominated by the hydrophytic mosses *Calliergidium austro-stramineum*, *Calliergon sarmentosum* and *Drepanocladus uncinatus* (83 quadrats) in permanently wet situations, with a tall ecotype of *Bryum algens* occurring in base-rich flushes. Although a *Pottia austro-georgica* association has been recognized on Signy Island, it is not an important community type and is considered as a modification of the calcicole *Tortula–Grimmia antarctici* association.

The separation of the stands representative of the base-rich flushes from those of the more acid, soligenous swamp communities is made at the $\chi^2_{\text{max.}} = 23 \cdot 0$ level, while a further division is also made of one of the "+ *Andreaea*" groups. The groups separated at this level correspond very closely to what have been classed as associations in the subjective classification. Thus groups AI, AII and AIII are all representative of the *Andreaea–Usnea* association, group B corresponds with the *Tortula–Grimmia antarctici* association, group C with the *Polytrichum alpestre–Chorisodontium aciphyllum* association, group D with the *Pottia austro-georgica* association, group E with the *Bryum algens–Drepanocladus uncinatus* association, and group F with the *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* association.

26 subgroups are separated at $\chi^2_{\text{max.}} = 6 \cdot 64$ (corresponding to the 1 per cent level) and these include all the sociations recognized from a subjective examination of the quadrat data, although in many instances some recur in separate groups. Few of these sub-groups contain less than five quadrats each. When the appropriate quadrats within each community sub-group in Fig. 2 are transferred to the map of each site, there is a distinct similarity in the distribution of the communities both in relation to the groups of the subjective classification (sociations) and to the groups derived from association analysis of the individual site data (see below) as well as to the features of the substratum. The distribution of the community groupings derived from the various analyses for site 1 (Foca Point) is illustrated in Fig. 5. The relationship between the community groups and sub-groups of the bulked data association analysis and the associations and sociations of the subjective classification is given in Table II.

Analysis of individual site data

The results of these analyses were briefly outlined by Gimingham (1967). The dendrograms (not illustrated) resulting from association analysis of the data of each of the three sites treated independently produce groupings very similar to those separated when the data were combined, although fewer classes were represented at each site due to the reduction of data being processed. For each site, dendrograms were produced for each of the three quadrat sizes.

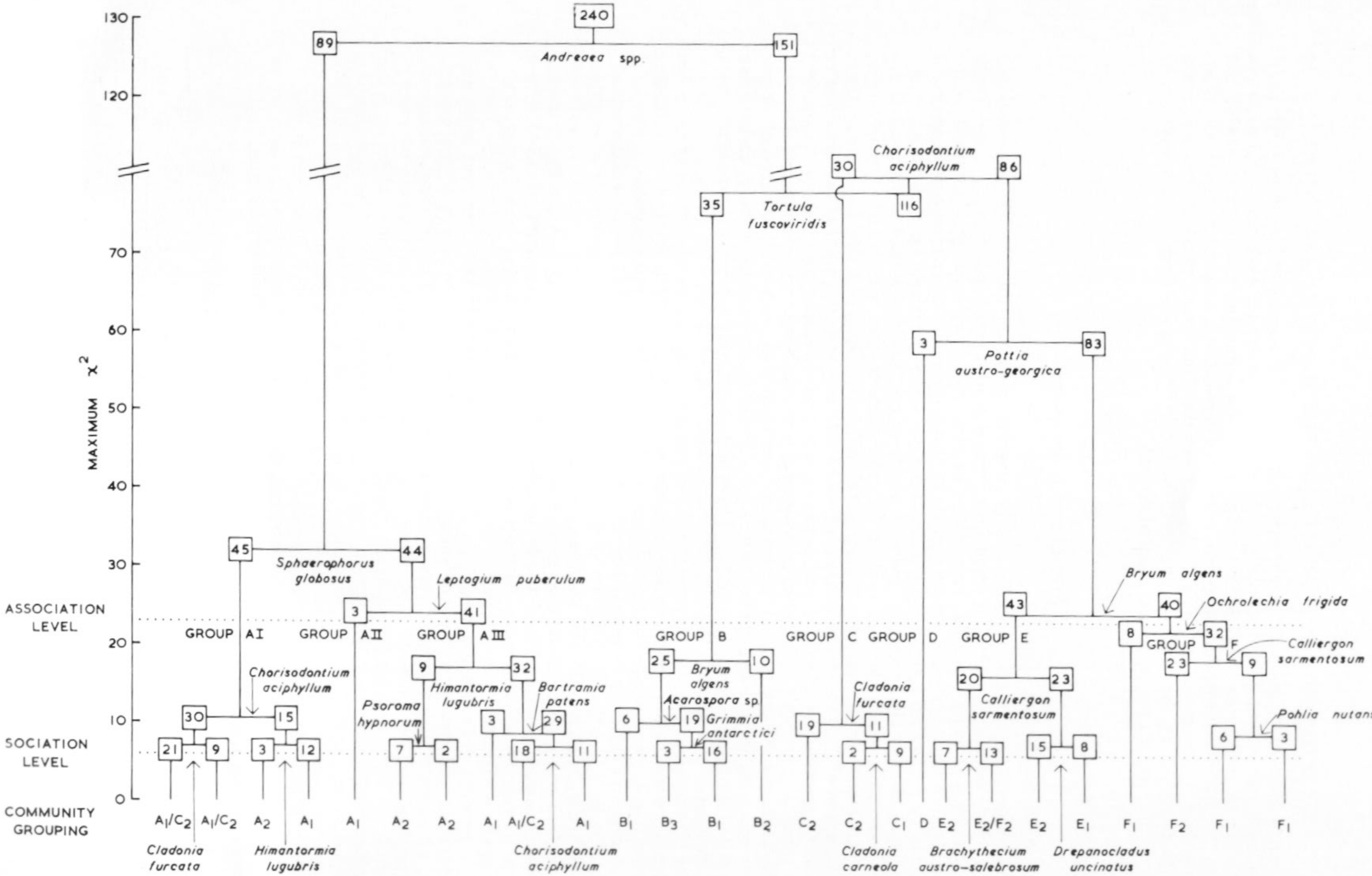


Fig. 2. Normal association analysis of combined data from three sites (240 stands) using 400 cm.² quadrats. Groups terminated at $\chi^2 = 23\cdot00$ correspond to associations of the subjective classification, those terminated at $\chi^2 =$ [illegible]64 correspond to sociations of the subjective classification. [illegible]e groupings are described in Table II.

TABLE II. RELATIONSHIP BETWEEN COMMUNITY GROUPS DERIVED FROM ASSOCIATION ANALYSIS OF COMBINED DATA FROM THREE SITES (FIG. 2) AND THE ASSOCIATIONS AND SOCIATIONS RECOGNIZED IN THE SUBJECTIVE CLASSIFICATION (TABLE I)

Association-analysis groups at $\chi^2 = 23\cdot00$	*Corresponding association in subjective classification*	*Association-analysis groups at* $\chi^2 = 6\cdot64$	*Corresponding sociation in subjective classification*	*Symbol used for community groups in Figs. 2, 3, 5 and 6*
AI, AII, AIII	*Andreaea–Usnea* association	AId, AIIa, AIIIc, AIIIe	*Andreaea*–lichen sociation and *Andreaea* sociation	A1
		AIa, AIb, AIIId	*Andreaea*–lichen sociation (usually with $>$20 per cent cover afforded by *Chorisodontium aciphyllum*)	A1/C2
		AIc, AIIIa, AIIIb	*Andreaea–Himantormia lugubris* sociation	A2
B	*Tortula–Grimmia antarctici* association	Ba, Bc	*Tortula* sociation (usually with $>$20 per cent cover afforded by *Bryum algens*)	B1
		Bd	*Tortula–Grimmia antarctici* sociation	B2
		Bb	*Grimmia antarctici* sociation	B3
C	*Polytrichum alpestre–Chorisodontium aciphyllum* association	Cc	*Chorisodontium aciphyllum* sociation	C1
		Ca, Cb	*Polytrichum alpestre–Chorisodontium aciphyllum*–lichen sociation and *Chorisodontium aciphyllum*–lichen sociation	C2*
D	*Pottia austro-georgica* association	Da	*Pottia austro-georgica* sociation	D
E	*Bryum algens–Drepanocladus uncinatus* association	Ed	*Bryum algens* sociation	E1
		Ea, Ec	*Bryum algens–Drepanocladus uncinatus* sociation	E2
		Eb	*Bryum algens–Drepanocladus uncinatus* sociation (usually with $>$15 per cent cover afforded by *Calliergon sarmentosum*)	E2/F2
F	*Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* association	Fa, Fc, Fd	*Drepanocladus uncinatus* sociation	F1
		Fb	*Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* sociation–and *Calliergon sarmentosum–Drepanocladus uncinatus* sociation	F2

* In the subjective classification of the quadrat data some stands representative of the *Polytrichum alpestre*–lichen sociation have been recognized and symbolized as C3 (e.g. in Figs. 5b and 7).

