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THE VEGETATION OF SUBANTARCTIC CAMPBELL ISLAND

Summary: The vegetation of Campbell Island and its offshore islets was sampled quantitatively at 140 sites. Data from the 134 sites with more than one vascular plant species were subjected to multivariate analysis. Out of a total of 140 indigenous and widespread adventive species known from the island group, 124 vascular species were recorded; 85 non-vascular cryptogams or species aggregates play a major role in the vegetation. Up to 19 factors of the physical environment were recorded or derived for each site. Agglomerative cluster analysis of the vegetation data was used to identify 21 plant communities. These (together with cryptogam associations) include: maritime crusts, turfs, megaherbfields, tussock grasslands, and shrublands; mid-elevation swamps, flushes, bogs, tussock grasslands, shrublands, dwarf forests, and induced meadows; and upland tundra-like tussock grasslands, tall and short turf-herbfields, bogs, flushes, rock-ledge herbfields, and fellfields.

Axis 1 of the DCA ordination is largely a soil gradient related to the eutrophying impact of marine spray, sea mammals and birds, and nutrient flushing. Axis 2 is an altitudinal (or thermal) gradient. Axis 3 is related to soil reaction and to different kinds of animal influence on vegetation stature and species richness, and Axis 4 also appears to have fertility and animal associations.

Autecological interpretation of the data demonstrates clear niche segregation of congeneric species and species with similar growth forms. The notable megaherbs and giant tussocks may be an adaptation to harvesting nutrients from the aerosol precipitate. Heat harvesting in the cool, cloudy, wet, and windy climate may also be implicated. The history of farming and natural disturbances has resulted in a complex mosaic of vegetation-soil systems of varying maturity. Their putative dynamic interrelationships are depicted in terms of impacts of burning, grazing, marine animals and climate change and subsequent recovery or primary and secondary succession.

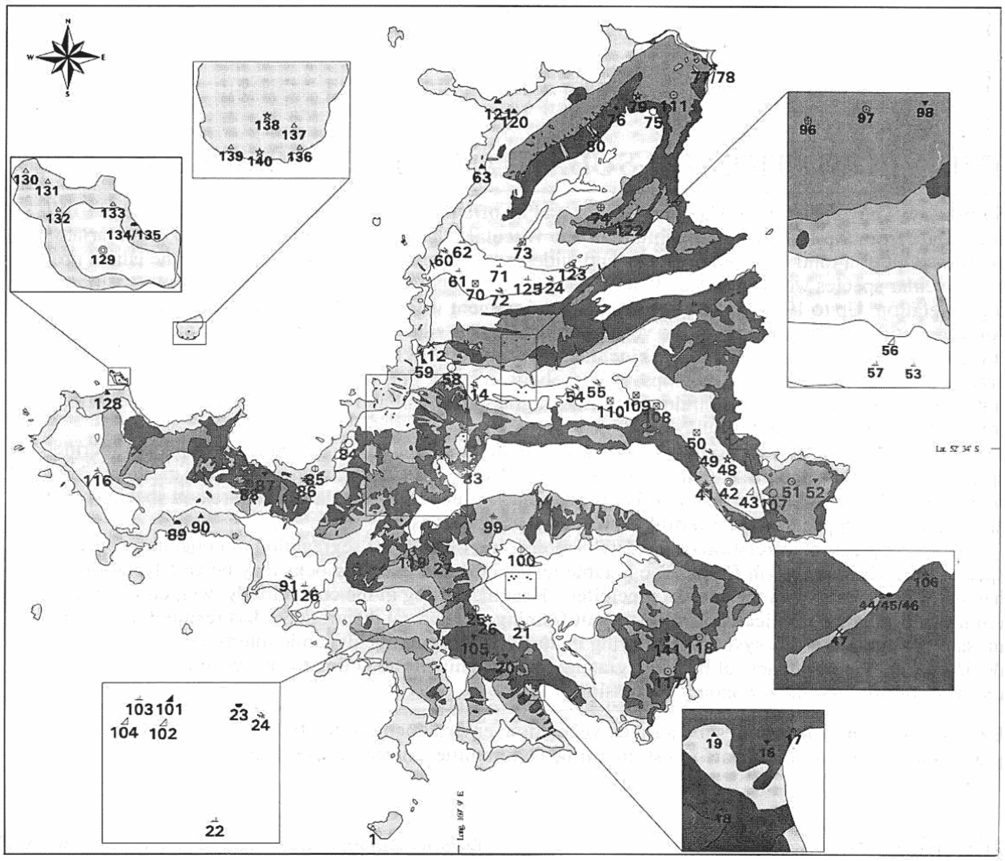
Keywords: Campbell Island; subantarctic; vegetation; environment; ordination; cluster analysis; tussock grasslands; tundra; scrub; dwarf forest; maritime communities; niche differentiation.

Introduction

Campbell Island (11 331 ha) is an isolated superoceanic, peat-covered island with numerous smaller offshore islets and stacks (Fig. 1), lying 700 km south of the New Zealand mainland at 52°33.7'S, 169°09'E (Clark and Dingwall, 1985; Meurk and Given, 1990). Extreme wind, cloudiness, high humidity, uniform cool temperatures (De Lisle, 1965), and soil fertility patterns (Campbell, 1981; Foggo and Meurk, 1983) establish the environmental gradients that influence vegetation patterns. The altitudinal range is from sea level to 558 m, which corresponds to mean January air temperatures of 9.3°C and 5.5°C respectively (Meurk and Given, 1990). Grounds for classifying Campbell Island as subantarctic are given in Meurk (1984). Domestic sheep and cattle, feral since the 1930s, were progressively eliminated between 1970 and 1990 (Dilks and Wilson, 1979; Rudge, 1986). Vegetation recovery from the farming and grazing era has been especially marked on more fertile sites or where there are abundant seed sources (Meurk, 1982, 1989). Thus, at the time of this study there was a mosaic of near-pristine, reduced, induced, and heavily modified/grazed vegetation. This presented a more complex and disrupted pattern (Meurk and Given, 1990) than exists on the other southern islands of New Zealand.

There have been numerous accounts of the plants and vegetative cover of Campbell Island since the first serious observations recorded by Hooker (1844). These general references are listed in Godley (1965, 1970, 1979, 1989). The only systematic descriptions of the vegetation are those of Cockayne (1904, 1909, 1928) and Oliver and Sorensen (1951).

Elsewhere in the southern circumpolar zone, a number of sampling studies have been described (Taylor, 1955, for Macquarie Island; Huntley, 1971, and Gremmen, 1982, for Marion and Prince



Legend

Map Units

- Tundra mosaic
- *Poa litorosa* meadow and Chionochloa
- Maritime complex
- *Coprosma*, slips and slumps
- Cushion bog
- *Dracophyllum* shrubland/dwarf forest

Scale: 1 : 85000

Community Type Symbols

CT:1	GOLE
CT:2	LBGE
CT:3	EYTU
CT:4	NHT
CT:5	TZJ
CT:6	RYFH
CT:7	WH
CT:8	THY
CT:9	BTL
CT:10	PSC
CT:11	RGB
CT:12	JBGH
CT:13	JBH
CT:14	FBH
CT:15	LBHA
CT:16	KHBU
CT:17	ACR
CT:18	CPDM
CT:19	QD
CT:20	DMCP
CT:21	AUD

Figure 1: *Simplified vegetation map (A) of Campbell Island, with locations of 140 vegetation sampling sites. The central boxed area is expanded as Fig. 1B (opposite). The base map and map unit symbols are derived by amalgamating related vegetation polygons from the original 1:25 000 map (Meurk and Given, 1990). Symbols used for the sample sites are coded according to their cluster analysis community type, with the letters referring to dominant species/growth forms (A* = Chionochloa **A**ntarctica, *B* = **B**ulbinella rossii, *C* = **C**oprosma *shrubs, D* = **D**racophyllum *spp., E = maritim**E**, F = **F**ellfield, G = me**G**aherbfield, H =* **H***erbfield, I =* **I***nduced/grazed, J =* Marsippospermum *and* **J**uncus *spp., K =* Rost**K**ovia magellanica, *L =* Poa **L**itorosa, *M =* **M**yrsine *d*ivaricata, *N = **N**est sites, O =* Poa f**O**liosa, *P =* **P**teridophytes, *Q =* Hebe elliptiC**A**, *R = **R**ock, S = **S**edge, T = **T**urf, U = c**U**shion bog, V = **V**arious slips/tracks, W = sea elephant **W**allow, X = e**X**otic/adventive plants, Y = non-vascular cr**Y**ptogams, Z = bare peat - **Z**ero vegetation).*

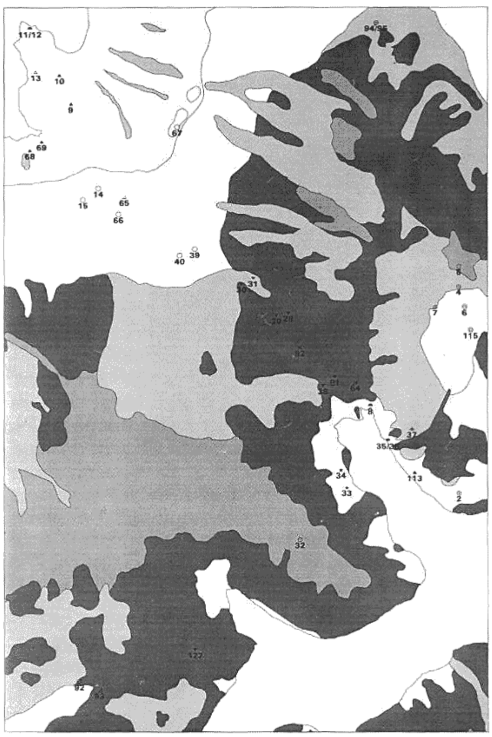


Figure 1B: Caption opposite.

Edward Islands; Greene, 1964, and Smith and Walton, 1975, for South Georgia; Smith, 1972, for South Orkney Island; Davies and Greene, 1976, for the Crozet Islands). Recently some numerical classifications have been performed on aquatic communities of Macquarie Island (Hughes, 1986). In most of these studies, environmental records were used only to infer cause of the vegetation pattern. Multivariate analysis has been employed to quantify these relationships in preliminary results (Meurk and Foggo, 1988) and a restricted analysis from the Auckland Islands (Lee *et al.*, 1991).

The vegetation pattern of these southern islands has a circumpolar unity, but the various elements are more or less well developed depending on latitude, isolation, age of substrate, and size of the landmass. Substrate fertility, as influenced by animals or maritime exposure, is also implicated (Smith and French, 1988). Wace (1960) and Bliss (1975, 1979) have attempted an integrated biogeographic classification for the circumpolar region. The main vegetation components are: littoral-fringe and submaritime zones of cryptogams, cushion, and turf species; eutrophic maritime tussock grasslands commonly associated with giant herbs; scrub or dwarf heath-like forests where there is sufficient warmth and shelter; oligotrophic hard-cushion bogs; eutrophic sedge swamps; mesotrophic inland tussock grasslands; and upland rushlands, wet cushion bogs, turf grasslands, or cushion fellfields (see Meurk and Given, 1990, and Infomap 260, 1991; Plates 1-4, pp. 126, 131).

This paper quantifies the vegetation-environment pattern for Campbell Island using multivariate statistical analysis. We see merit in expressing the complexity of vegetation in terms of both community and continuum concepts.

Methods

Sampling the vegetation

The difficulties of collecting adequately representative data in remote field situations are exacerbated by limitations of time and weather conditions. Our compromise was to stratify the vegetation and sample according to the 30 physiognomic categories (formations) of Meurk and Given (1990). Aproximately 100 samples taken in 1980-81 (by CDM and MNF) were supplemented by previous records from 1970-1975 (CDM) giving an overall total of 140. Of these, six sites with less than two vascular species were excluded from analysis.

Samples were spread evenly through vegetation and geographic space (Fig. 1). The approach, when working a catchment, mountainside, or other physiographic feature, was to cover the range of vegetation categories, usually by sampling at regular intervals along some gradient, but also including unusual or rarely seen associations. The northern, sheep-free half of the island was sampled more intensively in order to represent less modified vegetation (Meurk, 1982, 1989). Of some 140 indigenous and widespread adventive vascular species known from the islands, 134 appeared in the samples. Of these, 18 species were excluded from analysis, largely because they occurred only once. In addition 85 non-vascular cryptogams (or aggregates) were recorded.

Sample boundaries and sizes were flexible, but defined limits were imposed before recording commenced. Sampling was subject to the following constraints:

- the general location was chosen from some distance, or was predetermined at some regular interval along a gradient;

Plate 1: Panorama southeast from Col ridge across Perseverance Harbour to Mt Honey (558 m). Beeman Point Meteorological Station is in left midground and Homestead Ridge at right midground. The foreground (200 m) shows Poa litorosa short tussock meadow (CT 15), induced from former Chionochloa antarctica *tall tussock grassland (CT 17), and rock ledges (part CT 17). The shores support littoral fringe and maritime vegetation (CT 1, 2, 3, 7 and 19). The low plateau top of Homestead Ridge supports cushion bog-prostrate shrubland (CT 21) with fringing and interfingering* Dracophyllum *scrub and dwarf forest (CT 20). The lower slopes of Mt Honey have dark* Dracophyllum *woody vegetation (CT 20), slips (CT 8a), greyish* Coprosma-*fern*-Myrsine *shrubland (CT 18), and paler sedge swamps (CT 10). A pale midslope belt is dominated by the induced* Poa litorosa-Bulbinella rossii *meadow (CT 15), formerly the* Chionochloa *zone, and the darker vegetation of the upper slopes is the* Bulbinella-*dominated phase of CT 15 and 9, and the summit tundra mosaic (CT 6, 11, 12, 13, 14 and 16).*

Plate 2: A sheltered maritime cove (Davis Pt) with luxuriant megaherbfield, up to 1 m tall, of Stilbocarpa polaris, Anisotome latifolia *and a head of* Pleurophyllum *speciosum with shrubs of* Hebe elliptica *and the fern* Blechnum durum *against the rock wall (CT 1).*

- the vegetation stand was relatively large, physiognomically homogeneous, and ideally part of a broad zone, and the site was physiographically uniform;
- contiguous samples were avoided except on steep gradients, such as just above the littoral zone;
- a formation was sampled only once within approx. 2 km except where pre-established plots were used;
- each formation was limited to 3-6 samples.

In some instances where the microtopography formed a fine-scale mosaic a sample was defined which encompassed this variation. However, identifiable parts of such mosaics were usually treated as separate sampling entities even if these were irregular in shape or made up of several disjunct bits. From previous experience (Meurk, 1982; Smartt, Meacock and Lambert, 1974) it appears that either presence/absence (P/A) data or crude quantitative data give an adequate representation of a stand.

The following procedures were employed at each site.

- All species[1] were listed, with the top 10 or so in order of relative abundance.
- The average live vegetative height of each species was recorded according to a Raunkiaer-like, logarithmic progression of growth-form categories (Table 1).
- The cover was estimated for each species.
- A biomass index number was derived from the matrix (Table 1). This is the quantitative value used in subsequent analyses, and approximates a log transformation of absolute biomass.
- At all sites thorough collections were made of non-vascular cryptogams.

[1] Nomenclature for vascular plants follows Allan (1961), Moore and Edgar (1970), Zotov (1965), Webb, Sykes and Garnock-Jones (1988), Brownsey and Smith-Dodsworth (1989), and Edgar (1986). Lichen names are from Galloway (1985), and bryophytes from Hamlin (1972, 1973) and an unpublished checklist (A. Fife, *pers. comm.*). Four sites (37SG, 83QD, 86SL, 100BX) have forms of *Acaena* that are referable to *A. novae-zelandiae*. Earlier three indigenous species of *Ranunculus* were reported. However, Webb *et al.* (1988) consider that *R. subantarcticus* is merely a dwarfed upland form of *R. subscaposus*. Nevertheless, we have chosen to recognise the separate entities for this analysis, although accepting the clinal nature of the complex. *Phyllachne clavigera* appears to have taxonomic priority over the name *Phyllachne colensoi* (Allan, 1961). *Puccinellia chathamica* may include dwarfed entities that approach *P. macquariensis*. Hybrids are not distinguished in these analyses.

Sampling the physical environment

Altitude (m) - measured at each site using a calibrated altimeter.

Slope (°) - microtopographic slope of the site was measured using an Abney level held on a rod, 1.5 m long, laid on the ground/vegetation surface down the maximum slope.

Radiation (Langleys day^{-1}) - mean daily net radiation was derived from aspect, slope, and latitude using the method of Revfeim (1982).

Distance to open coast (km) - distances to the nearest open-sea coast were either estimated in the field or taken from a 1 : 250 000 map. Values were log transformed for statistical analysis.

Distance to any coast (km) - this differed from the above, when the nearest shoreline bordered an inlet or harbour.

Shelter (°) - angular elevation to the true westerly horizon (the source of the prevailing wind) was measured using an Abney level. Negative angles were recorded as zero.

Wind speed (m s^{-1}) - site windspeed was recorded using a hand-held cup anemometer. At the beginning and end of each site observation, six wind speeds were recorded at 10-second intervals, and the mean calculated (Sws). This was corrected to long term January wind speed in the following way. Standard January wind speed on the Beeman Meteorological Station (Bws) anemograph (1970-1979, based on Reid, 1982) is 8.5 m s^{-1}. Hand anemometer readings were found to be 0.52 x anemograph readings. Then, corrected site wind speed = Sws/Bws x 0.52 x 8.5 m s^{-1}.