Basically, the final groupings, terminated at $\chi^2_{max.} = 3 \cdot 84$ (corresponding to the 5 per cent level), are the same for each quadrat size at any one site, although those of the largest plot size tend to bear the closest resemblance to the sociations of the subjective classification. However, the species on which the divisions are made vary from one sample size to another, e.g. at site 1 (Thulla Point), the first divisions for each quadrat size are made on *Bryum algens* (100 cm.^{2} quadrat size), *Chorisodontium aciphyllum* (200 cm.^{2}) and *Brachythecium austro-salebrosum* (400 cm.^{2}), respectively.

Not all the groupings correspond exactly to the sociations of the subjective classification and certain quadrats of substantially different species composition are classed together on the basis of the presence of one or more relatively insignificant species. Since percentage cover is not considered in association analysis, a group may possess a species with anything from 1 to 100 per cent cover. In the subjective classification, however, a species with a high cover abundance is generally the dominant from which sociations derive their name, whereas one affording insignificant cover is usually treated as an accompanying species within the sociation. For example, stands in which *Bryum algens* is the predominant species (representative of the *Bryum algens* sociation in the subjective classification) are frequently grouped with stands in which this moss afforded low cover (e.g. as a component of the *Tortula* or *Tortula–Grimmia antarctici* sociations). Similarly, stands dominated by species of *Andreaea* and fruticose lichens (*Andreaea*–lichen sociation) are occasionally grouped with *Chorisodontium aciphyllum*-dominated stands. Thus *Andreaea* and/or lichen-dominated stands in which *C. aciphyllum* affords low cover are associated with stands formed solely by this tall turf-forming moss which often produces extensive banks exceeding 1 m. in depth.

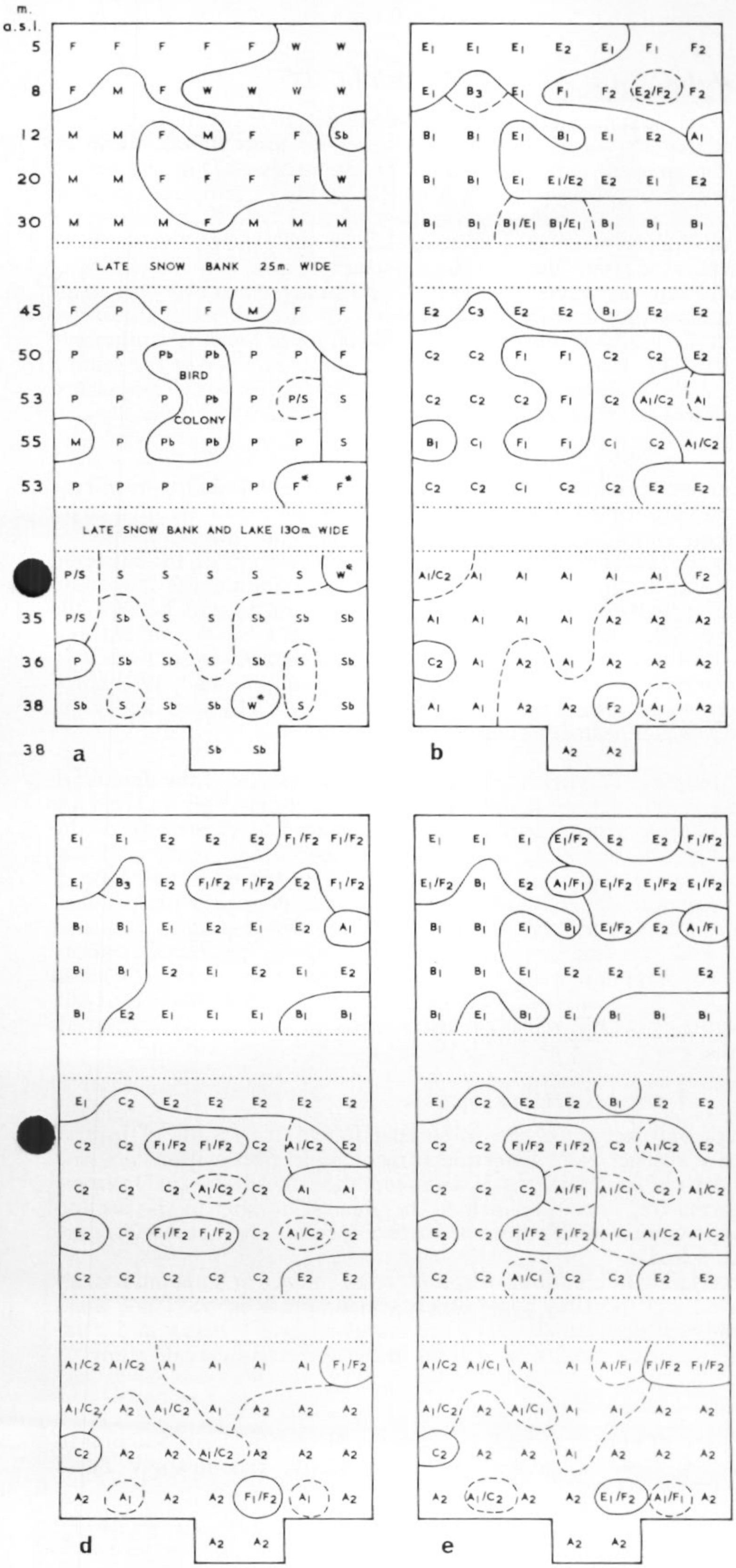
When the association-analysis groupings of the three quadrat sizes are entered on maps of the appropriate site (e.g. for site 1; see Fig. 3d, e and f) there is a fairly close correspondence both between the results for the different quadrat sizes within a site and between the different quantitative methods employed, bearing in mind that several of the groups are closely related with regard to species composition but not to abundance. Thus stands which in one analysis are classed as a *Bryum algens–Drepanocladus uncinatus* community (E2) may be classed as a *Drepanocladus uncinatus* community (F1) or *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* community (F2) in another analysis. Consequently, where an association-analysis grouping contains several stands representative of two sociations according to the subjective classification, this has been designated a "mixed group", e.g. A1/C2, A1/F1, E1/F2, etc. This also applies to certain groups produced by the association analysis of the bulked data from all the sites described above.

Site 1 (*Thulla Point*). For each quadrat size there is a fairly consistent demarcation between the distribution of certain of the association-analysis groupings corresponding to major features of the substratum (Fig. 3a). Thus, with occasional exceptions where a stand appears to be misclassified with regard to the subjective classification, there is a sharp boundary between stands dominated by *Calliergon sarmentosum* and *Drepanocladus uncinatus* in wet habitats, those dominated by *Bryum algens*, *Grimmia antarctici* and species of *Tortula* in wet or dry base-rich habitats, those dominated by species of *Andreaea* and fruticose lichens on more acid dry soils and those dominated by *Chorisodontium aciphyllum* and *Polytrichum alpestre* forming

Fig. 3. Maps of site 1 (Thulla Point) indicating at each sampling point features of topography and substratum, and community type derived from the subjective classification and various association analyses of quadrat data.
a. Topography and substrata.
b. Community groupings derived from subjective classification.
c. Community groupings derived from association analysis of 400 cm.^{2} quadrat size data combined from all sites.
d. Community groupings derived from association analysis of individual site 100 cm.^{2} quadrat data.
e. Community groupings derived from association analysis of individual site 200 cm.^{2} quadrat data.
f. Community groupings derived from association analysis of individual site 400 cm.^{2} quadrat data.

Key to symbols in (a): W, wet (acidic); F, wet (base-rich flush); S, dry or moist schist debris (acidic); M, dry or moist marble debris (basic); P, moist acidic moss peat, usually $>$ 25 cm. depth; b, boulders or large stones; * wet hollow.

For the key to symbols in (b)–(f), see Table II.


m. a.s.l.
5
8
12
20
30
45
50
53
55
53
35
36
38
38
LATE SNOW BANK 25m. WIDE
BIRD
COLONY
LATE SNOW BANK AND LAKE 130m. WIDE
a
b
c
d
e
f

deep peat banks. Because of the close similarity in species composition of many of the *Tortula–Grimmia antarctici* stands and the *Bryum algens–Drepanocladus uncinatus* stands, these are not clearly distinguished in the smallest and largest quadrat size analyses (Fig. 3d and f), but the distribution of these two communities resulting from the 200 cm.^{2} quadrat size analysis on the map (Fig. 3e) is remarkably close to that based on the subjective classification (Fig. 3b) and also that derived from the bulked data analysis (Fig. 3c). In these maps the stands in flushed habitats are clearly separated from those on the dry marble soils. It is interesting to note that the *Drepanocladus uncinatus*-dominated area (with high *Pohlia nutans* cover) occurring in the giant petrel colony features prominently in all analyses, as does a small *Calliergon sarmentosum*-dominated wet hollow amidst the *Andreaea–Himantormia lugubris* community at the south end of the site, and an *Andreaea*-dominated stand on a boulder in the swamp community at the north-east corner of the site. The analysis of each quadrat size distinguished between the closely related *Andreaea*–lichen stands and the *Andreaea–Himantormia lugubris* stands in the southern area.

Site 2 (*Tern Cove*). Only three major community types occurred at this site and each is prominent in the association-analysis groupings for all quadrat sizes. However, the relatively high cover of *Chorisodontium aciphyllum* in many *Andreaea*-dominated stands, and the occurrence of scattered cushions of *Andreaea* spp. amongst the shallow *C. aciphyllum* banks on the sheltered slope, gives rise to a large mixed group (A1/C2). The dendrograms for the 100 cm.^{2} and 200 cm.^{2} quadrat size data are virtually identical, with the first major dichotomy being made on *Usnea antarctica*. The first division in the 400 cm.^{2} size is made on *Cladonia furcata*, but the other divisions are similar to those of the smaller sizes. An important division is made in each quadrat size on *Chorisodontium aciphyllum*. One stand, occupying a small wet hollow dominated by *Calliergidium austro-stramineum* amidst an otherwise dry gravelly area supporting an *Andreaea*–lichen community, was repeatedly isolated in each analysis.

Site 3 (*Mirounga Flats*). The groupings derived from the association analysis of the data from the three quadrat sizes produce clearly defined communities when superimposed on the map of the site. The distribution of these groups corresponds closely to that derived from the subjective classification, although the boundary between the base-rich and more acid wet habitat stands varies from analysis to analysis. This is due largely to the preponderance of *Drepanocladus uncinatus* in communities of both the *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* and *Bryum algens–Drepanocladus uncinatus* associations represented. For each quadrat size the association analysis produced separate groups of calcicolous species representative of the *Tortula–Grimmia antarctici*, *Grimmia antarctici* and *Pottia austro-georgica* sociations. Two isolated stands representative of the *Andreaea*–lichen sociation occurring within more extensive areas of contrasting vegetation stand out clearly in all analyses.

Inverse association analysis

In general, minor differences only are apparent on comparison of the results of inverse association analysis of presence/absence data from the three sample sizes within any one study area. The dendrograms derived from analysis of data from the largest (400 cm.^{2}) sample size are perhaps the most informative, since they include the greatest number of species and are largely free from end groups composed of only one or two species. These, therefore, are shown for each site in Fig. 4a, b and c.

Despite variation in detail, certain combinations of species recur in two, or sometimes in all three study areas. These at least, and possibly some others which appear in one study area, may be expected to be of ecological significance. They are discussed briefly below and compared with the component species of categories recognized in the subjective classification.

Groups referable to the Andreaea–Usnea association

For each site the analyses have produced at least two groups of species corresponding to communities within the *Andreaea–Usnea* association of the subjective classification. These

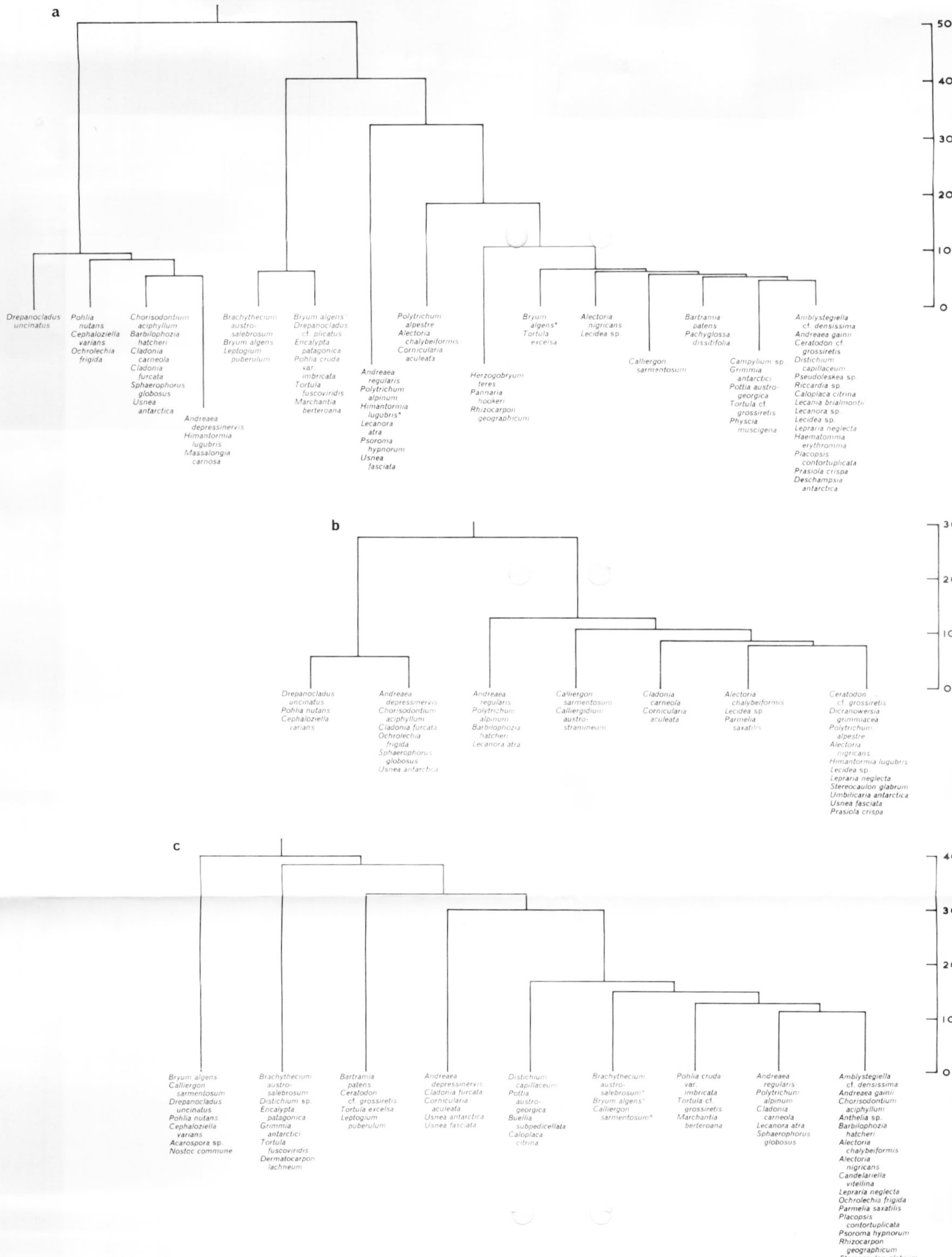


Fig. 4. Inverse association analysis of species in 400 cm.^{2} quadrats at each of three study areas. Species groups produced at the 1 per cent level (χ^2 = 6·64). (Note: In a few cases, marked with an asterisk, a species appears more than once in the same dendrogram. This results from recognition in the field of two apparently distinct taxa which were later found to be referable to the one species.)
a. Site 1 (Thulla Point).
b. Site 2 (Tern Cove).
c. Site 3 (Mirounga Flats).

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communities comprise several species of fruticose lichens and small moss cushions typical of exposed, comparatively acid dry rock and soil.