Soil temperature (°C) - site soil temperature (St) was measured (+/- 0.1°C) at 100 mm depth using an equilibrated electronic probe, and corrected in the following way. Long term mean January air temperature at Beeman Point is 9.3°C (N.Z. Met. Service, 1973). The mean of 25 days of 3 hourly, 100 mm soil temperature readings was 0.8°C greater than mean air temperature ((max+min)/2). Plots of the daily soil temperature curve from Beeman Point allowed extraction of the Beeman soil temperatures (Bt) synchronous with St. Thus long term January soil temperature at the field sample site is (St-Bt) + 0.8 + 9.3°C.

Soil moisture (% of dry weight) - determined for the 50-100 mm depth section from a 45-mm-diameter soil core, oven-dried for at least 24 hours.

Soil depth (m) - was the mean of five measurements using a thin steel probe 1.5 m long. Soils deeper than this were recorded as 1.5 m. For

Table 1: *Symbols displayed on the 2-way table to indicate stature/cover estimates for each species less than 10 m. The quantitative values used in the multivariate analyses range from 15 (symbol "0" in table) to 1 (symbol "-"). The symbols #, *, +, =, - are biomass indices of decreasing value. The height class symbols imply approximation to Raunkiaer's (1934) Microphanerophytes, Nanophanerophytes, Chamaephytes and Hemicryptophytes.*

	Cover description and upper limit of cover classes (%)									
Height classes (m)	Dominant, very abundant, continuous	Abundant, open	Frequent	Common, all fields of view	Fairly common, most fields	Occasional, some fields	Sparse, 1 field	Uncommon, requires search	Rare, 2 or 3 seen	Very rare, 1 seen
M_1 = 2.5-10.0	0	9	8	7	6	5	4	3	2	1
N_2 = 0.63-2.5	9	8	7	6	5	4	3	2	1	#
N_1 = 0.16-0.63	8	7	6	5	4	3	2	1	#	*
C_2 = 0.04-0.16	7	6	5	4	3	2	1	#	*	+
C_1 = 0.01-0.04	6	5	4	3	2	1	#	*	+	=
H = 0-0.01	5	4	3	2	1	#	*	+	=	-
Cover class upper limit (%)	100	75	50	25	12	5	2	1	0.5	<0.3

the shallow and variable mountain mineral soils, the mean was based on 10 measurements.

Redox potential (mv) - measured using an Orion portable specific ion meter with a platinum electrode that was inserted into the peat, and an Orion double-junction reference electrode (as described by Lee and Gibson, 1980). Readings were taken at 5 minute intervals until they had stabilised.

Soil samples to 150 mm depth were air-dried before storage and then analysed in Wellington within 2 months of collection. The samples were ground, including organic material and twigs of diameter less than 5 mm, but not sieved. The following measurements were made on this material.

Soil pH - was measured by the method of Blakemore, Seale and Daly (1977), except that the ratio of distilled water to soil was increased to 10:1.

Soil Ca, Mg, Na, K (mg cm^{-3}) - cation levels were measured by atomic absorption spectrophotometric analysis of ammonium acetate extractions (Blakemore *et al.*, 1977). The extracted solutions were measured three times, and the mean was corrected for bulk density of the original soil.

Soil conductivity (mmho) - determined in a conductivity cell (Blakemore *et al.*, 1977).

Growth index (scale of 0-5) - from bioassay data of Campbell Island soils (Foggo and Meurk, 1983) significant linear regression equations were derived for growth (of two species) against each of pH, Ca, Mg, and Na levels. These equations were used to predict bioassay growth for each of the sample soil pH, Ca, Mg, and Na levels. These eight values (after scaling the data from the two bioassay species) were averaged to give a soil growth index for each sample site.

Animal index (scale of 0-5) - grazing influence was estimated by recording the cover of sheep pellets (infrequently cowpats), combined with the lowest height class of the biomass matrix.

Other records - a subjective vegetation category was applied to each of the sample sites (Fig. 1 legend). A photograph was taken at each site (Figs. 3-6), and the locality mapped (Fig. 1) to permit relocation of the sample site for comparative studies.

Vegetation analyses

The sites were classified into vegetation groups on the basis of the quantitative vascular species information using Cluster Analysis (Sneath and Sokal, 1973). The sorting strategy was flexible (beta = -0.25). The measure of dissimilarity was City Block. An inverse classification of the species into ecological groups, on the basis of their co-occurrences in the stands, was performed using similar methods, but with double-zero matches excluded (Sneath and Sokal, 1973). Although Cluster Analysis is a fusing method, it is convenient, for interpretation, to work top-down, and the distinctions are therefore described here as splits. The normal and inverse clusters have been ordered to conform with Axis 1 of the Detrended Correspondence Analysis within the constraints of the dendrogram (Tables 2, 3, Fig. 2).

Differences in environmental factors between groups from the vegetational classification were tested by the non-parametric Mann-Whitney Test (Snedecor and Cochran, 1967). Ordination of stands and species was performed by Detrended Correspondence Analysis (Hill and Gauch, 1980).

Multiple regressions of the position of stands on the stand ordination were calculated against the environmental variables.

Results

Inverse Cluster Analysis (the species groups)

Twenty-seven main vascular plant groups were derived from the inverse cluster analysis (Fig. 2, Table 2). The ecological significance of these groups is elucidated from the positions of the individual species and their clusters within the DCA ordination diagrams (Figs. 7, 8), the axes of which have been environmentally characterised by multiple regression and by single-factor mapping (Figs. 11-17).

The individual ecological groups or guilds are characterised by average environmental values, derived from the concentration of occurrences within site groups (Appendix) and their attributes (Table 4). Some of the groups are coherent in that the environmental range is narrow and can be clearly segregated as low, medium, or high in one or more parameters. Other groups comprise widely distributed opportunistic species or mixtures of infrequently occurring species, with consequent poor guild definition. The coherent groups are those with specialised species that are confined to stressful environments such as the littoral fringe, acid cushion bogs, swamps, or exposed summit ridges. The following lists sketch out the broad growth form and habitat attributes of the species clusters. The signature species indicated are those within the cluster which attain the greatest biomass index (Tables 2, 3).

Vascular plant groups

Mesotrophic to eutrophic, middle to low altitude and maritime turf, megaherbfield, grassland and shrubland species:

A *Puccinellia chathamica* - common littoral fringe cushions and turfs of shallow, fertile soils;

B *Hebe elliptica* - maritime associates;

C *Stilbocarpa polaris* - sheltered, ungrazed rocks/ledges throughout;

D *Poa ramosissima* - seral or disclimax coastal grass on well drained, deep, acid soils often associated with bird colonies;

E *Callitriche antarctica* - mainly adventive grasses and forbs of coastal wet/flushed, shallow but fertile ground associated with animal disturbance;

F *Pleurophyllum criniferum* - herbs of sometimes grazed fertile swamps/flushes.

Largely oligotrophic to mesotrophic matrix forbs, graminoids, and ferns:

G *Anisotome antipoda* - exposed summit tundra cushions, turfs, ferns, and forbs of shallow, fairly fertile soils;

H *Poa annua* - weedy herbs of grazed, maritime to flushed, fertile, shallow soils;

I *Histiopteris incisa* - localised ferns and mat forbs, often grazed and fertile;

J *Hypolepis amaurorachis* - an uncommon fern of lowland, deep, well drained soils;

K *Cardamine depressa* - localised on fertile shallow soils of maritime cliff crests;

L *Ranunculus subantarcticus* - with G and Z the main obligate tundra cushions and forbs, usually of low cover in fellfields and ledges, on gentle, sheltered slopes with shallow soils;

M *Sagina procumbens*- scarce on mild, fertile, disturbed or bird nest sites. *Isolepis praetextata* - rare on saline, steep coastal rocks;

N *Cardamine subcarnosa* - upland rush-herbfield forb;

O *Chiloglottis cornuta* - orchid of lowland, sheltered shrublands on deep acid soils;

P *Lycopodium fastigiatum* - components of inter-tussock/shrub short grazed turfs on fertile soils. *Lyperanthus antarcticus* - orchid of lowland, acid cushion bogs;

Q *Lycopodium varium* - dwarf forest epiphytes, ground ferns, and sedges associated with deep, infertile soils;

R *Oreobolus pectinatus* - cushions and forbs of lowland, gently sloping, exposed and grazed, deep acid bogs.

Eutrophic maritime herbaceous dominants:

S *Poa foliosa* and *Anisotome latifolia* - dominants of enriched, ungrazed, sheltered megaherbfield-grassland on steep, maritime slopes.

Dominant tussock grass and summer-green lily of mesotrophic to eutrophic grassland:

T *Poa litorosa* and *Bulbinella rossii* - ubiquitous dominants of maritime and upland grazed tussock grasslands.

Dominant tussock grass of low altitude oligotrophic and middle altitude mesotrophic sites:

U *Chionochloa antarctica* - dominant tussock grass of ungrazed, deep acid soils on exposed slopes.

Eutrophic sedge-swamp dominants:

V *Carex appressa* and *Blechnum* "sp.2" - dominants of sheltered, lowland, fertile sedge swamps.

Largely oligotrophic to mesotrophic, middle to high altitude, open-space graminoids, forbs, mats, and cushions:

W *Uncinia hookeri* - ubiquitous matrix graminoids and forbs of upland grasslands, herbfields, and tall rushlands, including taller

Marsippospermum and *Hierochloe brunonis* confined to high altitude rushlands;

X *Juncus scheuchzerioides* - medium turfy rush, common on non-maritime, mesotrophic/ flushed, wet, often gently sloping, eroded sites;

Y *Isolepis aucklandica* - ubiquitous turfs or mats of infertile gentle surfaces;

Z *Rostkovia magellanica* - cushions, forbs, and turf rush typically of exposed, high altitude shallow acid bogs; the palatable *Pleurophyllum hookeri* flourishes only in the absence of grazing.

Scrub and dwarf forest dominants:

ZA *Dracophyllum scoparium* - dwarf forest, scrub, and gully tussock dominants on deep, well drained acid soils.

Non-vascular plant groups

a *Pertusaria graphica* - crustose/small foliose lichens of maritime to littoral fringe steep rocks.

b *Rinodina thiomella* - as for a.; both groups, including *Verrucaria* spp., are best developed on extreme sites in the absence of vascular plants.

c *Ochrolechia parella* - crustose lichen and moss of steep, exposed, upland rocks.

d liverworts and crustose lichens of exposed, high altitude steep rocks and relatively fertile fellfields.

e *Bryum billardierei* - mixed turfy-ground cryptogams on sheltered, gentle slopes.

f *Eriopus* - a moss of sheltered maritime banks.

g *Metzgeria* spp.- forest and scrub epiphytic lichens and hepatics.

h *Muelleriella* - a littoral fringe cushion moss.

i *Rhacocarpus purpurascens* - bryophytes of wet, acid tundra and exposed, grazed meadows.

j *Lepidozia* spp. - largely turfy bryophytes of upland meadows, herbfields, and shrublands.

k *Brachythecium* spp. - bryophytes of scrub and forest on deep, acid soils.

l *Ptychomnion densifolium* - fairly ubiquitous turf-meadow and scrub cryptogams of grazed sites.

m *Macromitrium* spp. - epiphytic scrub, forest, and rock-inhabiting foliose and squamulose lichens and bryophytes.

n *"Rhizocarpon?"* spp. - crustose lichens of exposed, high altitude rocks and fellfields.

o *Stereocaulon* spp. - a fruticose lichen aggregate on rock and fellfield.

p *Marchantia berteroana* - bryophytes of lowland, fertile, open, animal-disturbed sites.

q *Drepanocladus* spp. - aquatic mosses.

r *Dicranoloma* spp. - common tufted, cushion, matted, or foliose cryptogams.

s hepatics - unidentified species, ubiquitous apart from coastal rocks.

t *Breutelia* spp. - upland turfy mosses of wet to flushed but shallow soils.

u *Sphagnum* spp. - mosses of wet, deep, acid soils.

Normal Cluster Analysis (the vegetation)

The 134 vegetation stands are considered at the 21 group level (Tables 2-3). Sites with only one vascular plant species and those rock and riparian communities exclusively composed of lichens or bryophytes were not included in this treatment, which nonetheless covers about 95% of the land area. Reference is made to some of the lichen and bryophyte-dominated communities in the descriptive synopsis of plant community types (Appendix). Analyses of lichens and bryophytes produced patterns subtly different from the vascular-only analysis, but reliance was placed on the vascular plants because of their more comprehensive and accurate field identification. Table 3 demonstrates the dominant cryptogamic associates of the vascular clusters.

The highest-level split in the normal dendrogram (Fig. 2) separates a large group of maritime to high altitude, oligotrophic to eutrophic tussock, shrub, sedge, rush, cushion and forb vegetation (Group I) from low altitude, oligotrophic to mesotrophic forest, scrub, and tussock/shrubland/ cushion bog (Group I'). Environmental factors correlating simply with this split ($P<0.05$) are soil pH (+4.8)[2], shelter (-3.5), altitude (+176), soil temperature (-9.2), and soil Mg (-0.17). Not all these factors are independent. For example, soil temperature and soil Mg are negatively correlated with altitude (r = -0.73 and -0.54 respectively, Table 5). These five individual factors distinguish correctly between the two sides of the split for 60-68% of the stands, although a combination of all factors accounts for 86% of the stands.

The split between II and II' separates mainly maritime, low to middle altitude, eutrophic turfs, tussocklands, megaherbs and scrub from middle to high altitude meso-oligotrophic tussock, turf, forb, rush, and cushionfield. Environmental factors correlating simply with this split are soil temperature (+8.9), altitude (-206), distance from any coast (-0.35), soil Mg (+0.17), soil Ca (+0.25), soil Na (+0.21), shelter (+2.5), conductivity (+1.02), and soil moisture (-616). Altitude is positively

[2] The number in parentheses is the midpoint value of the environmental parameter to distinguish between vegetation groups of the two sides of the split. The sign before the number indicates whether the first-mentioned groups tend to have values higher (+) or lower (-) than this midpoint.

Plate 3: Grey-headed mollymawk colony, northeast coast at Bull Rock, looking south. The bright green grass is Poa ramosissima *(CT 4a). On the less biotically disturbed borders of the colony is maritime tall tussock grassland of* Poa litorosa, Polystichum vestitum *and* Bulbinella *(CT 2), and* Dracophyllum-Polystichum *scrub and dwarf forest (CT 20).*

Plate 4: Panorama south from Mt Azimuth (c. 470 m) to Col Ridge, Mt Dumas (500 m), Menhir, and Mt Paris (468 m). The limestone contrasts with the greyer basalt cliffs of Northwest Bay. The foreground supports Bulbinella-Stereocaulon*-moss fellfield (CT 14), the bronze, tall rush turf of* Marsippospermum gracile *with* Bulbinella *(CT 13), and on the boggy saddle below, the upland cushion bog of* Centrolepis pallida *with* Rostkovia magellanica *usually associated further upslope (CT 16b).*

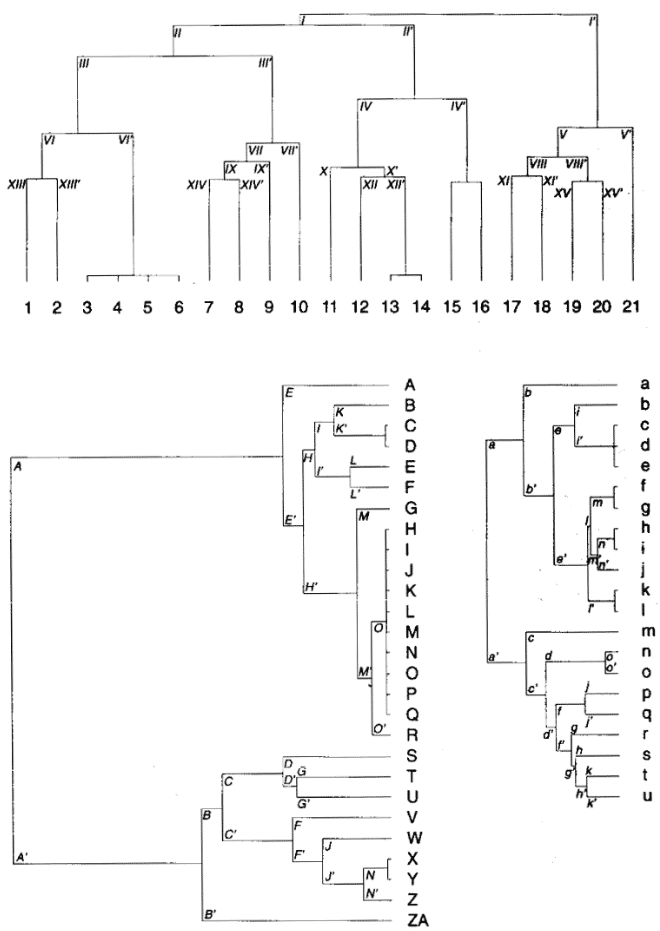


Figure 2: Dendrograms of association for the normal cluster analysis - above (sites, CT1-21), and inverse cluster analyses of vascular (A-ZA) - lower left, and non-vascular cryptogamic (a-u) species - lower right. The Roman numerals refer to the major ësplitsí and are replicated in the Appendix. Likewise the species' group letters (capitals for vascular species and lower case for cryptogams) are used in Tables 2 and 3. Italic letters denote the inverse ësplitsí. Dissimilarity scale for the normal analysis is from 0.0 up to an index value of 3.57 to the CT ìsplitî level (4.35 to the ultimate site level); for the inverse vascular analysis it is up to 11.12 at the speciesí group ìsplitsî (16.12 to the ultimate species level); for the inverse non-vascular plant analysis it is up to 3.84 (6.84 to speciesí ì splitsî).

correlated with distance from coasts, and moisture positively with soil depth and negatively with soil pH, K, and the growth index. With interactions, slope (+21) also becomes significant. Ninety percent of sites are correctly assigned, and individual significant factors are 58-88% accurate predictors.