The details of the species groups vary to some degree, but at sites 2 and 3 the classification has grouped *Andreaea depressinervis* with a species of *Usnea* and other fruticose lichens, while at each site *A. regularis* has been grouped with *Polytrichum alpinum*. Both groupings are representative of the *Andreaea*–lichen sociation; the presence of *P. alpinum* as an important associate in this sociation has been noted previously by Smith (1972). Other groupings may also be referred to this sociation, e.g. at site 1 the combinations of *Herzogobryum teres*, *Pannaria hookeri* and *Rhizocarpon geographicum*; *Alectoria nigricans* and *Lecidea* sp.; *Bartramia patens* and *Pachyglossa dissitifolia*; and at site 2 *Alectoria chalybeiformis*, *Lecidea* sp. and *Parmelia saxatilis*.

At site 1 there is a group containing *Andreaea depressinervis*, *Himantormia lugubris* and *Massalongia carnosa*, the latter lichen being epiphytic on *Andreaea*. Although only encountered in the one area, this corresponds with the *Andreaea–Himantormia lugubris* sociation.

Groups referable to the Tortula–Grimmia antarctici association

Several groupings are clearly referable to components of the *Tortula–Grimmia antarctici* association belonging to dry base-rich substrata. These groups are well represented at sites 1 and 3 where there was a strong influence from marble outcrops, but they are absent from site 2 where calcareous substrata were lacking.

At both sites there is a group containing *Grimmia antarctici*, a species of *Tortula* and several other calcicolous species, and a group in which another species of *Tortula* and calcicolous mosses occur. These assemblages can be compared with the *Tortula–Grimmia antarctici* sociation and the *Tortula* sociation, respectively. Groups containing *T. excelsa* may be covered by the *Bryum algens–Drepanocladus uncinatus–Tortula excelsa* sociation of flush habitats (see below). At each site, *Marchantia berteroana* occurs in one of the above groups. Although Gimingham and Smith (1970) described a *Marchantia berteroana* community under a "miscellaneous community types" heading, they commented that on Signy Island the bryophytic associates of *Marchantia* suggest that it probably belongs to an extreme variant of one of the *Tortula–Grimmia antarctici* sociations. Similarly, *Pottia austro-georgica* is a frequent associate in the calcicolous sociations, but where it assumes dominance the subjective classification recognizes a *Pottia austro-georgica* association. This is perhaps represented at site 3, where a group is constituted containing *P. austro-georgica*, *Distichium capillaceum* and two lichen species. The suggestion of affinity between this association and the *Tortula–Grimmia antarctici* association (Gimingham and Smith, 1970) is borne out at site 1, where *P. austro-georgica* is grouped with *Grimmia antarctici* and *Tortula* cf. *grossiretis*.

Groups referable to the Polytrichum alpestre–Chorisodontium aciphyllum association

Deep moss banks formed predominantly by *Chorisodontium aciphyllum*, typical of the *Polytrichum alpestre–Chorisodontium aciphyllum* association, were prominent features of the vegetation at sites 1 and 2. Epiphytic crustose and fruticose lichens were locally abundant and, while *P. alpestre* is commonly co-dominant with *C. aciphyllum* in such banks, it was sparse at both sites. However, one of the groups in the site 1 analysis comprises *P. alpestre* and the lichens *Alectoria chalybeiformis* and *Cornicularia aculeata*, a combination which corresponds with the *Polytrichum alpestre*–lichen sociation within this association. Also at site 1, *C. aciphyllum* is grouped with several species of fruticose lichens and the hepatic *Barbilophozia hatcheri*, a combination typical of the *Chorisodontium aciphyllum*–lichen sociation. The groups containing *Pohlia nutans*, *Cephaloziella varians* and *Ochrolechia frigida* at site 1, and *Cladonia carneola* and *Cornicularia aculeata* at site 2 are also representative of this sociation.

Although *C. aciphyllum* was the chief component of the moss banks, it was also prominent in many of the stands dominated by species of *Andreaea* and fruticose lichens representative of the *Andreaea*–lichen association. At site 2, a group containing several lichens, common to both the *Chorisodontium aciphyllum*–lichen and *Andreaea*–lichen sociations, are associated with *C. aciphyllum* and *A. depressinervis*. This perhaps reflects the tendency for small turves of the former moss to invade *Andreaea*-dominated communities, as noted by Gimingham and Smith (1970) and Smith (1972).

Groups referable to the Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus association

At each site some of the groups containing fewest species are composed of the hydrophytic mosses *Calliergidium austro-stramineum*, *Calliergon sarmentosum* or *Drepanocladus uncinatus*, sometimes including the associates *Pohlia nutans* and *Cephaloziella varians*. These groupings clearly represent the moss-carpet communities of moderately acid swampy areas, whose species frequently form extensive closed stands. These communities were treated in the subjective classification as monospecific or polyspecific sociations within the *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* association.

Groups referable to the Bryum algens–Drepanocladus uncinatus association

Flushed habitats below marble outcrops frequently support assemblages belonging to the *Bryum algens–Drepanocladus uncinatus* association in which *B. algens* and *D. uncinatus* predominate, with *Brachythecium austro-salebrosum* and *Calliergon sarmentosum* occasionally well represented. At site 1 the large hummock-forming cushions of *Bryum* and *Brachythecium* together with *Leptogium puberulum*, the only typical lichen of such habitats, constitute one group. Since *B. algens* was always dominant in such stands, this is referable in the subjective classification to the *Bryum algens* sociation. At site 3 *Bryum* is grouped with *Brachythecium* and *Calliergon*, a combination more characteristic of the *Bryum algens–Drepanocladus uncinatus* sociation. *Tortula excelsa* is grouped with *Bryum algens* at site 1 and with *Leptogium puberulum* at site 3. This corresponds with the closely related *Bryum algens–Drepanocladus uncinatus–Tortula excelsa* sociation.

Inverse association analyses produce a final miscellaneous group of species whose occurrences, with the exception of the site 2 group, are not strongly associated. However, in composition they are perhaps most closely correlated with the more heterogeneous and open communities of the *Andreaea–Usnea* association. These apart, not only can an ecological interpretation be placed on almost all the species groups but also in most instances they correspond effectively with categories contained in the original subjective phytosociological classification.

Agglomerative classification

For each site the dendrogram based on percentage cover data produces a number of fairly discrete groupings. Each, or in some instances more than one, of these groupings corresponds closely to communities (sociations) previously recognized in the subjective classification. Inevitably, as the species diversity increases, e.g. at site 1, a small number of quadrats is misplaced and a stand representative of one sociation is occasionally listed within a group of stands representative of a different sociation. Similarly, a few quadrats at site 1 do not have an acceptably close relationship with any community grouping and have not been classified. The dendrograms derived from the analysis of the presence/absence data for each of the quadrat sizes at site 2 do not distinguish between the groupings as clearly as those based on cover data. Because of many inconsistencies with regard to the linking of quadrats and to the comparison with the subjective classification, these results will not be discussed.

The dendrogram produced for the least floristically complex site (site 2, Tern Cove; Fig. 5) showed the most clearly defined groupings. The lowest link level with the similarity value of only 9 per cent (0·09 homogeneity) separates the dry from the wet habitat stands. Seven major and two single-membered groupings are separated between similarity values of 12 and 56 per cent. The latter two groups are subtended by long arms and bear little resemblance to any other stands with regard to their dominant species, although each is almost identical to other groups in species composition. Groups 1 and 2, as indicated in Fig. 5, represent the *Andreaea*–lichen sociation (A1) of the subjective classification; group 3 represents the *Andreaea*–lichen sociation in which most stands have >15 per cent cover afforded by *Chorisodontium aciphyllum* (A1/C2); group 4 represents a combination of the almost identical *Chorisodontium aciphyllum* and *Chorisodontium aciphyllum*–lichen sociations (C1/C2); group 5 comprises a single stand

Species									
Andreaea spp.	61	17	16	3	0	1	0	0	0
Calliergidium austro-stramineum	0	0	0	0	0	2	12	70	90
Calliergon sarmentosum	0	0	0	0	0	2	49	18	0
Chorisodontium aciphyllum	8	2	33	84	10	2	0	0	0
Drepanocladus uncinatus	5	3	11	2	5	80	41	8	15
Polytrichum alpestre	0	0	0	0	85	0	0	0	0
Usnea spp.	11	46	8	1	2	0	0	0	0
Community type (according to subjective classification)	A1	A1	A1/C2	C1/C2	C3	F1	F2	F2	F2

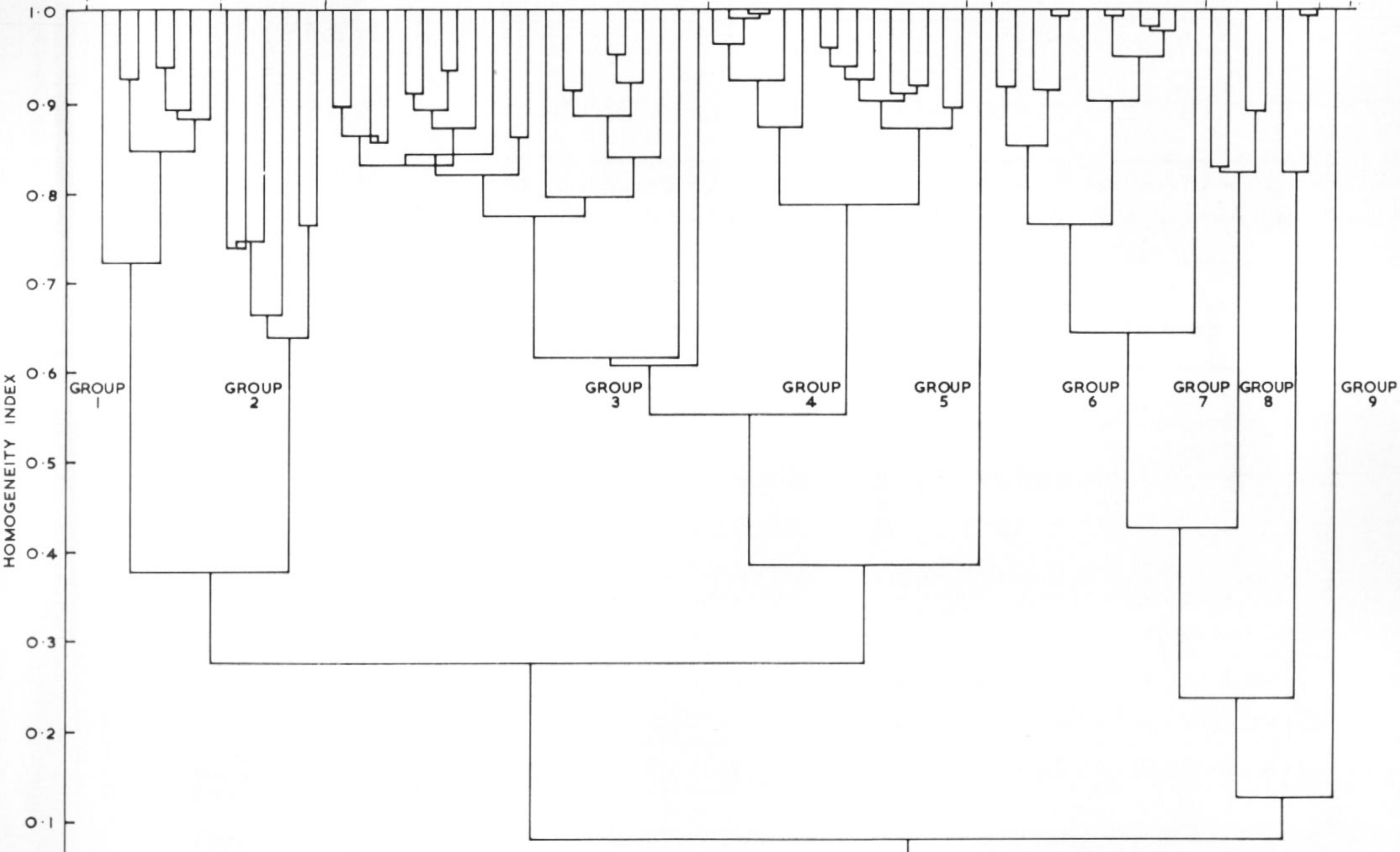


Fig. 5. Dendrogram, produced by agglomerative analysis of species cover data, showing the grouping of the 70 stands at site 2 (Tern Cove). The relatively compact groups correspond closely to sociations of the subjective classification and for each the mean percentage cover of species which attain dominance in one or more groups is tabulated. For the key to symbols of community groups, see Table II.

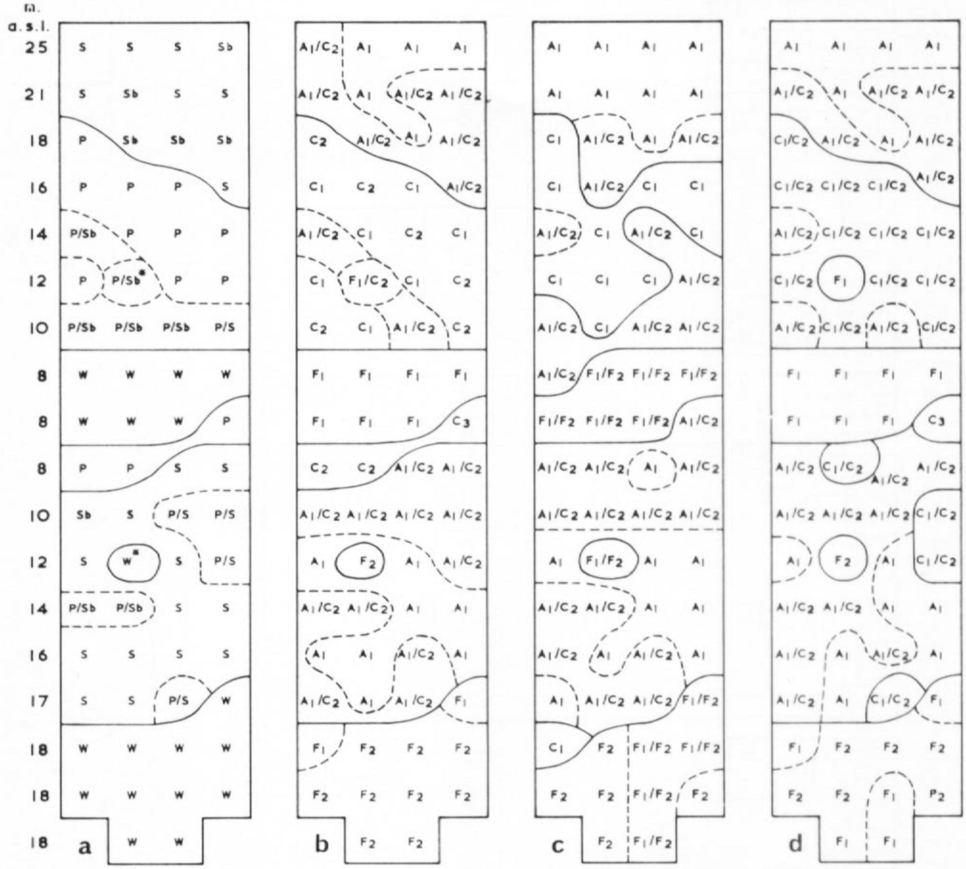


Fig. 6. Maps of site 2 (Tern Cove) indicating at each sampling point features of topography and substratum and community groupings derived from various classificatory analyses. For the key to symbols see Fig. 3 and Table II.
a. Topography and substrata.
b. Community groupings derived from subjective classification.
c. Community groupings derived from association analysis of 400 cm.^{2} quadrat data.
d. Community groupings derived from agglomerative analysis.

representing the *Polytrichum alpestre*–lichen sociation (C3) in which *P. alpestre*, which does not occur in any other stand, affords 85 per cent cover; group 6 represents the *Drepanocladus uncinatus* sociation (F1); groups 7–9 contain stands of the *Calliergon sarmentosum–Drepanocladus uncinatus*, *Calliergidium austro-stramineum–Calliergon sarmentosum* and *Calliergidium austro-stramineum–Calliergon sarmentosum–Drepanocladus uncinatus* sociations (F2). The single quadrat of group 9 is dominated by a tall robust form of *C. austro-stramineum* (90 per cent cover). In groups 7 and 8 a short slender form of this moss, formerly recognized as a separate species, sometimes predominates. The mean percentage cover of the species which achieve dominance in each of these groups is tabulated in Fig. 5. The distribution of these groupings in relation to those of the association analysis and of the subjective classification is indicated in Fig. 6.