The split between III and III' separates littoral-fringe, maritime tussock and megaherbfields, birdnest sites, upland rockfields, tarn margins, and peat scars from sedge-fern-shrub swamps, animal-modified tussock-meadows and turfs and slips, riparian belts, and tracks. The whole group comprises short vegetation of mesotrophic to eutrophic soils at low to middle elevations. Simple correlations occur with animal index (-0.5), distance from open coast (-0.31), soil Na (+0.41), and soil redox potential (-195). The sea-elephant wallow sites in Group III' are located around the inner harbours, and are therefore distant from the open coast. Soil Na is correlated with soil conductivity, K and Mg. Ninety four percent of sites are correctly assigned, and individual factors are 61-81% accurate predictors.

The split between VI and VI' separates maritime tussock and megaherbfield from short turfy or cushion communities of the littoral fringe, birdnest sites, rock ledges, tarn margins, and erosion scars (slips and deflated peat). The last group are generally at higher altitudes and have lower vascular plant cover, biomass, and species diversity. Simple correlates are growth index (+0.63), soil temperature (-10.1), soil K (+0.06), soil Mg (+0.17), slope (+6.5), distance to open coast (-0.97), soil Na (+0.32), soil pH (+4.53), and soil moisture (-381). All sites are correctly assigned, and individual factors are 63-79% accurate.

The split between IV and IV' separates high altitude, mesotrophic *Marsippospermum* rushland, herbfield, and fellfield from upland, meso-oligotrophic grassland, meadow, flushed and boggy short rushlands, and cushionfields. Simple correlates are altitude (+389), distance from any coast (+1.12), soil depth (-0.15), conductivity (-0.53), soil pH (+4.74), soil temperature (-7.9), soil moisture (-533), soil Ca (+0.21), soil Na (+0.26), growth index (+0.74), and soil K (+0.09). All sites are correctly assigned, and individual factors are 61-91% accurate.

The split between V and V' separates mesotrophic sedge-fern-mixed scrub, *Chionochloa* slope tussock grassland, scrub meadow, tall scrub, dwarf forest, and maritime tussock shrubland from oligotrophic *Chionochloa* tussock/dwarf shrub/ cushion bog. All are at low altitudes. Simple correlates are soil moisture (-639), soil Na (+0.15), soil K (+0.06), and soil temperature (-10.5), slope (+8.5), distance to open coast (-2.12), soil depth (-1.2), soil pH (+4.38), and animal index (-1.0). All sites are correctly assigned, and individual factors are 41-95% accurate. Beneath this level there are insufficient degrees of freedom to apply regression analyses.

Interpretation of analyses using all environmental factors must be tempered by the correlations between environmental factors (see above) which have no causative significance. Some of these are trivial or result from factors being mathematically derived from other factors, such as radiation from slope (as well as from latitude and aspect), and growth index from soil pH, soil Na, soil Mg, and soil Ca. Table 5 lists the significant, simply and partially correlated factors. Many of the soil nutrient factors are correlated by virtue of the importance of distance from the sea for all of them. The strong influence of distance from the sea, soil pH, and cations on the growth index, and of altitude on soil temperature, justifies removing the proxy factors from later analyses.

The Appendix names and characterises the 21 plant communities recognised on the basis of the cluster analysis (Fig. 2, Tables 2-3). Species richness values and vascular species guild dominance are also reported. Environmental attributes are derived from Table 4, from environmental correlations with cluster analysis splits (above), and from the ordination and environmental gradient analysis (below). Figures 3-6 illustrate examples of each of the groups.

Ordination (species and vegetation gradients)

The DCA ordinations of the vascular species are presented in Figs. 7-8. Similarly Figs. 9 and 10 present the normal stand ordinations and the overlayed communities.

Table 6 lists the regression coefficients, contributions, and significance levels from multiple regressions of environmental factors against the ordination scores. These statistics are presented for the 81 sites for which a full complement of 19 factors was recorded. Significant correlations on all 134 sites are also reported for the eight factors measured ubiquitously. Similarly, significant correlations are shown for when proxy environmental factors (altitude, slope, distance to coast) are excluded. Finally, the results of a simple regression for growth index is incorporated.

Table 2: *(overleaf) Two-way table of Campbell Island sample sites (designated by the row name whose first letter is aligned over the appropriate column), clustered at the 21 group level, and the vascular plant species clustered at the 27 group level (A-ZA). Quantitative values of species are explained in Table 1. Species followed by an asterisk are naturalised. The larger groupings of clusters (delineated by continuous lines) are understood in relation to the dendrograms of association (Fig. 4). Additional species are:* Acaena novae-zelandiae *(Sites 37SG, 83QD, 86SL, 100BX, Communities (CT) 9, 10, 19),* Acianthus viridis *(119UD, CT21),* Agrostis stolonifera* *(8ET, CT3),* Arrhenatherum elatius* *(113LE, CT2),* Asplenium obtusatum *(46EQ, CT1),* Grammitis patagonica *(101RG, CT11),* Hypochaeris radicata* *(2LX, CT18),* Juncus articulatus* *(64TX, CT8),* Leptinella dispersa *(68BT, 69GL, CT2),* Lycopodium australianum *(101RG, CT11),* Myosotis capitata *(101RG, CT11),* Poa trivialis* *(85BT, CT9),* Rumex obtusifolius* *(113LE, CT2),* Schizaea australis *(32UD, 117UA, 119UD, CT21),* Tmesipteris tannensis *(119UD, CT21),* Uncinia divaricata *(116JH, CT12),* Urtica australis *(17EG, CT1).*

Table 2: *(caption on previous page; continued opposite)*

SPECIES GROUPS	COMMUNITY TYPES	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	SAMPLE SITES	1OG 137GO 133OG 13OG 130GL 131GL 132LE 17EG 46EQ 106OG 136OL	9LE 63LE 59GL 10BG 120BG 19LB 90LE 128BE 113LE 68BT 69GL	8ET 135ET 134EH 11EF 121NT 44EU 35EU 89ET	26NH 79NH 48NH 138LE 77NT 78NT	50ZT 73ZT 110JT 70YT 109JT	43RY 102RY 56RY 104HY 93RY	33WH 34WX	47VY 80TH 112FH 64TX 82ST	25LB 100BX 85BT	18PC 99PC 37SG 41SP 86SL 122SP	101RG	53JG 116JH 61JB 71JH	22JB 125JF 126JH 103JB	123FB 57FH 62FH
A	Colobanthus muscoides	= - =	= # * = -	+ 4 1 2 5 5					=						
	Crassula moschata	- = 2	+ # - +	* # 5 1 4 4 #											
	Isolepis cernua	# + - # -	= = 2 - - 1 -	1 * 2 2 4 2 3				#		1					
	Puccinellia chathamica			6 6 * 1 2 2 -											
	Leptinella lanata	#		# 5 * 2 1											
B	Acaena minor var. antarctica	3 2 = 1	= 1		6 = -				-		1 # * *		1		
	Carex trifida	2 3 +	#	-											
	Lachnagrostis leptostachys	2 # 1 #		=					= - 2	=	1 1				
	Blechnum durum	4 3 - 1	# -												
	Hebe elliptica	4 7 *													
C	Hebe benthamii	1	2				-		#			+			
	Stilbocarpa polaris	2 6 3	2 * 6								=	#	- - 3	#	
	Pleurophyllum speciosum	2	- 3 3 3 3 1						= + *		=	3	5 - # -	# +	+
	Poa pratensis*		2 2 + 1 4					5			*				-
D	Poa ramosissima	2 * - 1		-	2 7 8										
E	Agrostis capillaris*		#	+				3 3	2 =	4		-			
	Callitriche antarctica	1	* = +		* 2			5 2	+ *				-		
	Leptinella plumosa	1	+ = =	1 = 1 +	=			# 2	+						
	Deschampsia chapmanii	#	- 1 * 2 2	+				# 2	- 2	-	# -	-			
	Rumex acetosella*		-					3 1			1				
	Anthoxanthum odoratum*		*					-	=		1				
	Holcus lanatus*		#						+		2				
	Festuca rubra*		3 1					1	*		2				
F	Acaena anserinifolia		+		2			-		3 1 2	# 2 # 3	-			
	Cerastium fontanum*	*	- - = * = # 2 1		# 2			+	= - =	2 1 #	+ * 1 * 1 1		= *	1	
	Epilobium pedunculare	= = *	+ * = = 1 + =		# 1 -			* *	2 * +	* * +	1 # * 1 #	*	# #		
	Isolepis habra		+						2 # = 2	1 #	# 1 2 4 2	-			
	Corybas trilobus		*							+	# 1 # * 1	-	1 1		
	Epilobium alsinoides							#	1	= *	* 1 2 # # 1		= *		
	Hierochloe fusca	3				1			1 - 1 2		+ 4 # +				
	Pleurophyllum criniferum										5 5				
G	Abrotanella rosulata						= - + =		=			#	-	1 * * +	1 * #
	Deschampsia gracillima						* +			2		+	- * =	1 # +	2 1 =
	Agrostis subulata						- - =							# *	2 2 1
	Anisotome antipoda											4	4 -	-	- # +
	Damnamenia vernicosa						-					2	- 1 #	# -	1 #
	Ranunculus pinguis											1			+ # -
	Ranunculus subscaposus										1 +	1	=		
	Grammitis poeppigiana						# = * * =					#		# * *	# + +
	Hymenophyllum villosum						* +					#	=	# * -	1 #
	Poa aucklandica						- +					#		# # + 1	= - 1
	Polystichum cystostegia											#		- * - *	
	Trisetum spicatum	=	* =				+ =				#	2	1 *	# + +	* - 1
H	Cardamine corymbosa	+ -	- # # # = 1 1 # # # #				+			= 1	-	1	2 #	+	=
	Colobanthus apetalus	- -	* * - # # =	-	=		*			2 -		=			
	Stellaria media*	-	= 2 = * #					=		1					
	Neopaxia australasica		- + 1 * +						* *	#	+				-
	Poa annua*		* - # 3 - * *	-	-			4 1	+ *	= # 1	+				
	Epilobium brunnescens	#	+ * = =			= =		#	- + #	+ = #	+ * *	#	- * # #	- +	# =
	Montia fontana		2 + = *			1		#	+ * +	= + *	*				
I	Histiopteris incisa	+							*						
	Hydrocotyle microphylla									2 - #	=				
	Hypolepis millefolium								*	3	-				
	Pratia arenaria									#	=				
J	Hypolepis amaurorachis	*									1				
K	Cardamine depressa		= * -	* *											
L	Colobanthus hookeri						+ - =								= *
	Craspedia uniflora											=		- -	* *
	Myosotis antarctica						- -					*		+ -	* =
	Ranunculus subantarcticus											+	#	= -	+
	Grammitis givenii											+			
	Epilobium pernitens														-
	Taraxacum magellanicum		+ + + +						-	-					
M	Sagina procumbens*	* +	*						-	-	=				
	Isolepis praetextata	# =		*											
N	Cardamine subcarnosa		= -										# = 1	* +	
O	Chiloglottis cornuta								=						
P	Juncus antarcticus								1 1	- *					
	Lagenifera petiolata	-	- - =						# #	1 2 #	# +		+		
	Lycopodium fastigiatum								#	-					
	Lyperanthus antarcticus								+						
Q	Grammitis magellanica														
	Hymenophyllum minimum														
	Lycopodium varium	1									- =				
	Uncinia aucklandica														
R	Aporostylis bifolia														
	Drosera stenopetala								-						
	Astelia subulata														
	Centrolepis ciliata								=						
	Gonocarpus aggregatus								+						
	Oreobolus pectinatus														
	Blechnum procerum														
S	Anisotome latifolia	5 2 6 4 6 6 5 3 3 2	4 6 4 7 3 - = 3	= #			=		- 2		-				+
	Poa foliosa	7 3 8 7 4 5 5 7 7	4 3 3	# 2	= =		*		1 + 2			#	*		
T	Bulbinella rossii	5 2 3 6 5 4 5 2 3 4	5 5 6 8 6 6 6 7 4 6 7	2	2 2 4 =	1 1 1	-		1 * -	5 4 8	2 4 2 3 3 5	4	6 5 5 5	5 5 5 6	3 3 2
	Poa litorosa	5 5 4 8 5 5 3 6	7 7 5 4 4 7 7 = 8 5	* 1	1 2 1 7 1		#		# 2 + =	5 3	4 3 3 4 4 4	-	2 5 # #	# 2	
U	Chionochloa antarctica	4 2 3									+				
V	Blechnum sp2								- 3		4 3 5				
	Carex appressa	3						2 3	# # 4	3	+ 3 + 4 7 6				
W	Acaena minor var. minor		2 # + + + #		2 #		=		1 +	* # #	2	2	1 1 2	2 * # 2	2 * 1
	Poa breviglumis		2 - 2 - # # 1		#		+		1 1 1 -	4 # 4	1 1 1 - #	2	+ 1 # 2	= #	- *
	Epilobium confertifolium	- * #	= = + - 1 * = +	*	# 1 1 = 1	= +	= =		# # * -	# *	- +	1	1 * * *	# * # *	# - #
	Geranium microphyllum		* - 1 =		=				+ *	* # -	# * 1	*	- # # 2	= +	
	Stellaria decipiens	# = 1 3 2	+ - * 1 1 # #		* # * 3 +	* * + *	*	+		* * 1	* = - +	*	* * + #	* + + =	
	Agrostis magellanica	+	2 1			- *	#		+ 4 2 1 2	+	1 - 1	2	# 1	+	
	Helichrysum bellidioides		# # # = * *			=	+ 1		3 3 1 * 2	* * =	+ * 4 1 2	1	2 2 2 3	1 # 1	2 2 1
	Luzula crinita	= -	- = +	*	+ * 2	# + 1	- - + -		3 1 1	- =	* #	1	= 2 3	1 # 3 +	1 1 1
	Uncinia hookeri		1 * + 2 1 2		+			-		1 =	* + = 2	2	2 2 # 1	1 1 # -	2 2 #
	Hierochloe brunonis						-		1 +		4	1	2 4 4	1 3 3 *	#
	Marsippospermum gracile											#	4 7 8 5	5 5 6 5	2
X	Juncus scheuchzerioides		1			2 2 5 5 6		3	= # - 1 4	=	3 1 4 2	-	*		
Y	Coprosma perpusilla					+			1	-	+	=	# -	- =	# # =
	Isolepis aucklandica				=	# + 3 # *	*		* 1 4 1	+	= #		* -	- *	+ +
	Hymenophyllum multifidum								+	1 =	#	=	= #		+
Z	Abrotanella spathulata				+				- =	+		=	* +		
	Gentiana antarctica	#	1						- + #	+		*	# +	- *	- # *
	Phyllachne clavigera											+		=	1 # 1
	Pleurophyllum hookeri											-	2 # 2	-	* *
	Centrolepis pallida					1						*			1
	Rostkovia magellanica													# 1 #	#
ZA	Coprosma ciliata								= *	= -	3 6 3 1 = 2				
	Polystichum vestitum	3 = 5	5 5 2 * * = 1		+ + -		=	-		+ * -	8 6 2 3 * #	2	= = =		
	Coprosma cuneata		*				-		+ 1		7 # + 2	#			
	Myrsine divaricata	=							#		# 3 -				
	Dracophyllum longifolium		-						=	=	1 = +				
	Dracophyllum scoparium							3	- +		+				