The nature of the group clusters in the dendrograms is revealed by the size of the similarity value in the series of resemblance maps for each site. There is some degree of variation within each community, as reflected by the range of similarity values. Stands within the more distinctive communities (e.g. those belonging to the *Polytrichum alpestre–Chorisodontium* *aciphyllum* association) show little variation in similarity value, indicating that they are relatively uniform in species composition and the cover abundance of individual species. Where two or more communities have several species in common (e.g. the *Andreaea*–lichen sociation and the *Andreaea*–lichen sociation with frequent *Chorisodontium aciphyllum*; or the *Tortula–Grimmia antarctici* sociation and the *Bryum algens–Drepanocladus uncinatus* sociation) these resemblances are reflected by the wider range of similarity values within each community and the trend towards other community types can be followed in each resemblance map. In such instances this is clear evidence that certain groups of communities represent a continuum of variation. The trends based on the core of three widely differing community types at site 1 (Thulla Point) are illustrated in Fig. 7.

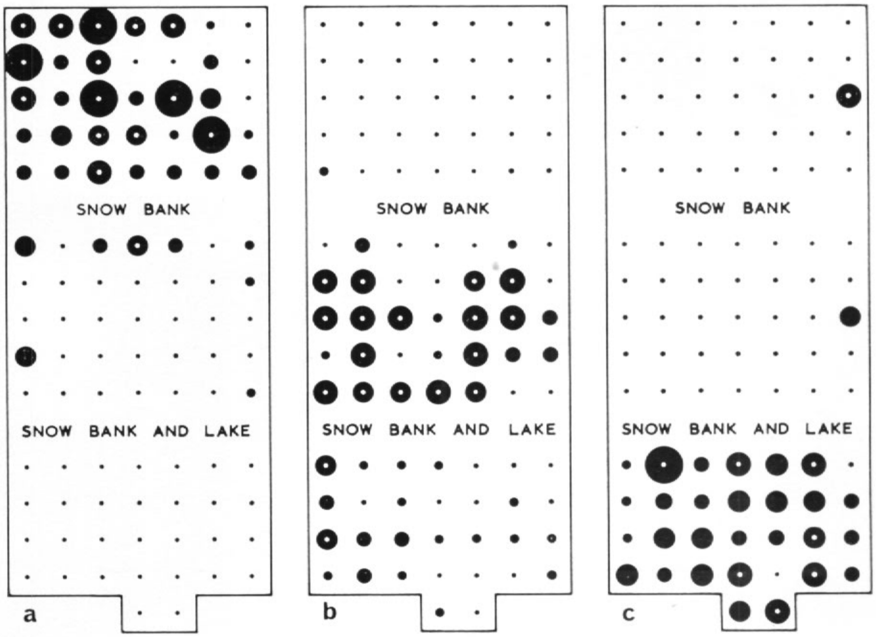
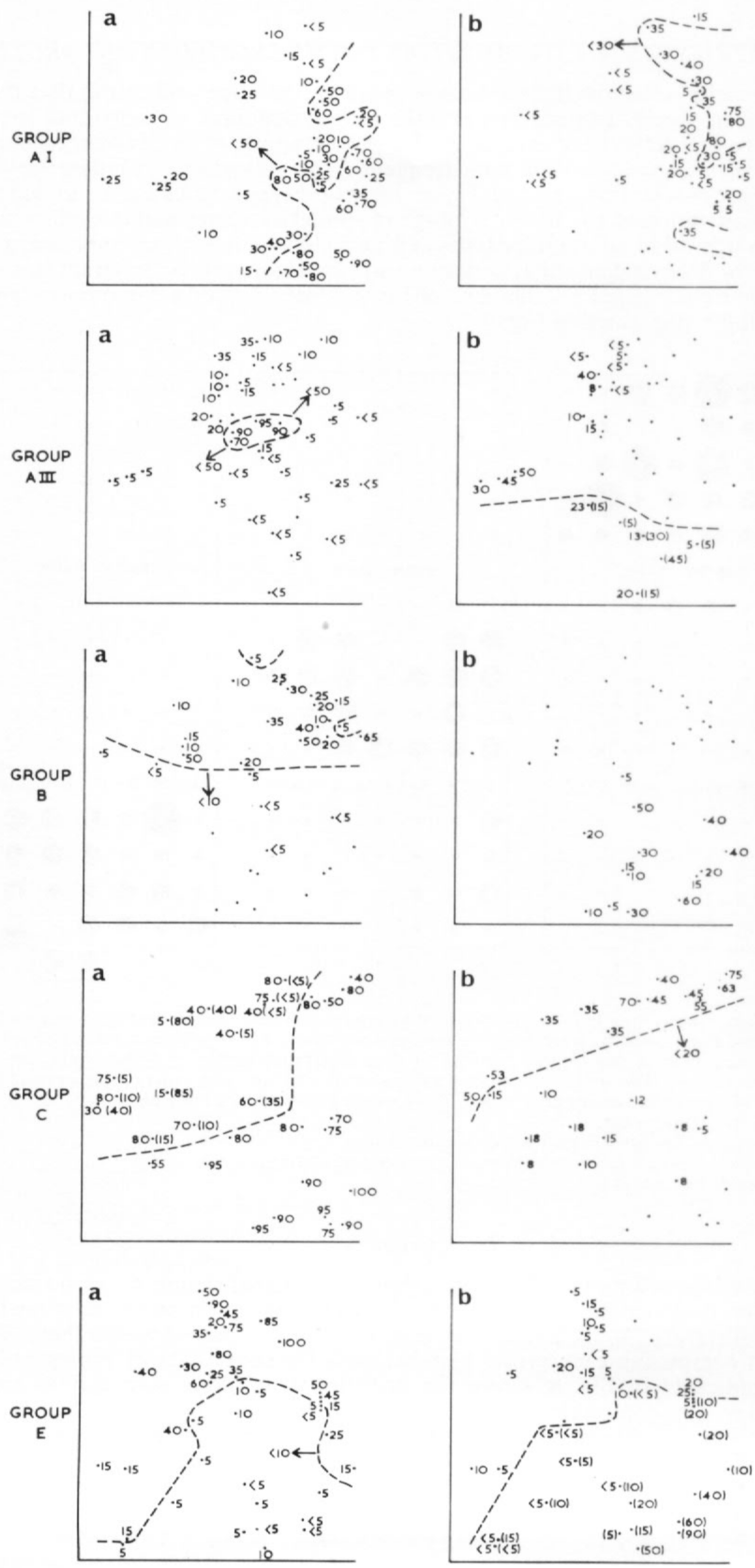


Fig. 7. Resemblance maps for site 1 (Thulla Point) showing the similarity between each sample and three putative communities, established by averaging the species cover data from the community centroid (open-centred circles) derived from a dendrogram similar to that illustrated in Fig. 5. Solid circles are "outside" the community centroid. The similarity value of a stand relative to the mean value of the centroid is proportional to the size of the circle, the range of values from smallest to largest circles being 0–9, 10–19, 20–39, 40–59, 60–79 and 80–100 per cent.
a. *Bryum algens–Drepanocladus uncinatus* community.
b. *Polytrichum alpestre–Chorisodontium aciphyllum* community.
c. *Andreaea*–lichen community.

Ordination

The results of the ordination of stands within the principal groups of the normal association analysis of the combined data provide some further information on the relationships between the main classificatory groups and the range of variation contained within them. The positions of the stands comprising each group together with the cover data of ecologically important species are indicated in Fig. 8. From the distribution of these data certain environmental gradients are readily detectable. However, it should be noted that these diagrams do not refer to individual sites but incorporate data from all three sites. Ordination was not carried out for the two minor groups, each of which comprises only three quadrats, and the final group (indicated in Fig. 2 as groups AII, D and E, respectively).


a
b
GROUP A I
a
b
GROUP A III
a
b
GROUP B
a
b
GROUP C
a
b
GROUP E

Groups referable to the Andreaea–Usnea association

Group AI comprises stands most of which were situated on relatively acidic schistose debris, grouped with a small number incorporating some degree of moss-peat formation. Fruticose lichens (particularly species of *Cladonia* and *Usnea*) and species of *Andreaea* are well represented throughout, but the result of plotting the cover abundance of the latter species and of the tall turf-forming moss, *Chorisodontium aciphyllum*, on to the ordination indicates a gradient of increasing moisture and shelter towards the upper right of the diagram, which contains those quadrats in which peat accumulation was recorded. This reinforces the view that *C. aciphyllum* is inclined to invade the coalesced cushions of *Andreaea* and to initiate peat formation.