Table 2: *contd.*

Group	Species	14LH	15LH	95UT	39LB	65LP	40LB	66LB	58AL	75AL	67ZT	84LZ	107UD	121BK	54KH	49UH	60KY	114JB	24UK	72UK	55UK	123UB	91KB	124KH
	Community type	15												16										
A	Colobanthus muscoides																							
	Crassula moschata																							
	Isolepis cernua																							
	Puccinellia chathamica																							
	Leptinella lanata																							
B	Acaena minor var. antarctica												•											
	Carex trifida																							
	Lachnagrostis leptostachys																							
	Blechnum durum																							
	Hebe elliptica																							
C	Hebe benthamii																							
	Stilbocarpa polaris		-																					
	Pleurophyllum speciosum	#	+														-	#	=				+	
	Poa pratensis*																							
D	Poa ramosissima																							
E	Agrostis capillaris*																							
	Callitriche antarctica																							
	Leptinella plumosa																							
	Deschampsia chapmanii											=												
	Rumex acetosella*																							
	Anthoxanthum odoratum*																							
	Holcus lanatus*																							
	Festuca rubra*																							
F	Acaena anserinifolia																							
	Cerastium fontanum*						=	=	-		•	•	-										=	
	Epilobium pedunculare					+		+			+													
	Isolepis habra																							
	Corybas trilobus										#													
	Epilobium alsinoides				+																			
	Hierochloe fusca																							
	Pleurophyllum criniferum																							
G	Abrotanella rosulata											•					+	-	#	1			+	•
	Deschampsia gracillima											•							2	1			#	#
	Agrostis subulata																		1		-			#
	Anisotome antipoda														-			1	+					
	Damnamenia vernicosa		-								-		#		•	•	=	#	1	#	•	-	+	
	Ranunculus pinguis																			•				
	Ranunculus subscaposus																							
	Grammitis poeppigiana																	+	#	-			•	
	Hymenophyllum villosum												-											
	Poa aucklandica																		+					
	Polystichum cystostegia																							
	Trisetum spicatum																	-						
H	Cardamine corymbosa																							
	Colobanthus apetalus																							
	Stellaria media*																							
	Neopaxia australasica																			-				
	Poa annua*																							
	Epilobium brunnescens																							•
	Montia fontana																							
I	Histiopteris incisa																							
	Hydrocotyle microphylla																							
	Hypolepis millefolium																							
	Pratia arenaria											-												
J	Hypolepis amaurorachis																							
K	Cardamine depressa																							
L	Colobanthus hookeri																							
	Craspedia uniflora																						=	
	Myosotis antarctica																						-	
	Ranunculus subantarcticus																-							
	Grammitis givenii								=		=			=			•							
	Epilobium pernitens																		+	•				
	Taraxacum magellanicum																							
M	Sagina procumbens*																							
	Isolepis praetextata																							
N	Cardamine subcarnosa																							
O	Chiloglottis cornuta																							
P	Juncus antarcticus	•	#																				#	
	Lagenifera petiolata	=	#																					
	Lycopodium fastigiatum	#	#	#	=	=			#	2		=												•
	Lyperanthus antarcticus																							
Q	Grammitis magellanica																							
	Hymenophyllum minimum																							
	Lycopodium varium						-	=	+	•		-	•											
	Uncinia aucklandica																							
R	Aporostylis bifolia												-											
	Drosera stenopetala												•											
	Astelia subulata		=										#											
	Centrolepis ciliata		+										-											
	Gonocarpus aggregatus												=											
	Oreobolus pectinatus												#											
	Blechnum procerum																							
S	Anisotome latifolia	•	+									+												
	Poa foliosa																							
T	Bulbinella rossii	2	2	#	4	4	4	5	4	3	5	3	5	4	4	2	1	4	1	2	1	2	2	3
	Poa litorosa	2	2	2	6	7	5	5	5	3	5	5	4	1	#	2								
U	Chionochloa antarctica	1			3	1			7	8	2		•				•							
V	Blechnum sp2																							
	Carex appressa																							
W	Acaena minor var. minor			-		#		+				#					=							
	Poa breviglumis							=				#												
	Epilobium confertifolium	#	#	+	•	#	#	+	•	+	=	1	+	+	=	+		+		-			•	•
	Geranium microphyllum	#	#	+	•	1	2	1	•	•	•	•		•	=		-	#					#	•
	Stellaria decipiens				-	•	+	•	•	•	#	#		+				=						
	Agrostis magellanica	=	=				#					#	=	-	+	•	#			1			#	
	Helichrysum bellidioides	•	-	2			=	=	-			+	•	+		+	1	#	•	+			•	#
	Luzula crinita	2	#		2	1	2	#	2	1	2	1	2		#	1		1	-	1	#	+	1	2
	Uncinia hookeri	#	#	+	3	2	3	1	3	2	1	2	#	1	1	1	1	#	1	#			2	1
	Hierochloe brunonis	1	•	•	1	2		=									2	1		-				
	Marsippospermum gracile														+		1	5						
X	Juncus scheuchzerioides	1	1	1										#	#	2		#			•		4	
Y	Coprosma perpusilla	1	•		2	#	1	#	#	1	-	-	1	1	1	#	2	2	•	#	#	•	2	#
	Isolepis aucklandica	4	4	#	•	1	#	2		=	•	4	#	2	2	1	1	1	2	2	#	#	1	1
	Hymenophyllum multifidum	#	1	#	3	2	3	2		+	•	=		#	-			=						
Z	Abrotanella spathulata	•	=		#	=	•	#	+	-	-	#	=	•	•	•	+	=		=	#		•	
	Gentiana antarctica	1	#	+	3	1	2	1	•	+	+	#	#	=	•	#	=	1	=	=	1	•	+	#
	Phyllachne clavigera	1	#		•	•	#	#	+	=		#	#	#	#	2	1	#	#	•	#	#	#	
	Pleurophyllum hookeri	#	=										3	•	4	4	•	3				=		
	Centrolepis pallida												=			1	#	#	3	4	4	4		•
	Rostkovia magellanica													3	4		4	3	3	1	1		4	4
ZA	Coprosma ciliata			•			•		-	1		-												
	Polystichum vestitum	-		-	4	6	1	3	3	1	#	-	=											
	Coprosma cuneata		-	-	1	#		+		1	=	+	1											
	Myrsine divaricata									-														
	Dracophyllum longifolium				2			2	2	=														
	Dracophyllum scoparium	=		=	1				=	3			4		=									

Group	Species	6AP	115AC	92RC	129AG	42RC	2LX	88TD	4CP	74PC	7PS	94BC	96DA	83QD
	Community type	17					18							19
A	Colobanthus muscoides					-								+
	Crassula moschata													+
	Isolepis cernua				-									-
	Puccinellia chathamica													
	Leptinella lanata													
B	Acaena minor var. antarctica							#						2
	Carex trifida													2
	Lachnagrostis leptostachys			-	#			-				•		
	Blechnum durum													2
	Hebe elliptica													6
C	Hebe benthamii			=		#								
	Stilbocarpa polaris													
	Pleurophyllum speciosum	3	1		#							#		
	Poa pratensis*													
D	Poa ramosissima					=								
E	Agrostis capillaris*													
	Callitriche antarctica													
	Leptinella plumosa													
	Deschampsia chapmanii													=
	Rumex acetosella*						3							
	Anthoxanthum odoratum*						2							
	Holcus lanatus*													
	Festuca rubra*										-			=
F	Acaena anserinifolia								-					
	Cerastium fontanum*						•	-	-					
	Epilobium pedunculare			+		•	=		•					+
	Isolepis habra								+					
	Corybas trilobus						-							
	Epilobium alsinoides													
	Hierochloe fusca			-			2		+	2	1	3	2	
	Pleurophyllum criniferum						+		-		5	1		
G	Abrotanella rosulata					=								
	Deschampsia gracillima													
	Agrostis subulata					•								
	Anisotome antipoda													
	Damnamenia vernicosa					#								
	Ranunculus pinguis					+								
	Ranunculus subscaposus													
	Grammitis poeppigiana					#								
	Hymenophyllum villosum					=								
	Poa aucklandica													
	Polystichum cystostegia													
	Trisetum spicatum				1	#								
H	Cardamine corymbosa													•
	Colobanthus apetalus			+	-	=								•
	Stellaria media*													
	Neopaxia australasica													
	Poa annua*													
	Epilobium brunnescens			-										
	Montia fontana													
I	Histiopteris incisa						-	•						#
	Hydrocotyle microphylla													
	Hypolepis millefolium													
	Pratia arenaria							1						
J	Hypolepis amaurorachis													
K	Cardamine depressa													
L	Colobanthus hookeri					-								
	Craspedia uniflora													
	Myosotis antarctica													
	Ranunculus subantarcticus													
	Grammitis givenii					=								
	Epilobium pernitens													
	Taraxacum magellanicum													
M	Sagina procumbens*													
	Isolepis praetextata													
N	Cardamine subcarnosa													
O	Chiloglottis cornuta						1		-			-		
P	Juncus antarcticus													
	Lagenifera petiolata						-	-						
	Lycopodium fastigiatum											1	+	
	Lyperanthus antarcticus												#	
Q	Grammitis magellanica					#								
	Hymenophyllum minimum													
	Lycopodium varium	-	#			1	-	#	-	-			1	
	Uncinia aucklandica													
R	Aporostylis bifolia												•	
	Drosera stenopetala												+	
	Astelia subulata													
	Centrolepis ciliata													
	Gonocarpus aggregatus													
	Oreobolus pectinatus													
	Blechnum procerum													
S	Anisotome latifolia	-	•	=	4									
	Poa foliosa			=	+	2								
T	Bulbinella rossii	3	4	3	5	5	4	3	4	4	4	5	2	3
	Poa litorosa	•	2	5	5	3	5	5	4	3	4	4	3	3
U	Chionochloa antarctica	8	8	5	7	4			-			2	5	
V	Blechnum sp2								4	5	6	1	#	
	Carex appressa		1		+		5	2	3		5		2	#
W	Acaena minor var. minor			+			+			=		•		
	Poa breviglumis					=								1
	Epilobium confertifolium	•				•	1	•	•	-	-	+	-	
	Geranium microphyllum	•		+			#	+	+			+	#	
	Stellaria decipiens				#	=	•	•		-		-		1
	Agrostis magellanica			+						1		+	=	
	Helichrysum bellidioides	1		#	-	2	+		1	2		1	1	
	Luzula crinita		+	#	•	1	3	#	-			=		
	Uncinia hookeri	=			1	1	3	1	2	1	#	3	2	
	Hierochloe brunonis	+			#						#	#		
	Marsippospermum gracile													
X	Juncus scheuchzerioides										2	#	3	
Y	Coprosma perpusilla					+						-	3	
	Isolepis aucklandica	-					#	4			#	#	2	
	Hymenophyllum multifidum	#				•			=	#	1	2	=	
Z	Abrotanella spathulata						+	#				=	-	
	Gentiana antarctica				•	#	+	#			•	•	#	
	Phyllachne clavigera					#						+	-	
	Pleurophyllum hookeri											•		
	Centrolepis pallida													
	Rostkovia magellanica													
ZA	Coprosma ciliata	4	4	7	1	2	3	+	7	4	5	4	1	3
	Polystichum vestitum	4	5	2	1	2	4	5	5	4	4	4	1	3
	Coprosma cuneata	3	5	4	1	4	=	-	6	3	3	4	2	2
	Myrsine divaricata	3	1	3	•	#	+	3	2	3	3	1	2	2
	Dracophyllum longifolium	-	•	=	=		-	5	2			+	2	7
	Dracophyllum scoparium	1	•				2	#	3	=	3	3	6	3

Group	Species	3DM	16DM	87DM	76DC	127D	20DC	38DM	81DM	98DM	28DC	105DP	30DL	31DA	29DM	52DM	5AU	51AU	111AU	32UD	117UA	119UD	27UD	118AD	97AD
	Community type	20															21								
A	Colobanthus muscoides																								
	Crassula moschata																								
	Isolepis cernua					2																			
	Puccinellia chathamica																								
	Leptinella lanata																								
B	Acaena minor var. antarctica		-									=													
	Carex trifida																								
	Lachnagrostis leptostachys																								
	Blechnum durum		-	•																					
	Hebe elliptica																								
C	Hebe benthamii																								
	Stilbocarpa polaris																								
	Pleurophyllum speciosum													-										-	
	Poa pratensis*																								
D	Poa ramosissima																								
E	Agrostis capillaris*																								
	Callitriche antarctica		1																						
	Leptinella plumosa																								
	Deschampsia chapmanii																								
	Rumex acetosella*																								
	Anthoxanthum odoratum*																								
	Holcus lanatus*																								
	Festuca rubra*																								
F	Acaena anserinifolia																								
	Cerastium fontanum*											-													
	Epilobium pedunculare	=	=	•						•															
	Isolepis habra																								
	Corybas trilobus	-	-		#	2	2	2	+	=		-				-									
	Epilobium alsinoides																								
	Hierochloe fusca																		1						
	Pleurophyllum criniferum																					-			
G	Abrotanella rosulata																								
	Deschampsia gracillima																								
	Agrostis subulata																								
	Anisotome antipoda																								
	Damnamenia vernicosa																-	1	+	+	+	•	=	-	-
	Ranunculus pinguis																								
	Ranunculus subscaposus																								
	Grammitis poeppigiana																								
	Hymenophyllum villosum															•							-		#
	Poa aucklandica																								
	Polystichum cystostegia																								
	Trisetum spicatum																								
H	Cardamine corymbosa		-																						
	Colobanthus apetalus																								
	Stellaria media*		-																						
	Neopaxia australasica																								
	Poa annua*		-																						
	Epilobium brunnescens																								
	Montia fontana		-																						
I	Histiopteris incisa	-	=	2		3																			
	Hydrocotyle microphylla																								
	Hypolepis millefolium	-																							
	Pratia arenaria																								
J	Hypolepis amaurorachis		=																						
K	Cardamine depressa																								
L	Colobanthus hookeri																								
	Craspedia uniflora																								
	Myosotis antarctica																								
	Ranunculus subantarcticus																								
	Grammitis givenii																								
	Epilobium pernitens																								
	Taraxacum magellanicum																								
M	Sagina procumbens*																								
	Isolepis praetextata																								
N	Cardamine subcarnosa																								
O	Chiloglottis cornuta	•	=	•							1	#					-								
P	Juncus antarcticus																								
	Lagenifera petiolata																								
	Lycopodium fastigiatum										-		-	-	-				-						
	Lyperanthus antarcticus																			-	#	-	1	#	
Q	Grammitis magellanica		•				#			1															+
	Hymenophyllum minimum		+							1															+
	Lycopodium varium						2	•	=	3	1		+	-	1	#	3	•	+	-		-	-	=	
	Uncinia aucklandica	-	-	-	#		-	2	+	#															
R	Aporostylis bifolia										-						+		•	-	-	#	-		
	Drosera stenopetala																+			+	+	•			
	Astelia subulata																1	-	•	#	#	•			
	Centrolepis ciliata																-			2	+	=			
	Gonocarpus aggregatus																			+	#				
	Oreobolus pectinatus																			3	•	1	1		
	Blechnum procerum																					2		2	
S	Anisotome latifolia																								
	Poa foliosa																								
T	Bulbinella rossii		-		4	3	-				3	3	4	3	2	#	1	1	2	2	#	1	1	1	
	Poa litorosa			•	2	4					4	3	5	2	2	#	-								
U	Chionochloa antarctica				3						-			6			6	6	6	2	5	1	4	7	7
V	Blechnum sp2							1	3	6													-	+	3
	Carex appressa																								
W	Acaena minor var. minor												=		•										
	Poa breviglumis		-				=																		
	Epilobium confertifolium			•	-							#	•	•	=		-		=						
	Geranium microphyllum										-	•	-	•											
	Stellaria decipiens		=	•	-	+	=	1	#			-	+												
	Agrostis magellanica																								
	Helichrysum bellidioides				#						#	•	=	-					+						
	Luzula crinita										=	#	•	-			-								
	Uncinia hookeri										=	1	4	2	1	-	-	-	-				-	#	
	Hierochloe brunonis													2			•								
	Marsippospermum gracile																								
X	Juncus scheuchzerioides													•											
Y	Coprosma perpusilla										1		1	1		#	1	1	1	#	1	#	3	1	2
	Isolepis aucklandica										3	#	-	1	1		2	2	3	1	1	2	2	#	
	Hymenophyllum multifidum						3	•	•	2	2	1	3	1	2	2	-			-	#			1	1
Z	Abrotanella spathulata												-	-											
	Gentiana antarctica				-						-	-			=		+	•	1	+	+	=	-	#	+
	Phyllachne clavigera																1	#	•	•	•		#		
	Pleurophyllum hookeri																	1				-			
	Centrolepis pallida																-								
	Rostkovia magellanica																								
ZA	Coprosma ciliata	•	-	1	5	5	4	2	2	3	3	3	4	3	3	3	=	-	3	=					
	Polystichum vestitum	7	1	3	4	5	5	3	3	3	3	4	4	4	4	2			=					#	2
	Coprosma cuneata	3	•	+	4	3	6	3	4	4	3	3	4	2	3	2	2	1	-	=	-	1	2	3	3
	Myrsine divaricata	7	4	3	1	4	6	5	4	4	5	3	3	4	6	4	2	•	#	•	+	3	4	3	4
	Dracophyllum longifolium	8	8	4	3	1	3	5	4	8	3	6	5	2	+		3	#							4
	Dracophyllum scoparium	8	8	0	8	8	8	9	9	3	7	7	4	7	8	8	5	5	6	5	5	5			7

Table 3: *Two-way table of Campbell Island sample sites, clustered at the 21 group level, and the non-vascular cryptogamic species or aggregates clustered at the 21 group level (a-u). See legend for Table 2. Continued opposite.*

SPECIES GROUPS	COMMUNITY TYPES	1	2	3	4	5	6	7	8	9	10	11
	SAMPLE SITES	1OG 137GO 133OG 13OG 130GL 131GL 132LE 17EG 46EQ 106OG 136OL	9LE 63LE 59GL 10BG 120BG 19LB 90LE 128BE 113LE 68BT 69GL	8ET 135ET 134EH 11EF 121NT 44EU 35EU 89ET	26NH 79NH 48NH 138LE 77NT 78NT	50ZT 73ZT 110JT 70YT 109JT	43RY 102RY 56RY 104HY 93RY	33WH 34WX	47VY 80TH 112FH 64TX 82ST	25LB 100BX 85BT	18PC 99PC 37SG 41SP 86SL 122SP	101RG
a	*Pertusaria graphica*			=			· ·					
	Xanthoparmelia sp.	=	-	=								
	Verrucaria maura						-					
b	*Physcia caesia*											
	Verrucaria durietzii											
	Rinodina thiomela						-					
	script lichen											
c	*Leptostomum inclinans*						- ·					
	Ochrolechia parella						1 ·					
d	*Lepicolea scolopendra*											+
	Pertusaria 'lime'						- -					
	pink lichen crust						- +					
e	*Aneura sp.*		+								=	
	Bryum billardierei		= - +		1						- +	
	Trichocolea mollissima											
	Cladonia 'green'				=							
	Lepidozia laevifolia											
	Schistochila spp.											
	Sticta latifrons											=
	Weymouthia cochlearifolia						·					
	Campylopus introflexus											
	Knightiella splachnirima											
	Usnea 'green'											
	moss spp.	· = ·	- - ·						+			
	agaric yellow		=			· = =			+			
	Cladonia 'brown'						- ·					
	Sphaerophorus melanocarpus						+					
	Hypogymnia lugubris						-					
	Bryum laevigatum											+
	Conostomum pusillum						=					
	Campylopus spp.				# -							-
f	*Calyptrochaeta apiculata*	·		=								
g	*Metzgeria spp.*	+	= ·									
	Collema spp.	+	+ ·				+				=	
	Pseudocyphellaria rubella											
	Lecidea s.l.	=									# -	
	Coccotrema sp.						+					
	Megalospora gompholoma						=				=	
	Menegazzia spp.						+ + =					
	Usnea 'yellow'						1 ·					
h	*Muelleriella crassifolia*		-	2 1 2								
i	*Adelanthus occlusus*						=			-		
	Lepidozia spp.								=			
	Rhacocarpus purpurascens						= =					
j	Anthocerotae	·				=			# # = ·		- #	
	Bartramia patens		=				+		= · +	+	+	·
	Fossombronia spp.		= -	=					+	-	=	#
	Plagiochila spp.									+		1
	Porella elegantula		-				+					
	Pseudocyphellaria homoeophylla											·
	Lophocolea spp.		#			- -	=	-	+		1	
	Riccardia sp.		+						=		+	
	Lepidolaena spp.									·		
	Thuidium furfurosum		- =							+ 1	· =	=
	Polytrichum spp.									+		
k	Lejeuneaceae						=				=	
	Brachytheciaceae										1 + #	
l	*Achrophyllum dentatum*	· +	+ · · 1						#	- #	- = 1 +	=
	Peltigera spp.	· +	# # - - + · = -	+			-		· 1 ·	=	- - = + + ·	
	Sticta colina	·	= · + + # - = -	+						=	=	
	Ptychomnion densifolium		+ # # - =							3 = =	1 · · +	
	Acrocladium chlamydophyllum		· + # =							+ +	1 · + +	=
m	*Frullania spp.*	+					= =				= + =	
	Psoroma 'no prothallus'						# ·					
	Macromitrium spp.	+		-			# · ·				= -	· +
	Pseudocyphellaria coronata										-	
	Pseudocyphellaria faveolata						#					#
	Psoroma 'prothallus'						- =					
n	'Rhizocarpon black-white'						1 2 = ·					
	Placopsis spp.						+ · =		1 #			
o	*Stereocaulon/Argopsis*						1 3 4 1 +		# -			+
p	*Marchantia berteroana*	· · #	· # 1 · # ·		3 # + # #	= · +		2 #	· = + -	# = #	- · # -	
	Ceratodon purpureus				# 1			# ·			+ +	
q	*Drepanocladus sp.*					1 5		+				
r	*Riccardia cochleata*								#	-		
	Hypnum cupressiforme								·		-	
	Dicranum robustum		· =		#		= + #		=			#
	Cladia aggregata		-		# ·	+ -	· ·		= -	·		·
	Sphaerophorus tener					+	+			= +		=
	Pseudocyphellaria glabra		= + -				1 - · +			· +	= -	·
s	hepatic spp.	+ ·	· = # + # · #	#	- # ·	= -	2 ·		· 1 -	1 # =	2 · # 1	
t	*Breutelia elongata*					- · +			·			#
	Breutelia pendula		- =			·			- 3 2 = +	- ·	= 1 2 +	#
u	*Sphagnum spp.*					1 #			# 3 #			

Table 3: *contd.*

COMMUNITY TYPES: 12, 13, 14, 15, 16, 17, 18, 19, 20, 21

SAMPLE SITES:

53JG, 57FH, 58AL, 114JB, 92RC, 96DA, 81DM, 51AU
116JH, 62FH, 75AL, 24UK, 129AG, 83QD, 98DM, 111AU
61JB, 14LH, 67ZT, 72UK, 42RC, 3DM, 28DC, 32UD
71JH, 15LH, 84LZ, 55UK, 2LX, 16DM, 105DP, 117UA
22JB, 95UT, 107UD, 123UB, 88TD, 87DM, 30DL, 119UD
125JF, 39LB, 21BK, 91KB, 4CP, 76DC, 31DA, 27UD
126JH, 65LP, 54KH, 124KH, 74PC, 127D, 29DM, 118AD
103JB, 40LB, 49UH, 6AP, 7PS, 20DC, 52DM, 97AD
123FB, 66LB, 60KY, 115AC, 94B, 38DM, 5AU

SPECIES GROUPS		12	13	14	15	16	17	18	19	20	21
a	*Pertusaria graphica*										
	Xanthoparmelia sp.										
	Verrucaria maura										
b	*Physcia caesia*										
	Verrucaria durietzii										
	Rinodina thiomela										
	script lichen										
c	*Leptostomum inclinans*						=				
	Ochrolechia parella										
d	*Lepicolea scolopendra*			+		-					
	Pertusaria "lime"			+							
	pink lichen crust			· =							
e	*Aneura sp.*				+			+ + =		= +	
	Bryum billardierei				- - - + -			= · +		- # = · - = = +	
	Trichocolea mollissima						+	#		=	
	Cladonia "green"			-	= + + -			- ·		-	+ = ·
	Lepidozia laevifolia				- ·	+	=			# -	=
	Schistochila spp.	·	-			-					
	Sticta latifrons	=			=	=		-			
	Weymouthia cochlearifolia	- +		- ·		- -	·				
	Campylopus introflexus							+			-
	Knightiella splachnirima				- + -			= -		- -	+ = = -
	Usnea "green"								=	= = =	
	moss spp.				- -		- #			·	=
	agaric yellow				· -	+		· -		=	
	Cladonia "brown"				- = =		+	- -		+ - = -	- + = =
	Sphaerophorus melanocarpus					-	+			#	· + - -
	Hypogymnia lugubris		=	-	+	· - ·	=			-	· = - # ·
	Bryum laevigatum					= = +					
	Conostomum pusillum		-	=		- · #	+				
	Campylopus spp.			#	- +	· ·					= = -
f	*Calyptrochaeta apiculata*								#		
g	*Metzgeria spp.*	=						- +	#	= + # · · 1 + · ·	
	Collema spp.				-	=		+ + -	#	- - = + + - · =	= +
	Pseudocyphellaria rubella						= +	= + =		= = = + · ·	=
	Lecidea s.l.				- - +		·	+ - =	·	= - + + +	
	Coccotrema sp.								-	+ · = + #	-
	Megalospora gompholoma							- = ·	-	+ · = · + · · · = +	· -
	Menegazzia spp.								·	= = · = + +	=
	Usnea "yellow"			· = ·	·	= - = #	+	-	=	+ = = · = = = -	- + =
h	*Muelleriella crassifolia*										
i	*Adelanthus occlusus*	+	+ · +		+ + = = + = · -	# # +		-		- · - =	+ -
	Lepidozia spp.			=	+ + = = · + =	1 #				· + =	
	Rhacocarpus purpurascens		- ·	# =		# - 1 · + ·				+	
j	Anthocerotae	·						-			
	Bartramia patens	+ #	= · =	=		- =					·
	Fossombronia spp.				+ = #	# +		= =			
	Plagiochila spp.	+ ·	= =		· -	=		- +		= # =	-
	Porella elegantula				+ · # - - +		+ · ·	· ·		- · - -	+
	Pseudocyphellaria homoeophylla	=	#		- # # #	- =	+	= =			
	Lophocolea spp.	2 #	+							· = ·	·
	Riccardia sp.	- #			= - = - -	+ - +		=		= - - · + ·	+ # · ·
	Lepidolaena spp.	+ =	·					-		+ 1 =	+ ·
	Thuidium furfurosum							-		·	=
	Polytrichum spp.	·			- ·	3		- +			
k	Lejeuneaceae							#		# · 1 # - +	
	Brachytheciaceae						=			+ + · # + =	
l	*Achrophyllum dentatum*	# ·			+			· · + =		= - # + = · # +	=
	Peltigera spp.	# 2	· + =		=	= · -	· -	# = ·	+	- · =	
	Sticta colina	+ #	+		- + +	# - #	+	- - = · =		+ =	
	Ptychomnion densifolium	· +		+	+ + · + # = -	·	+	= · # · - · =		- + - - = = = -	# ·
	Acrocladium chlamydophyllum	+	+ + + -	+	= · = -	= -		= · = -		+ # - - +	+
m	*Frullania spp.*				- ·		- · =	- = # = - +	#	= + # # 2 # = 1 + = 1 #	· = #
	Psoroma "no prothallus"				+		- = ·	= · + = ·	+	1 · + # + 1 # = + · + · #	= ·
	Macromitrium spp.				= +			= - = +	1	1 3 # # 2 1 1 # # +	- · +
	Pseudocyphellaria coronata				1		#	- + - #		1 · 1 1 = · # # = = 1 2 #	+ - - + #
	Pseudocyphellaria faveolata				·	-	·	=		1 # + = · # + = · #	- - + #
	Psoroma "prothallus"				+			2		- 2 · 2 + # · + · = # -	- · #
n	"Rhizocarpon black-white"			1 =							
	Placopsis spp.			= 1 ·							
o	*Stereocaulon/Argopsis*		·	2 2	=	+ # · ·	#				
p	*Marchantia berteroana*				· =		·	# 1		+	
	Ceratodon purpureus				+ · - =		·	- -		+	=
q	*Drepanocladus sp.*										
r	*Riccardia cochleata*				# # · = + # =	=		· #		= · - + ·	3 # # · = # - # #
	Hypnum cupressiforme				- # = + # =		#	= - - ·		- 3 + = = +	+ # # + + + + #
	Dicranum robustum	· = +	· 1 =	+ ·	+ · # - · · · - #	· · = + # + · = = ·	#	= = - = +		+ - 2 2 # +	3 4 # 2 2 · = # 1
	Cladia aggregata	+	= + -	· = -	= = + = · # 1 # # 2	= # - = #	+	1 + - = - -		# - = + # = -	+ · + + + ·
	Sphaerophorus tener	·	= # ·	# ·	+ + # · · # 1 3 + · #	+ + # ·	#	= = - =		# = · # = = ·	2 # 2 · 1 # + · =
	Pseudocyphellaria glabra	+ - + ·	= · +	# # #	+ · 1 # + # · # - = #	= + - + · -	· + · · 1	- # - · · · +		1 1 = · 1 + · # · + 2 1 =	· # - · · # 1
s	hepatic spp.	· 1	1 1	1	1 1 # · # # 1 + + #	# 2 1 2 = # 1	+ · #	3 1 2 · 1 ·	1	2 3 · # 4 # = 2 · · 1 #	+ · # = 1
t	*Breutelia elongata*	1 # +	# · # -	# · +	# # +	· 1 # · # # + = + + ·		·			
	Breutelia pendula	+ · 1 1	# # -	= #		= # + = #	=	=			
u	*Sphagnum spp.*				1 1 4 = # + = +	4 # 2 1 3 = + + ·		- + # 3			- # = #

Table 4: *Mean environmental factors for each of the Normal Clusters (Community Types 1-21). Radiation is in Langleys day^{-1}, conductivity in mmho.*

	Community Types																				
Factor	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Altitude (m)	54	135	46	132	319	376	5	85	200	57	543	389	498	469	204	376	136	94	1	70	79
Soil temp (°)	9.8	8.9	10.8	10.6	8.4	6.9	10.7	11.5	10.6	9.5	6.6	7.3	5.6	6.5	8.2	8.0	9.3	9.8	11.3	9.0	10.2
Slope (°)	26	21	16	13	2	41	10	16	18	12	12	15	13	21	10	10	35	8	18	10	5
Radiation	368	379	382	376	393	352	323	384	379	392	396	371	382	385	383	385	365	392	370	387	393
Windspeed (m s^{-1})	4.0	7.1	7.6	4.9	14.4	10.5	4.2	2.1	6.7	6.4	0.1	7.8	11.2	10.4	11.1	14.0	6.6	8.0	1.2	5.7	12.3
Shelter (°)	11	7	7	9	4	5	7	11	12	5	14	0	0	0	3	3	7	8	8	12	5
Open coast (km)	0.06	0.16	0.09	0.24	1.79	2.52	2.25	0.80	1.31	1.40	3.50	1.31	2.03	2.04	0.75	1.87	1.23	1.32	3.00	1.21	1.04
Any coast (km)	0.03	0.08	0.02	0.18	1.15	1.13	0.03	0.52	0.81	0.24	2.00	1.03	1.50	1.23	0.74	0.94	0.53	0.63	0.01	0.47	0.39
Soil depth (m)	0.82	1.22	0.14	1.16	1.50	0.04	0.45	0.51	0.95	1.05	0.12	0.99	0.25	0.08	1.50	0.66	0.69	1.08	0.90	1.30	1.50
Soil moisture (%)	354	378	315	588	984	51	454	655	560	591	308	676	413	202	731	838	529	515	559	456	785
Soil redox (mv)	-223	-289	-220	-292	-147	-342	+143	-51	-172	-234	-120	-227	-282	-326	-243	-216	-294	-12	-399	-331	-294
Conductivity	3.47	1.00	7.37	1.09	0.64	0.14	0.85	0.71	0.66	0.85	0.18	0.61	0.31	0.15	0.78	0.53	1.08	0.07	1.65	1.37	0.90
Soil pH	5.3	5.1	6.1	4.3	4.5	5.6	5.8	4.8	5.5	4.8	5.9	5.0	5.4	5.4	4.5	4.9	4.6	4.6	4.5	4.2	4.2
Soil Ca (mg cm^{-3})	0.65	0.45	0.56	0.29	0.11	0.16	0.32	0.25	1.27	0.40	0.22	0.12	0.23	0.55	0.17	0.18	0.16	0.31	0.41	0.37	0.20
Soil Na (mg cm^{-3})	0.89	0.43	2.09	0.19	0.09	0.30	0.21	0.23	0.24	0.20	0.15	0.14	0.33	0.38	0.18	0.20	0.24	0.21	0.50	0.26	0.20
Soil Mg (mg cm^{-3})	0.45	0.31	0.60	0.15	0.09	0.06	0.23	0.21	0.18	0.20	0.16	0.09	0.09	0.10	0.16	0.12	0.13	0.27	0.29	0.28	0.24
Soil K (mg cm^{-3})	0.13	0.10	0.22	0.04	0.02	0.11	0.40	0.06	0.08	0.08	0.05	0.07	0.10	0.08	0.05	0.06	0.08	0.14	0.07	0.07	0.06
Growth index	2.35	1.54	2.50	0.57	0.35	0.45	1.52	0.84	2.15	1.00	1.29	0.64	1.05	1.68	0.58	0.70	0.57	0.99	1.24	0.87	0.59
Animal index	0.0	1.1	0.6	0.0	0.0	0.0	2.0	0.2	4.3	1.5	0.0	0.3	0.5	0.0	1.5	0.4	0.0	1.0	0.0	1.1	1.2

Axis 1

The negative end of the axis (eigenvalue = 0.65) is characterised by the species groups R (e.g., *Oreobolus, Centrolepis ciliata, Astelia*), Q, ZA (e.g., scrub, fern, and epiphyte species), Y (*Isolepis aucklandica, Coprosma perpusilla*), and Z (*Centrolepis pallida, Phyllachne*). The positive end of the axis is characterised by the groups A (e.g., *Puccinellia, Leptinella lanata, Crassula, Isolepis cernua*), K (*Cardamine depressa*), M (*Isolepis praetextata*), S (*Anisotome latifolia, Poa foliosa*), E (*Leptinella plumosa, Deschampsia chapmanii*), D (*Poa ramosissima*), B (*Hebe elliptica, Blechnum durum*), H (*Poa annua*), C (*Stilbocarpa, Pleurophyllum speciosum*), I (*Hydrocotyle*), F (*Isolepis habra*), T (*Poa litorosa, Bulbinella*), and V (*Carex appressa*).

The vegetation gradient is related primarily to the complex of factors associated with proximity to the coast (Table 6). Shallowing of the peat/soil depth along the same gradient is the single most significant contributor to the 61% variation in stand positions accounted for using all sites. Upland rock ledge and outcrop vegetation have some affinities with maritime communities on shallow soils, which are reflected in their similar ordination positions. This relates to the higher mineral content of the rock ledge soils resulting in higher pH, and also the low grazing pressure allowing some palatable, typically maritime species to survive. The more coastal sites tend to be less steep, more shaded, and of course at lower altitude.

Using the 81 sites with the full complement of factors the multiple regression accounts for 73% of the variation (Table 6). Distance from the open coast is the most important contributor, with high soil Na levels and soil pH associated with more maritime, flushed, or biotically influenced sites. Wind speed tends to decline with proximity to the coast (or at low elevations).

By excluding proxy factors, the variation accounted for declines to 60% (Table 6). Presumably this is because the true causal factors are less accurately measured. Soil Na is strongly positively related to the gradient, and soil pH less strongly. Soil temperature increases and wind decreases along the fertility gradient.

Finally, when the growth index alone is considered the regression is significant but accounts for only 21% of the variation (Table 6). The altitude-related trends in soil temperature, and to some extent windiness, are incidental to this axis, since they are tied to the fertility gradient's dependence on distance from the coast, and therefore indirectly to the inland higher-altitude sites at the negative end of Axis 1.