Group AIII is also composed largely of stands representing mixed *Andreaea* and lichen communities on acid mineral soils. Stands in the lower part of the diagram occurred on dry schist debris or rock, others just above the middle on wetter mineral substrata, while moist peat was recorded in those at the top. The vertical axis thus approximately corresponds with an increasing gradient of moisture and shelter. Species of *Andreaea* are again prominent throughout but the cover of several other mosses and lichens varies according to the degree of moisture or exposure. *Himantormia lugubris*, typical of the most windswept situations, is represented only in the lower part of the diagram, the hydrophytic moss *Drepanocladus uncinatus* reaches its highest cover value just above the middle and *Chorisodontium aciphyllum* at the top. These results agree with those of group AI, showing in addition that the mat-forming *D. uncinatus* enters *Andreaea* and fruticose lichen-dominated communities where the substratum is moist.

Group referable to the Tortula–Grimmia antarctici association

The majority of stands in group B were situated on a substratum of high base status, mainly marble debris. Some of those in the upper part of the diagram occupied moist or flushed habitats; hence increasing substratum wetness again appears to correspond with the vertical axis. Species of *Tortula* (*T. excelsa*, *T. fuscoviridis* and *T.* cf. *grossiretis*) are present in most stands, but *Grimmia antarctici* and other short acrocarpous calcicolous mosses (*Distichium* spp., *Encalypta patagonica* and *Pottia austro-georgica*) and the foliose lichen *Dermatocarpon lachneum*, are restricted to the lower "drier" part of the diagram. *Bryum algens*, *Brachythecium austro-salebrosum* and *Drepanocladus* cf. *plicatus*, typical flush species, are concentrated in the upper "wetter" part. This ordination indicates a continuous range from the *Grimmia antarctici* and *Tortula* sociations (within the fruticose lichen and moss-cushion sub-formation) on the driest substrata to the *Bryum algens–Drepanocladus uncinatus* sociation (within the moss-hummock sub-formation) of wet situations. The restriction of *Marchantia berteroana* to the upper part of the diagram is of interest in the light of the comment on p. 37.

Group referable to the Polytrichum alpestre–Chorisodontium aciphyllum association

Group C consists of stands dominated by tall turf-forming mosses. Since these species develop a highly organic acid peat of varying depth, there is no discernible trend in the descriptions of the substratum. However, with increasing exposure and dryness, both *Polytrichum alpestre* and a large group of fruticose and crustose lichens increase in cover towards the

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Fig. 8. Ordination, in relation to the first two axes obtained by principal-components analysis, of stands belonging to five major groups derived from normal association analysis of the combined data from all study areas (see Fig. 2). Percentage cover values for selected species are plotted on to the ordination; high and low values are usually separated by a broken line. Group AI (a) *Andreaea* spp. (*A. depressinervis*, *A. gainii*, *A. regularis*); (b) *Chorisodontium aciphyllum*. Group AIII (a) *Drepanocladus uncinatus*; (b) *Usnea* spp. (*U. antarctica*, *U. fasciata*) and *Himantormia lugubris* (in brackets below the broken line). Group B (a) *Bryum algens*; (b) *Grimmia antarctici*. Group C (a) *Chorisodontium aciphyllum* and *Polytrichum alpestre* (in brackets above the broken line); (b) fruticose and crustose lichens (mainly *Cladonia carneola*, *C. furcata*, *Usnea antarctica* and *Ochrolechia frigida* but including *Alectoria chalybeiformis*, *A. nigricans*, *Cornicularia aculeata*, *Sphaerophorus globosus*, *Stereocaulon glabrum*, and *Buellia* cf. *punctata*). Group E (a) *Bryum algens*; (b) *Brachythecium austro-salebrosum* and *Calliergon sarmentosum* (in brackets below the broken line).

upper left of the diagram, where *Chorisodontium aciphyllum* declines. Although the latter species is prominent throughout, it predominates where the peat is moister. The considerable reduction of lichens towards the foot of the diagram is indicative of increased shelter and greater snow accumulation in winter. The distribution of these principal species illustrates a small continuum which commonly occurs in this type of community. Lichen-free stands of the *Chorisodontium aciphyllum* sociation (lower right) intergrade with stands of the *C. aciphyllum*–lichen sociation (middle and upper right) and those of the *C. aciphyllum–P. alpestre*–lichen sociation (upper left). This represents a successional development in which the proportion of *P. alpestre* increases as drainage improves and, where exposure to wind is greatest (preventing snow accumulation in winter, thereby subjecting the surface to very low temperatures and desiccation), the moss is killed, the surface erodes and the exposed peat becomes colonized by epiphytic lichens (see Smith, 1972).

Group referable to the Bryum algens–Drepanocladus uncinatus association

All stands in group E belong to wet sites, and the ordination separates those which were recorded as occupying calcareous habitats (flushed by drainage from nearby marble outcrops) from a group in which this influence was less marked or lacking. The vertical axis of the diagram therefore corresponds with a gradient of increasing base status. In the former type of habitat, *Bryum algens* is associated with *Brachythecium austro-salebrosum* and *Leptogium puberulum*, whereas *Calliergon sarmentosum* and *Psoroma hypnorum* are strongly associated with the less basic habitats. *Drepanocladus uncinatus* is best represented in intermediate situations. The relationship shown here between the extensive moss carpets of the more acid swamp areas (*Calliergon sarmentosum*, etc.) and the comparatively calcicolous moss-hummock communities of *Bryum algens* and its associates in flushed areas extends to the stands of group B, in which there is a series from the latter type through to the *Tortula–Grimmia antarctici* communities of dry marble debris.

Discussion

A subjective approach to a phytosociological investigation inevitably involves the selection of the more favourable sites or stands with regard to uniformity of species composition and distribution, for purposes of recording floristic data in a number of quadrats at each site. Furthermore, if a number of stands representative of the same community type is to be analysed, some degree of bias is unavoidable in their selection. Consequently, when a large-scale survey is being undertaken of the vegetation of an area, the smaller or less well-developed stands and the more heterogeneous vegetation often representing ecotones tend to be neglected. They are considered as being atypical communities which, if they are recurring, are usually inconsistent in species composition and species abundance. A worker undertaking such a phytosociological survey generally commences with a pre-conceived vision of the vegetation comprising a range of discrete assemblages which can then be readily classified, irrespective of whether or not they comprise noda in a continuum. An indication of the existence of a continuum may be obtained by further examination of the species lists.

However, an objective approach to vegetation analysis eliminates most bias regarding stand selection, although the choice of the study area itself may be pre-determined to some extent. Data are obtained for all categories of vegetation ranging from closed stands of uniform composition to open heterogeneous stands or even bare ground. Statistical techniques applied to classify such data provide no indication of continua, but the data are amenable to further analysis designed to detect floristic gradients.

The subjectively derived classification of the vegetation of Signy Island (Smith, 1972) compares favourably with that produced by the statistical methods of normal and inverse association analyses and agglomerative analysis. All the groupings produced by these analyses could be readily ascribed to associations and sociations previously established by the subjective approach. Each statistical system of analysis produced almost the same groupings of stands. Where different quadrat sizes were employed at a site, the resulting groups were similar, although those obtained from the largest (400 $cm.^2$) bore the closest resemblance to the subjectively derived community types of sociations. One of the objections to the normal and inverse association analyses is that only presence and absence data are required and consequently several quadrats are misplaced with regard to the subjective system. Thus, while the sociations of the subjective classification are based on the dominance of one or more species and the cover abundance of all associated species, such quantitative data are not considered in association analysis. One of the characteristics of many of the cryptogamic communities of the maritime Antarctic is their similarity in species composition. Although several community types may have almost identical species lists, in each a different species assumes dominance due to minor variations in the environment, and this criterion is used as the basis for separating sociations, although recognizing the possible existence of continua. However, association analysis tends not to differentiate between such sets of data and no consideration is given to the contribution afforded by respective species in terms of abundance. A species affording only 1 per cent cover is given the same weighting as one with 100 per cent cover. Stands apparently belonging to one sociation are frequently grouped with those representative of another.