Thus, Axis 1 is essentially a fertility gradient related to the eutrophic impact of marine spray, sea mammals and birds, and flushed soils. The species distributions described above and the associations that mirror these patterns (Fig. 9) clearly reflect the impress of suboptimal, optimal, and excessive levels of the cation and pH gradient. Community types (CT) 21 and 16 are respectively the lowland and upland variants of oligotrophic, acid cushion

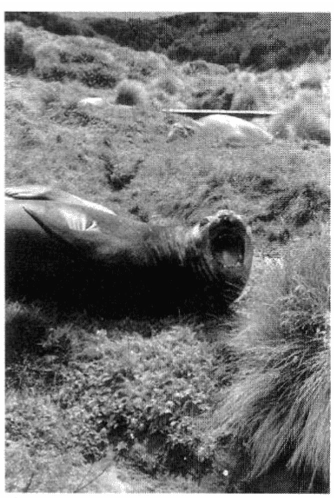
Figure 3: *Typical examples of each of the Community Types (CT1-4). Altitude (in m) and distance from any coast (in km) are given for each sample site. A: Sample 13OG, CT1 - Maritime megaherb - tussock grassland (23 m, 0.02 km); dominated by* Poa foliosa, Anisotome latifolia, Poa litorosa, *and* Bulbinella rossii. *B: Sample 19LB, CT2a - Upper maritime* Poa-Bulbinella *tall tussock grassland (27 m, 0.2 km); dominated by* Poa litorosa, Bulbinella rossii, *and* Polystichum vestitum. *C: Sample 10BG, CT2b - Upper maritime* Poa-Bulbinella-*megaherb tall tussock grassland (130 m, 0.25 km); dominated by* Anisotome latifolia, Bulbinella rossii, Stilbocarpa polaris, Poa litorosa, Pleurophyllum speciosum, *and* Poa foliosa. *D: Sample 35EU, CT3a/b - Littoral lichen-moss rockfield and littoral fringe cushion-turf-mat-lichenfield on rock (1 m, 0.01 km); dominated by* Pertusaria, Verrucaria, Muelleriella *(all on rock),* Colobanthus muscoides, Crassula moschata, Isolepis cernua, Poa litorosa, Puccinellia chathamica, Leptinella plumosa, *and* Bulbinella rossii. *E: Sample 8ET, CT3b - Littoral fringe salt marsh turf (0 m, 0.01 km); dominated by* Puccinellia chathamica, Crassula moschata, Isolepis cernua, *and* Leptinella plumosa. *Note* Poa litorosa *tussocks (CT2a) and sea elephants (CT7) in background. F: Sample 79NH, CT4b - Middle altitude biotic-seral, mat-turf herbfield on abandoned royal albatross nests (183 m, 1.75 km); dominated by* Poa litorosa, Marchantia berteroana, Luzula crinita, Acaena minor, Epilobium *spp.,* Stellaria decipiens, Bulbinella rossii, *mosses (*Bryum billardierei*) and other creeping indigenous and adventive herbs.* Poa litorosa, Bulbinella rossii, *and* Polystichum vestitum *dominate the induced short tussock grassland (CT15) beyond.*


A


D


B


E


C


F

Figure 4: Typical examples of each of the Community Types (CT5-10). Altitude (in m) and distance from any coast (in km) are given for each sample site. A: Sample 70YT, CT5b - Middle altitude rush-sedge-moss turf tarn margin (396 m, 1.25 km); dominated by Juncus scheuchzerioides, Isolepis aucklandica, Drepanocladus, Sphagnum, *and other mosses and forbs. B: Sample 104HY, CT6b - High altitude basalt talus (539 m, 2 km); dominated by* Argopsis megalospora, Stereocaulon *spp.,* Grammitis poeppigiana, Stellaria decipiens, *other small forbs, turf grasses, and mosses. C: Sample 33WH, CT7 - Harbourside turf-mat-forb grassland of sea-elephant wallows (8 m, 0.1 km); dominated by adventive grasses such as* Agrostis capillaris, Poa pratensis *and* P. annua, *the daisy* Leptinella plumosa, *the thallose liverwort* Marchantia berteroana, *and semi-aquatics such as* Callitriche antarctica. *Around the fringes of the fresh wallows are taller* Poa litorosa, Polystichum vestitum, Carex appressa, *and* Bulbinella rossii *(CT10), and in the background* Dracophyllum *and* Coprosma *spp. on older, less fertile peats (CT20a). D: Sample 80TH, CT8a - Low to middle altitude turf-mat-forb grassland on old slip surface (122 m, 1.5 km); dominated by Agrostis magellanica, Helichrysum bellidioides,* Luzula crinita, Breutelia pendula, Bulbinella rossii, Poa litorosa, Acaena minor, Poa breviglumis, Hierochloe brunonis, *and the lichens* Peltigera *and* Placopsis *(rock). E: Sample 100BX, CT9 - Middle altitude* Bulbinella*/turf-mat grassland (310 m, 1.5 km); dominated by* B. rossii, *some* Poa litorosa, Agrostis capillaris, Acaena *spp.,* Poa breviglumis, Epilobium *spp.,* Helichrysum bellidioides, Lagenifera petiolata, *mosses (*Thuidium*), lichens, and other forbs. F: Sample 37SG, CT10 - Low-middle altitude divaricate shrub-forb-tall fern-sedgeland swamp (12 m, 0.05 km); dominated by* Pleurophyllum criniferum, Carex appressa, Poa litorosa, Hierochloe fusca, Bulbinella rossii, Juncus scheuchzerioides, Coprosma ciliata, *and* Polystichum vestitum, *with some bryophytes.*

Figure 5: *Typical examples of each of the Community Types (CT11-16). Altitude (in m) and distance from any coast (in km) are given for each sample site. A: Sample 101RG, CT11 - High altitude turf-meadow with megaherbs on rock ledges (543 m, 2 km); dominated by* Pleurophyllum speciosum, Anisotome antipoda, Bulbinella rossii, Damnamenia vernicosa, Polystichum *spp.,* Agrostis magellanica, Uncinia hookeri, Poa breviglumis, Acaena minor, Trisetum spicatum, *bryophytes, and lichens. The slopes are occupied by* B. rossii *and* Marsippospermum gracile *(CT13). B: Sample 71JH, CT12 - Moderately high altitude* Marsippospermum *tall turf rushland with megaherbs (457 m, 1.5 km); dominated by* M. gracile, Bulbinella rossii, Stilbocarpa polaris, Pleurophyllum hookeri, Hierochloe brunonis, Poa litorosa, Acaena minor, Uncinia hookeri, Helichrysum bellidioides, Poa breviglumis, Geranium microphyllum, Luzula crinita, Damnamenia vernicosa, *bryophytes, and lichens. C: Sample 103JB, CT13 - High altitude* Marsippospermum-Bulbinella *tall turf rushland (549 m, 2 km); dominated by* M. gracile, B. rossii, Luzula crinita, Acaena minor, Poa aucklandica, Cerastium*, and bryophytes. Fellfields (CT14), rock ledges (CT11), and short turf rushlands and cushion bogs (CT16a/b) form a mosaic beyond. D: Sample 62FH, CT14 - High altitude* Bulbinella*/turf-forb-cryptogam fellfield/talus on solifluction terrace (457 m, 0.75 km); dominated by* B. rossii, Stereocaulon *spp.,* Uncinia hookeri, Agrostis subulata, Phyllachne clavigera, Deschampsia gracillima, Helichrysum bellidioides, Trisetum spicatum, Luzula crinita, Poa aucklandica, *and* Acaena minor *subsp.* minor. *E: Sample 58AL, CT15 - Middle altitude* Poa litorosa-Bulbinella *short tussock meadow with reinvading* Chionochloa *(213 m, 1.5 km); dominated by* C. antarctica, Poa litorosa, B. rossii, Uncinia hookeri, Luzula crinita*, lichens and bryophytes, with* Polystichum vestitum *and* Dracophyllum *shrubs (CT20a) in the background. F: Sample 55UK, CT16a/b - mosaic of high altitude* Rostkovia-Bulbinella*/sedge short turf rushland and* Centrolepis pallida *cushion bog (381 m, 1 km); dominated by* Pleurophyllum hookeri, B. rossii, Rostkovia magellanica, Isolepis aucklandica, Juncus scheuchzerioides, C. pallida, Phyllachne clavigera, Damnamenia vernicosa, Gentiana antarctica, *and bryophytes.*

Figure 6: *Typical examples of each of the Community Types (CT17-21). Altitude (in m) and distance from any coast (in km) are given for each sample site. A: Sample 6AP, CT17 - Middle altitude* Chionochloa-*divaricating shrub-fern tussock grassland (123 m, 0.75 km); dominated by* C. antarctica. *Associated species are* Dracophyllum *spp.,* Coprosma *spp.,* Myrsine divaricata, Polystichum vestitum, Pleurophyllum speciosum, *and* Bulbinella rossii. *B: Sample 4CP, CT18 - Low to middle altitude* Coprosma-*fern*-Myrsine *divaricating shrubland (107 m, 0.5 km); dominated by* Coprosma ciliata, C. cuneata, Carex appressa, Bulbinella rossii, Polystichum vestitum, Blechnum *sp.2,* Poa litorosa, *and* Dracophyllum *spp. C: Sample 83QD, CT19 - Sheltered maritime* Hebe elliptica-*mixed tussock shrubland (1 m, 0.01 km); dominated by* H. elliptica *(flowering),* Coprosma ciliata, Poa litorosa, Polystichum vestitum, Dracophyllum longifolium, Blechnum durum, *and* Bulbinella rossii, *with hepatics and epiphytic* Macromitrium. *D: Sample 3DM, CT20b - Low altitude* Dracophyllum *dwarf forest (69 m, 0.25 km); dominated by* D. longifolium, D. scoparium, Polystichum vestitum, Coprosma cuneata, C. ciliata, *and epiphytic* Macromitrium, Pseudocyphellaria, *and* Psoroma *spp. E: Sample 32UD, CT21 - Low altitude* Chionochloa *tall tussock*/Dracophyllum *prostrate shrub/cushion-turf bog (23 m, 0.25 km); dominated by* D. scoparium, C. antarctica *(recovering grazed stumps),* Oreobolus pectinatus, Phyllachne clavigera, Astelia subulata, Isolepis aucklandica, Dicranum robustum, Coprosma perpusilla, Centrolepis ciliata, Bulbinella rossii, Schizaea australis, *and* Drosera stenopetala.

bog vegetation. On better drained and slightly less impoverished soils are dense, lowland heath (*Dracophyllum*) scrub and forest (CT20) and *Coprosma*-fern-*Myrsine* scrub (CT18); at middle elevations are the *Chionochloa* tussock shrublands (CT17) and derivative *Poa* meadows (CT15); and on the summits turf rush herbfields and fellfields (CT13, 14). Mesotrophic community types are in the middle band of the ordination, and receive some additional nutrients. Variously these come from some marine influence (CT19), flushing by enriched or oxygenated waters (CT10 - sedge swamp, CT5 - tarns and upland swamps), supplementation from guano (CT4), disturbance or grazing (CT5, 8, 9), or from being on free-draining, shallow mineral soils (CT6, 11, 12). At the most eutrophic end of the spectrum are maritime shrublands, tussock grasslands, and megaherbfields (CT1, 2), sea-elephant wallows (CT7), and bird colonies (CT4). At near-toxic cation levels are the littoral fringe cushions and turfs (CT3).

Axis 2

Species groups at the negative end of Axis 2 (eigenvalue = 0.48) are Q (dwarf forest associates), ZA (scrub and forest species), O (a lowland orchid associated with scrub margins), V (sedge swamp dominants), J (lowland fern), F (sedge swamp associates), U (the low to middle altitude *Chionochloa*), R (lowland cushion bog species), and the various maritime species groups (A, B, M, D, E, S, K). The mid-axis segment includes T (*Bulbinella, Poa litorosa*), Y, P, I, and H (matrix turf species), X (low to middle altitude rush), C (megaherbs, shrub and grass), and W (widely distributed matrix species and upland *Marsippospermum*). The positive end of the axis includes summit tundra groups L (*Colobanthus hookeri, Epilobium pernitens*), G (*Grammitis poeppigiana, Poa aucklandica, Agrostis subulata*), Z (*Centrolepis pallida, Rostkovia, Pleurophyllum hookeri*), and N (*Cardamine subcarnosa*). Groups W, Y, and T have species of wide amplitude.

The multiple regression on all sites accounts for 74% of the variation, and is overwhelmingly dominated by altitude (Table 6). Soil depth decreases with altitude (although this will be confounded with shallow soils near the littoral fringe). Higher altitude sites are less sheltered from the prevailing west wind. (The primary altitudinal gradient is negatively related to proximity to the coast.)

The full factor multiple regression accounts for 85% of variation. Altitude is still the major contributor, with minor contributions from soil Na (+ve), conductivity (-ve), soil Mg (-ve), and growth index (+ve).

The exclusion of proxy factors reduces the variation accounted for to 69%. The main contributors are soil Mg (-ve), soil temperature (-ve), Na (+ve), shelter (-ve), windspeed (+ve, $P < 0.1$), soil pH (+ve), and growth index. However, the failure of growth index on its own to show any correlation with Axis 2, and the generally ambiguous contribution of the nutrient factors, is evidence that this second component of variation in the vegetation is principally altitude-controlled (via adiabatic air and ground cooling and by greater exposure to the wind). Soil depth declines towards rocky, eroding tops and other middle elevation outcrops that are at the top end of the ordination. And, whereas several nutrient factors decline towards the colder and more leaching environment of the summits, the important soil pH, soil Na, and the derivative growth index increase as a function of the freer draining mineral nature of the soils.

Thus, Axis 2 is simply an altitudinal (or thermal) gradient. The vegetation picture (Fig. 9) along this gradient conforms well with the environmental relations just described. At the base are sheltered dwarf forests and scrub (CT18, 19, 20), lowland bogs (CT21), swamps (CT10), and maritime or biotically induced communities (CT1, 2, 3, 4, 7). In mid-gradient are the middle elevation tussock grasslands (CT17) and induced meadows (CT4, 8, 9, 15); and at the top are the summit bogs (CT16), flushes or swamps (parts CT5, 12, 13, 16), rushlands (CT12, 13), fellfields (CT14), and rockfields (CT6, 11).

Axis 3

Axis 3 has an eigenvalue of 0.31. Species groups at the negative end are E (*Rumex acetosella, Agrostis capillaris*), H (*Poa annua, Montia*), K (*Cardamine depressa*), F (*Pleurophyllum criniferum, Epilobium alsinoides*), P (*Juncus antarcticus*), I (*Hydrocotyle*), X (*Juncus scheuchzerioides*), V (*Carex appressa*), and A (*Colobanthus muscoides*). The positive end of Axis 3 is characterised by groups D (*Poa ramosissima*), C (*Stilbocarpa, Hebe benthamii*), S (*Poa foliosa, Anisotome latifolia*), M (*Isolepis praetextata*), B (*Hebe elliptica*), N (*Cardamine subcarnosa*), and J (*Hypolepis amaurorachis*).

The multiple regression on all sites accounts for 29% of variation. There is a partly bimodal fertility gradient with high fertility at the negative end associated with mammals (animal index) and inland flushes, and again at the positive end associated with maritime influence (distance to open coast). Along this gradient there are increases in slope, soil depth and distance from any coast.

With full factor sites the multiple regression improves to 63%. This is associated with a highly

Table 5: *Simple and partial correlation coefficients* (r)*, and their probabilities* (P)*, between pairs of environmental factors. Only significant correlations are listed.*

Attribute	Correlate	Simple correlation r	Simple correlation P	Partial correlation r	Partial correlation P
Altitude	Soil temperature	-0.725	0.000	-0.500	0.000
	Shelter	-0.290	0.009		
	Distance to open coast	0.248	0.026		
	Distance to any coast	0.610	0.000	0.441	0.000
	Conductivity	-0.242	0.030		
	Soil Na	-0.223	0.046		
	Soil Mg	-0.535	0.000	-0.303	0.015
	Growth index	-0.236	0.034		
Soil temperature	Windspeed	-0.376	0.001		
	Shelter	0.264	0.017		
	Distance to any coast	-0.448	0.000		
	Conductivity	0.250	0.025		
	Soil Mg	0.347	0.002		
Slope	Radiation	-0.689	0.000	-0.635	0.000
	Windspeed	-0.292	0.008		
	Shelter	0.356	0.001	0.328	0.008
	Distance to open coast	-0.291	0.008	-0.314	0.012
	Distance to any coast	-0.276	0.013		
	Soil depth	-0.450	0.000	-0.256	0.042
	Soil moisture	-0.245	0.028		
	Soil pH	0.339	0.002		
	Growth index	0.336	0.002		
Radiation	Windspeed	0.356	0.001		
	Distance to open coast			-0.278	0.026
	Distance to any coast	0.277	0.012		
	Soil depth	0.346	0.001		
	Soil pH	-0.302	0.006		
	Growth index	-0.221	0.047		
Windspeed	Shelter	-0.369	0.001		
	Distance to any coast	0.389	0.000		
	Soil moisture	0.330	0.003	0.263	0.036
	Soil Mg	-0.261	0.019		
Shelter	Distance to any coast	-0.363	0.001		
Distance to open coast	Distance to any coast	0.605	0.000	0.567	0.000
	Conductivity	-0.338	0.002		
	Soil Ca	-0.263	0.018		
	Soil Na	-0.249	0.025		
	Soil Mg	-0.360	0.001		
	Growth index	-0.416	0.000		
Distance to any coast	Soil moisture	0.318	0.004		
	Conductivity	-0.314	0.004		
	Soil pH	-0.365	0.001		
	Soil Ca	-0.291	0.008		
	Soil Na	-0.457	0.000		
	Soil Mg	-0.595	0.000		
	Soil K	-0.307	0.005		
	Growth index	-0.480	0.000		
Soil depth	Soil moisture	0.459	0.000	0.322	0.009
	Soil pH	-0.489	0.000		
	Soil Ca			0.283	0.023
	Soil Na	-0.354	0.001		
	Soil Mg			0.275	0.029
	Soil K	-0.378	0.001		
	Growth index	-0.268	0.016		
	Animal index	0.217	0.051		
Soil moisture	Soil pH	-0.485	0.000		
	Soil Ca	-0.381	0.000		
	Soil Na	-0.403	0.000		
	Soil Mg	-0.442	0.000		
	Soil K	-0.559	0.000	-0.252	0.044
	Growth index	-0.497	0.000		
Soil Redox	Soil pH			0.327	0.008
	Soil Na			-0.288	0.021
	Soil Mg			0.275	0.028
Conductivity	Soil pH			-0.638	0.000
	Soil Ca			-0.392	0.001
	Soil Na	0.610	0.000	0.805	0.000
	Soil Mg	0.402	0.000	-0.518	0.000
	Growth index	0.348	0.001	0.676	0.000
Soil pH	Soil Ca	0.507	0.000	-0.256	0.041
	Soil Na	0.427	0.000	0.523	0.000
	Soil Mg	0.376	0.001	-0.499	0.000
	Soil K	0.497	0.000		
	Growth index	0.686	0.000	0.691	0.000
Soil Ca	Soil Na			0.269	0.031
	Soil Mg	0.417	0.000	-0.408	0.001
	Soil K	0.225	0.044		
	Growth index	0.821	0.000	0.761	0.000
Soil Na	Soil Mg	0.704	0.000	0.671	0.000
	Soil K	0.724	0.000	0.353	0.004
	Growth index	0.360	0.001	-0.599	0.000
Soil Mg	Soil K	0.594	0.000		
	Growth index	0.633	0.000	0.710	0.000
Soil K	Growth index	0.335	0.002		

Table 6: *Statistics for multiple regression of environmental factors on vegetation ordination axes. The data are for those factor combinations with highest probability regressions (see below). Significance for 81 sites where the full complement of 19 environmental factors were measured is shown by asterisks (*). Regressions on all 134 sites but with only the 8 factors that were measured at all those sites (*viz. *altitude, slope, radiation, shelter, distance to open coast, distance to any coast, soil depth, and animal index), are indicated by +; • indicates significant regressions of factors at 81 sites excluding the proxy factors altitude, distance from open coast and distance from any coast (i.e., proxy factors where related direct factors were measured); # indicates significance of simple regression for 81 sites between vegetation scores and growth index. Probability levels are, respectively* P < *0.05, 0.01 and 0.001 for 1-3 symbols of any type. Slope only is given where* P < *0.1.*

Environmental factor	Axis 1 Slope	Axis 1 Contribution	Axis 2 Slope	Axis 2 Contribution	Axis 3 Slope	Axis 3 Contribution	Axis 4 Slope	Axis 4 Contribution
Altitude	-0.001	5.1+	0.005	91***+++			0.001	42*++
Soil temperature	0.137	4.0•	-0.135	8.6••	-0.095	5.1•	0.069	
Slope	-0.022	7.2+			0.017	17++	-0.014	5.5*+
Radiation	-0.012	5.9+						
Shelter			-0.015	5.8*+	0.021	8.0*••		
Distance to open coast	-0.273	25**+++			-0.150	29**+++		
Distance to any coast	-0.291	19+++			0.097	8.0+		
Soil depth	-0.802	38+++	-0.239	3.6++	0.257	15++		
Soil redox					-0.001	5.0•		
Conductivity			-0.099	6.8*	-0.102	5.1*		
Soil pH	0.577		0.411		-1.003	24***•••		
Soil Ca							0.658	7.7**•
Soil Na	1.110	5.1*•	0.753	7.5**•				
Soil Mg			-4.136	14*•••				
Growth index	0.597	21###	0.355		0.601	5.2•	-0.109	4.2#
Animal index					-0.110	23*++•	-0.049	
Intercept	0.757		-0.437		6.658		3.598	

significant soil pH (-ve) and distance to open coast (-ve) effect. The gradient also relates to shelter (+ve). Other significant soil factors are conductivity (-ve), soil redox potential (-ve), growth index (+ve), and soil Na (+ve). The significant animal index (-ve) is confirmed.

The multiple regression excluding proxy factors accounts for 52% of variation and has similar characteristics to the full factors regression. However, the significance of soil Na decreases and that of growth index and animal index increases. Soil temperature also decreases along the gradient, which perhaps reflects the environmental trends in the middle section of the ordination.

The soil factors which contribute to the growth index are contradictory here (i.e., Na and pH), and result in a non-significant simple regression with Axis 3.

Thus, the negative end of the Axis 3 gradient appears to be a miscellaneous assemblage of communities that are reduced in stature when compared with the zonal or optimal communities of the altitude sequence. These appressed turfs are on mammal-disturbed/grazed sites (CT7, 8), eroded peats (CT5), trampled tracks (CT9), flushed, waterlogged footslopes (CT10), and extreme maritime exposed rockfields (CT3). Flushing appears to result in slightly reduced acidity, but this is not necessarily linked to other fertility factors. The fertility associated with the positive end of the axis results from maritime salt spray and seabird colonies on open coasts. There is a gradient from grazed sea elephant wallow banks (CT7), littoral-fringe cushion-turfs on rock (CT3), other short and/or discontinuous turf-mat grasslands, rushlands, and taller reed-like sedgelands (CT5, 8, 9, 10) on the one hand, to predominantly tall tussock grassland, megaherbfield (CT1, 2), scrub (CT19), and species-poor, stable seabird-induced swards (CT4). This may be understood in terms of a gradient from seral or rejuvenated (disclimax) communities to stable, more mature (climax or post climax) communities.

Axis 4

The species groups characteristic of the negative end of the axis (eigenvalue = 0.18) are C (*Stilbocarpa*), S (*Anisotome latifolia*), U (*Chionochloa*), and parts of A (*Leptinella lanata*), F (*Pleurophyllum criniferum*), E (*Holcus*), L (*Taraxacum magellanicum*), G (*Ranunculus subscaposus*), and V (*Blechnum* "sp.2"). The positive end of the axis is characterised by D (*Poa ramosissima*), part E (*Callitriche*), M (*Isolepis praetextata, Sagina*), J (*Hypolepis*

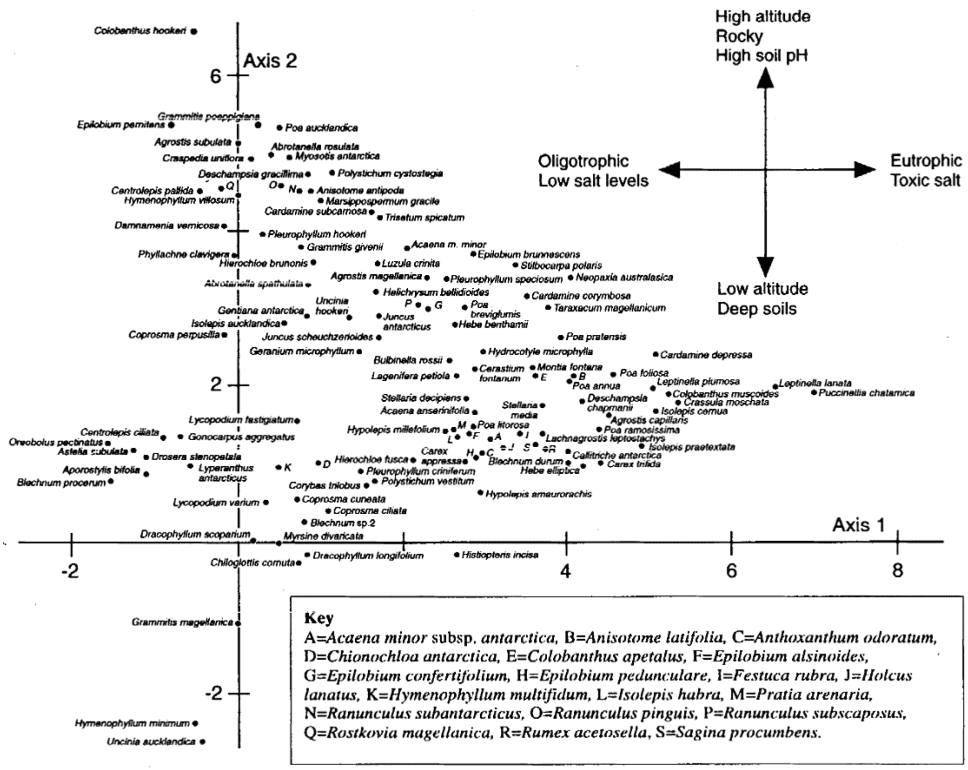


Figure 7: *Inverse (species) DCA ordination diagram for Axes 1 and 2. Axis 1 represents a fertility gradient with maritime species on the right, mesotrophic species in the centre, and bog species to the left. The vertical axis reflects an altitudinal gradient. Speciesí groups (guilds) are indicated by capital letters (see key).*

amaurorachis), I (*Hydrocotyle, Histiopteris, Pratia, Hypolepis millefolium*), and parts of W *(Stellaria decipiens*), H (*Stellaria media, Montia*), and B (*Hebe elliptica, Carex trifida*).

The all sites multiple regression accounts for 14% of the variation. Altitude (+ve), slope (-ve), and animal index (+ve) are the significant contributors. The full factor sites multiple regression accounts for 41%, with soil Ca (+ve), slope (-ve), altitude (+ve), soil temperature (+ve), and growth index (-ve) the major contributors. With exclusion of proxy factors the multiple regression accounts for only 26% of variation and the overall regression is non-significant, with only soil Ca (+ve) a significant component. However, the simple growth index regression produces a significant negative relationship, although only 5% of the variation is accounted for.

Overall, Axis 4 appears to be a trend from tall tussocks, sedges, rushes, megaherbs, and shrubs of relatively pristine and fertile condition (perhaps preserved in some instances by being associated with steep slopes) to appressed turfs and mats of grazed, disturbed, eroding, or rocky uplands accessible to feral mammals.

Autecology of the species

Individual species in isolation can be presumed to distribute themselves along environmental gradients according to the range of their physiological tolerances. Ecological limitations to this ideal are imposed by plant competition, which may result in skewed, truncated, or bimodal distributions (see Meurk and Foggo, 1988), by dispersal failure, and by incomplete vegetation development. Through our numerical analysis we are able to identify less-than-ideal distributions of some species, and hence

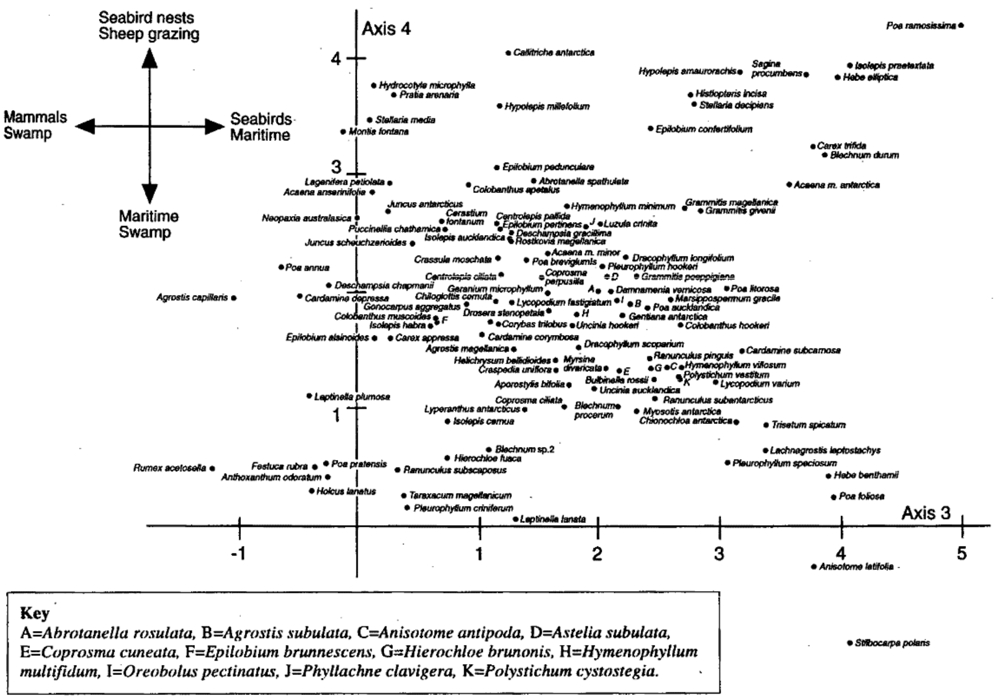


Figure 8: *Inverse (species) ordination diagram for Axes 3 and 4. Axis 3 represents a gradient of mammal to seabird biotic-influence with littoral fringe, swamp, and adventive ìgrazing increaserî species on the left and tall or palatable species of maritime or seabird sites to the right. Axis 4 has palatable maritime or swamp species at the base and species tolerant of sheep or seabirds at the top. Species groups are indicated by capital letters (see key).*

their imperfect contribution to the species associations and vegetation patterns. While the positions of species on the inverse ordination (Figs. 7, 8) indicate only their centroids in multidimensional, environmental space, the mapping of species abundance at the individual stand loci on the normal ordination provides niche diagrams which offer a fuller appreciation of speciesí ecological limits (Figs. 11-15).

The species niche diagrams are juxtaposed to show the relationships of closely related or complementary species or growth forms in ordination space. Absolute environmental definition can be inferred from the factor overlays (Figs. 16, 17). In general the vertical axis of ordination 1 x 2 is treated as an altitudinal gradient and the horizontal axis as a fertility gradient from oligotrophic, acid soils on the left, through mesotrophic sites in the middle range, and eutrophic to maritime soils on the right. However, interpretation of the diagrams should bear in mind the following causes of distortion.

ï The ordination envelope is narrower at the top, presumably because the extreme summit environment tends to dampen the expression of other gradients that may be present.

ï The axes are only abstractions of real space, plant association gradients. Summit cushion bogs may tolerate the same degree of cold as fellfields, but because the latter form discontinuous vegetation the ordination analysis views them as more extreme than the mature, mesic herbfields below. Thus the uppermost sites within the envelope are not necessarily at the highest altitudes.

ï Likewise, the bottom of the diagram does not represent altitudes lower than those just above the Y-axis origin. It merely reflects the most sheltered, highly developed (forest) vegetation on the island, whereas the similarly elevated sites above the origin represent natural or induced open vegetation (mimicking tundra). Thus, species that fail to extend down to this origin are generally restricted to open spaces.

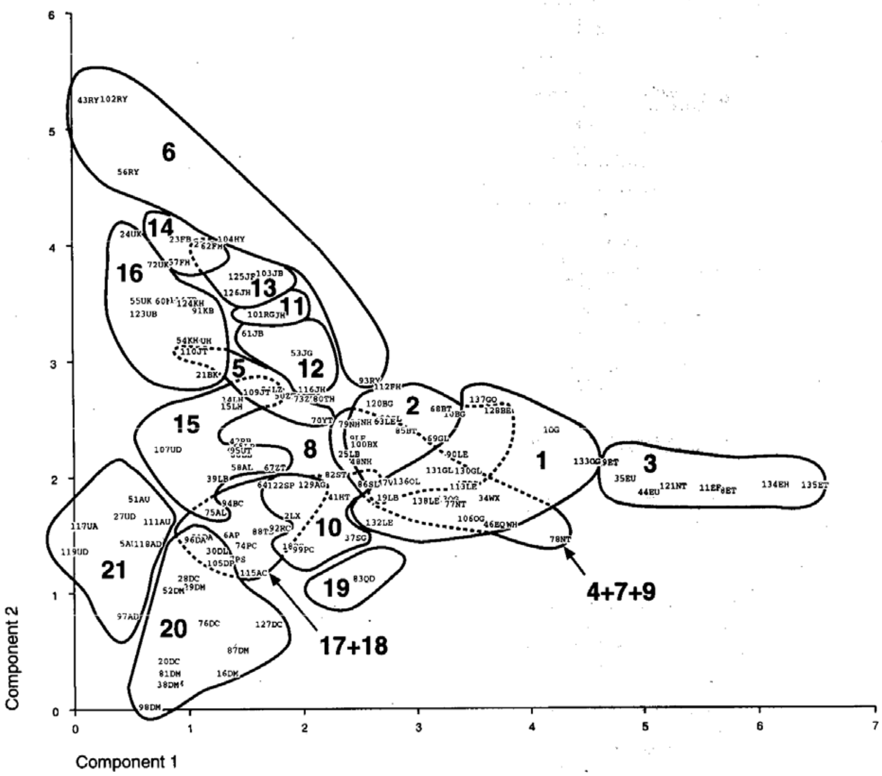


Figure 9: *Normal (sites) DCA ordination diagram for Axes 1 and 2. Community Types are indicated by bold numbers.*

- Some species, seriously depleted by past grazing history (or competition in part of their potential range), may not have reattained their full expression in the diagram. On the other hand, reduced competition will have allowed some herbaceous species to realise their physiological niche.