For instance, sociations dominated by *Bryum algens*, *Grimmia antarctici* or species of *Tortula* which occupy base-rich soils on Signy Island are unsatisfactorily grouped together. In the subjective classification these are distinguished as separate sociations each with its own habitat characteristics. Similarly, species with a relatively wide ecological amplitude such as *Drepanocladus uncinatus* and to a lesser extent *Chorisodontium aciphyllum*, which are present in varying quantities in many sociations, tend to oversimplify the association-analysis classification. For this reason, a number of stands in the present survey belonging to two or more distinct sociations have, in terms of the subjective classification, been misclassified and associated in the same group. For example, some stands in which *Drepanocladus uncinatus* occurs as a casual associate affording less than 5 per cent cover in an open fellfield stand dominated by species of *Andreaea* and *Usnea* may be unsatisfactorily classified in the same group as those stands dominated by *Drepanocladus uncinatus*, *Calliergon sarmentosum* or *Calliergidium austro-stramineum* in bog habitats. Frequently stands dominated by species of *Andreaea* and lichens, but which possess a few per cent cover of *Chorisodontium aciphyllum*, are grouped with stands dominated by the latter species which, because of its tall turf growth form, typically produces deep moss banks. Some discrepancies have also become apparent when the grouping of certain stands derived from the association analysis of individual sites and of the bulked data of the three sites are compared. For an individual site, each association analysis of the three quadrat sizes usually grouped a particular stand in the same sociation according to the subjective classification, although the bulked data analysis frequently placed it in a different sociation.

At each site there are several examples of an isolated stand representative of a sociation which is distinctly different from the surrounding vegetation, e.g. where a group of calcifuge species (*Andreaea*, *Usnea*, etc.) occupies a pocket of acidic schistose soil occurring amongst a predominantly basic marble soil dominated by calcicolous species (*Bryum*, *Grimmia*, *Tortula*, etc.). In most instances the association analysis classifies such a stand correctly, i.e. in a group corresponding to the *Andreaea*–lichen sociation, whereas the surrounding stands would be in a group corresponding to one of the sociations belonging to the *Tortula–Grimmia antarctici* association.

Unless the worker has a detailed knowledge of the vegetation, it would not be known that heterogeneous groups such as are occasionally produced by association analysis do not, in fact, portray an accurate description of community composition. What they signify, however, is the continuous variation prevalent in the vegetation, although this would not be evident without prior knowledge of the community types and their interrelationships. Nevertheless, despite these apparent discrepancies, the association-analysis groupings bear a close resemblance to the associations, and often the sociations, of the subjective classification.

The grouping procedure of the agglomerative technique is much more satisfactory since it is based on quantitative cover data and incorporates a system of weighting species with higher abundances. Such species often achieve dominance and, being generally associated with specific environmental features, are important in the classification of communities. The application of this method to the Signy Island data resulted in a number of groups closely resembling sociations of the subjective classification. However, with increasing floristic complexity, the dendrograms become more difficult to interpret. Site 1, having the greatest diversity of community types, had a large number of indistinctly separated groups, although only five associations were represented. Conversely, the site with least floristic diversity (site 2) produced clearly defined groupings almost identical with those of the subjective classification. Further support for the validity of the subjective classification is provided by the various categories resulting from the inverse association analysis. Most of these groups comprised species lists almost identical to those provided by Smith (1972) for several sociations.

When the major groupings of the classificatory dendrograms are examined for trends within the putative communities, it is clear that the vegetation cannot be considered entirely as comprising readily defined discrete units. Ordination by principal-components analysis of association-analysis groupings reveals floristic trends related to certain environmental gradients. Trends within a site are also illustrated by an evaluation of the agglomerative analysis groupings. These are shown in resemblance maps which illustrate the distribution patterns of similarity values for a given community centroid and each respective stand. Both methods clearly indicate the existence of continua within the vegetation which are not otherwise revealed directly by the classificatory techniques.

In considering the merits of subjective and objective approaches to the study of the relatively simple plant communities of the maritime Antarctic, the results of the present survey indicate that the vegetation can be classified into floristic categories, many of which may be considered as components of a continuum of variation. Also, the categories or sociations recognized by a subjective technique bear a close resemblance to those derived from more objective methods. Although only a small number of sociations was revealed by the latter approach this was largely due to the restricted size of the study areas and limited range of edaphic and other environmental factors which are responsible for the floristic complexity and diversity of community types.

While it is desirable to eliminate bias as much as possible from phytosociological surveys, some degree of site selection is often essential so as to incorporate the maximum floristic variation within a study area of convenient working size. In the Antarctic, vegetation seldom forms extensive closed stands. In order to include the widest range of community types in the subjective survey of Signy Island, sites were selected, following a preliminary examination of the entire area, with respect to homogeneity in species composition within a stand often as small as 25 m.^{2}. Replicates of each community type were chosen, as far apart as possible, with regard to similarity of species composition and habitat (Smith, 1972). In contrast to most other regions of the world, Antarctic plant communities are relatively simple both floristically and physiognomically, and occupy small areas. Ecotones are frequently narrow in area and inconsistent in composition.

For an objective approach to be effective, a comparatively large study area is required so that a diversity of habitats and consequently of plant communities is enclosed. However, even if several study areas are examined, it is unlikely that all community types representative of the region will be included. Such an approach will therefore result only in a partial survey or classification of the vegetation. Furthermore, the present field survey of three small study areas (240 quadrats) took about 60 man hours. When an opportunity arises for the examination of a previously unstudied area, time is likely to be at a premium and, since the worker frequently has to contend with sub-zero temperatures, strong winds and precipitation, the most satisfactory method of carrying out a phytosociological survey would employ the subjective approach. Nevertheless, small-scale surveys by objective methods employing the non-random selection of sample points are useful and important in demonstrating the validity of much larger-scale surveys relying on subjective methods.

While the results of the present study barely demonstrate the hierarchical categories of the classification as established by the subjective method of Gimingham and Smith (1970) and Smith (1972), they strongly support the validity of the community groupings or sociations. There is no evidence that the subjective classification requires amending or that a new classification need be erected. However, the advantage of certain statistical procedures is that they may be usefully employed to examine the network of variation throughout the vegetation complex of Antarctic regions.

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REFERENCES

AUSTIN, M. P. *and* L. ORLOCI. 1966. Geometric models in ecology. II. An evaluation of some ordination techniques. *J. Ecol.*, **54**, No. 1, 217–27.

GIMINGHAM, C. H. 1967. Quantitative community analysis and bryophyte ecology on Signy Island. (*In* SMITH, J. E., *organizer*. A discussion on the terrestrial Antarctic ecosystem. *Phil. Trans. R. Soc.*, Ser. B, **252**, No. 777, 251–59.)

————. *and* R. I. L. SMITH. 1970. Bryophyte and lichen communities in the maritime Antarctic. (*In* HOLDGATE, M. W., *ed. Antarctic ecology*. London and New York, Academic Press, 752–85.)

HALL, A. V. 1967. Methods for demonstrating resemblance in taxonomy and ecology. *Nature, Lond.*, **214**, No. 5090, 830–31.

————. 1969. Avoiding informational distortion in automatic grouping programs. *Syst. Zool.*, **18,** No. 3, 318–29.

————. 1970. A computer based method for showing continua and communities in ecology. *J. Ecol.*, **58,** No. 3, 591–602.

HOLDGATE, M. W. 1964. Terrestrial ecology in the maritime Antarctic. (*In* CARRICK, R., HOLDGATE, M. *and* J. PRÉVOST, *ed. Biologie antarctique*. Paris, Hermann, 181–94.)

LONGTON, R. E. 1967. Vegetation in the maritime Antarctic. (*In* SMITH, J. E., *organizer*. A discussion on the terrestrial Antarctic ecosystem. *Phil. Trans. R. Soc.*, Ser. B, **252**, No. 777, 213–35.)

ORLOCI, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. *J. Ecol.*, **54**, No. 1, 193–215.

SMITH, R. I. L. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. *British Antarctic Survey Scientific Reports*, No. 68, 124 pp.

WILLIAMS, W. T. *and* J. M. LAMBERT. 1959. Multivariate methods in plant ecology: I. Association-analysis in plant communities. *J. Ecol.*, **47,** No. 1, 83–101.

————. *and* ————. 1960. Multivariate methods in plant ecology: II: The use of an electronic digital computer for association-analysis. *J. Ecol.*, **48,** No. 3, 689–710.

————. *and* ————. 1961. Multivariate methods in plant ecology: III. Inverse association-analysis. *J. Ecol.*, **49,** No. 3, 717–29.