Fig. 11 displays the major shrub species. The order of diminishing tolerance of poor soils or occurrence on richer soils is *Dracophyllum scoparium* (a calcifuge species), *D. longifolium* (a feature of riparian dwarf forests), *Coprosma cuneata, Myrsine divaricata, Coprosma ciliata, Hebe benthamii*, and *H. elliptica*. The mat-forming *Coprosma perpusilla* occurs on the poorest soils alongside stunted *Dracophyllum scoparium*. All species may occur at or near sealevel, with adaptation to cold and exposure increasing in the order *H. elliptica, M. divaricata, D. longifolium, C. ciliata, D. scoparium, C. cuneata, H. benthamii,* and *C. perpusilla*.

Several cushion plants are typical of the saturated, oligotrophic, acid habitats. *Centrolepis pallida* is virtually confined to the uplands, while *C. ciliata* is the lowland representative of this genus (Fig. 11), usually occurring together with *Oreobolus pectinatus* and *Astelia subulata*. *Phyllachne clavigera* is similarly restricted to impoverished soils, with a slight extension into summit fellfields and with greater tolerance of taller but open grassland vegetation. It differs from the other cushions mainly in straddling the complete altitudinal range.

The unusually large megaherb species were greatly reduced in distribution by grazing, and are now only partly recovered. Nevertheless, Fig. 11 demonstrates the way in which these plants are ecologically segregated. *Pleurophyllum criniferum*

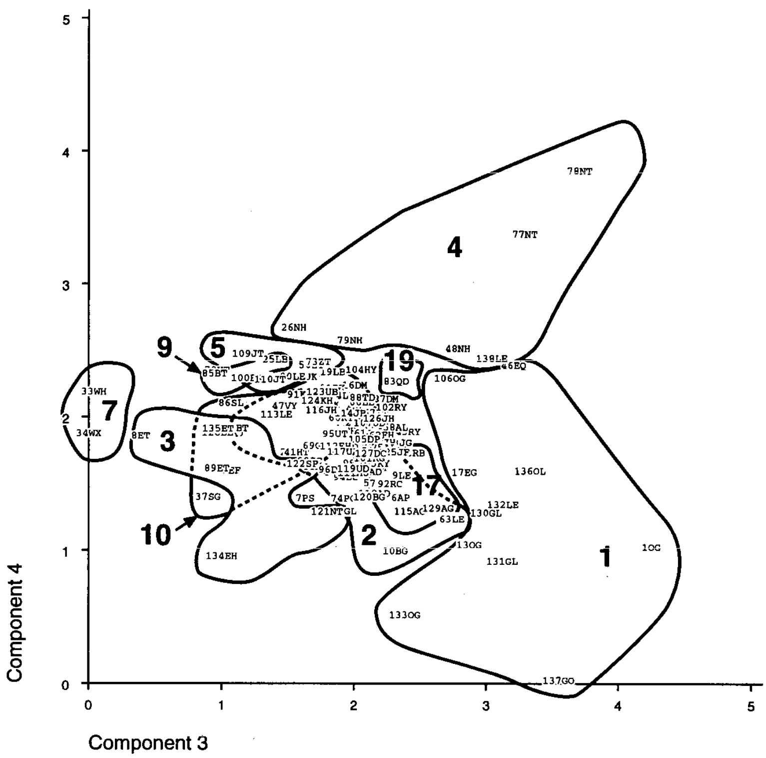


Figure 10: *Normal (sites) DCA ordination diagram for Axes 3 and 4. To the left on Axis 3 are sheep-grazed, sea elephant-disturbed, swamp, highly saline, littoral fringe and salt marsh sites. To the right is tall or dense maritime vegetation which may also be affected by seabirds. Axis 4 provides a different contrast between sheep-grazed and seabird nest sites above and maritime vegetation and swamps below.*

is a summer-green, tall forb of mesotrophic lowland swamps and flushes. It is probably the least recovered species because (ecologically) it could not retreat from grazing animals into inaccessible refugia. Its habitat is island-like and therefore slow to be recolonised. The upland equivalent is the evergreen *P. hookeri*, although it frequents infertile as well as flushed, shallow soils. The widely tolerant and naturally widespread *P. speciosum* occurs at all elevations, from open maritime conditions to high altitude ledges on fertile to somewhat poor tussock grassland soils. The outlier of *P. criniferum* to the left of the diagram is a good example of the occasional anomalies that relate to some undetected micro-environment or chance occupation of an otherwise inhospitable habitat. *Stilbocarpa polaris* is another species of wide altitudinal range which also thrives on the richer to maritime sites.

The pair of *Anisotome* species are clearly separated. The maritime to lowland, mesotrophic *A. latifolia* is seldom sympatric with the high altitude *A. antipoda*, although this may change with their recovery. Interestingly, the latter species fills the lowland role on the Antipodes Islands in the absence of *A. latifolia* (Godley, 1989). Hybrids are known among the species of both *Anisotome* and *Pleurophyllum*. *Bulbinella rossii* is ubiquitous, extending even further into poor or very high sites than its nearly constant companion *P. litorosa*. It is a little less tolerant of extreme maritime sites, is summer-green, but seasonally dominates most unwooded vegetation, as its broad niche indicates. Its unpalatable foliage (Meurk, 1977) has undoubtedly contributed to its recent success. In contrast it is an uncommon plant on Auckland Island, where feral pigs eat the fleshy underground roots and stems. The smaller, endemic *Gentiana*

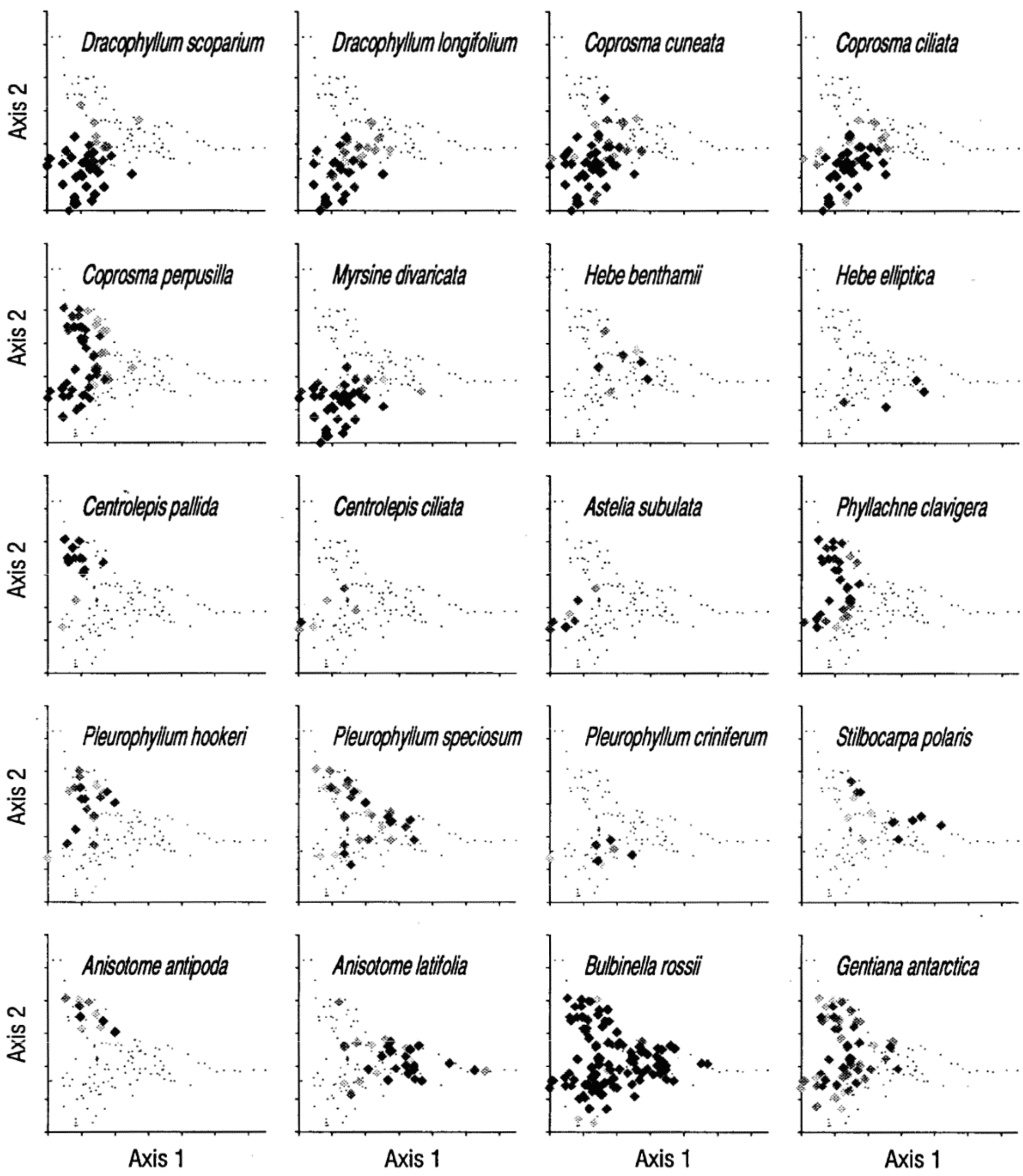


Figure 11: *Distribution and dominance of principal shrub, cushion, and megaherb or forb species in ecological space (Axes 1 and 2 of site ordination). Sites for which the species are absent are indicated by fine dots. The dominance of the species at each site is indicated by 5 levels of shading (black = highest level, with dominance value of 8-10 inclusive from Table 1).*

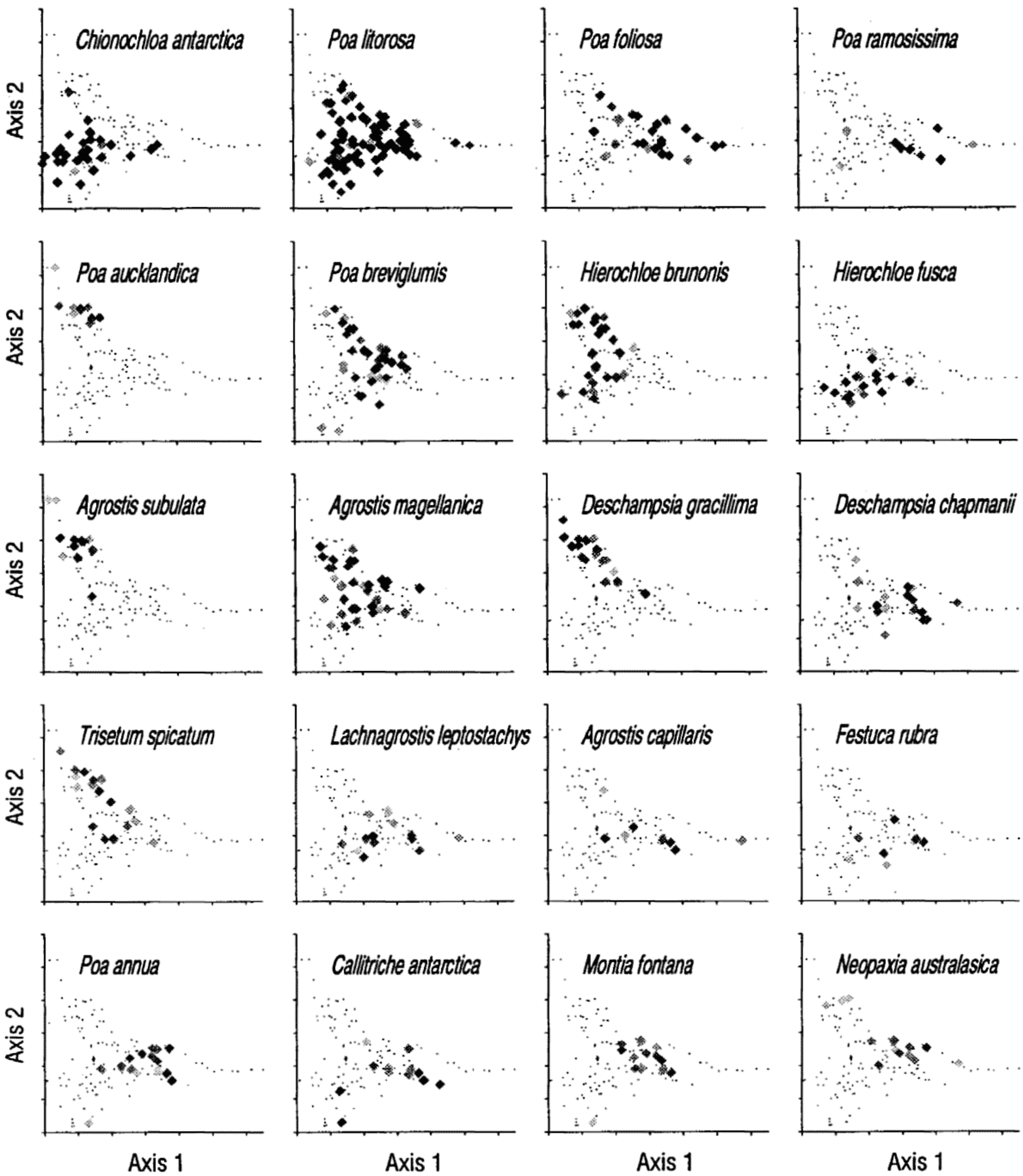


Figure 12: *Distribution and dominance of principal grass and semi-aquatic forb species in ecological space (Axes 1 and 2 of site ordination). Sites for which the species are absent are indicated by fine dots. The dominance of the species at each site is indicated by 5 levels of shading (black = highest level, with dominance value of 8-10 inclusive from Table 1).*

antarctica is also widely spread in the open, inland communities which tend towards the oligotrophic.

Fig. 12 portrays the relationships of the grasses. The maritime *Poa foliosa* appears at the eutrophic end of the diagram where animal enrichment is also a factor. *Poa litorosa* in its giant maritime phase extends almost as far. However, it is a much more versatile species and can cope with relatively oligotrophic sites and higher elevations as a bunch grass. The distribution of *P. foliosa* has nevertheless been greatly reduced by grazing history, which may account for gaps at the base of the ordination diagram. *Chionochloa antarctica* is a low to middle altitude dominant (restricted at upper reaches by previous grazing), but especially tolerant of oligotrophic, acid bog soils. Although *P. litorosa* has replaced the palatable *Chionochloa* over much of its former range, it is clearly vigorous (darker symbols) only in maritime or otherwise fertile flushes or sites influenced by sea animals. With the removal of sheep there is a gradual recovery of *Chionochloa*, from resprouted bases or seed (Meurk, 1982), into the short tussock meadows (CT15) that have occupied the middle altitudes for most of this century.

The other tall grasses are *Hierochloe* species; *H. fusca* is typical of low-altitude, non-maritime though fertile sites such as swamps, whereas *H. brunonis* is an upland, mesotrophic, shorter-statured grass. The smaller matrix grasses fit among the taller dominants. *Poa ramosissima* is very restricted at the eutrophic end of the spectrum being associated with seabird colonies. *Poa breviglumis, Agrostis magellanica*, and *Deschampsia chapmanii* are low to middle elevation, mesotrophic species, whereas *P. aucklandica, Agrostis subulata*, and *Deschampsia gracillima* are high altitude oligo-mesotrophs often associated with fellfields or rocks. Finally, three representative adventives (*Agrostis capillaris, Festuca rubra, Poa annua*), widely dispersed in the grazed meadows, are seen to require mesotrophic soils in this climate, and although the first two are known from high elevations on sheltered and sunny aspects they do not tolerate the exposed summit fellfields and bogs. Both the *Agrostis* and *Poa* are found in eutrophic sea elephant wallows.

Finally there are three forbs of saturated to semi-aquatic habitats (Fig. 12). *Callitriche* and *Montia* are sympatric in maritime and lowland eutrophic pools or on wet bare peat, especially in places disturbed and manured by seabirds and mammals. *Neopaxia* occurs at middle to higher elevations, also on flushed bare peat or among pebbles of talus and fellfield.

Rushes and sedges are presented in Fig. 13. *Marsippospermum* is the dominant tall turf of closed vegetation on high altitude, mesotrophic, sheltered sites and *Juncus scheuchzerioides* occupies the mesotrophic, seral flushes, swamps, and eroded peats at middle to low elevations. *Rostkovia* has a role in the high altitude oligo-mesotrophic bogs and turf herbfields. *Juncus antarcticus* has a rather restricted distribution at middle altitudes in mesotrophic, short (grazed) turfy vegetation. *Luzula* and *Uncinia hookeri* are nearly ubiquitous open-space matrix species, the former spreading out a little further onto rock bluffs and ledges (upper extension of diagram), but neither tolerating extreme acidity. *Uncinia aucklandica* is confined to dwarf forests (lowland, oligotrophic part of spectrum). *Carex appressa* dominates lowland, mesotrophic swamps, but *C. trifida* is a much less prevalent tussock of sheltered maritime sites. The four turf *Isolepis* species encompass the entire fertility spectrum of the island. Thus, *Isolepis cernua* and the rarer *I. praetextata* are maritime species, *I. habra* occupies mesotrophic flushes and disturbed ground to moderate elevation, and *I. aucklandica* is ubiquitous in open, meso-oligotrophic conditions.

The last group of larger physiognomic dominants comprises the ferns (Fig. 13). *Polystichum vestitum* is most versatile in the lower to middle country, often defining gullies in both grasslands and dwarf forest, although avoiding extremes of soil fertility. The smaller, summer-green *P. cystostegia* is restricted to the high altitude turf, rushlands, herbfields, and among rocks. *Blechnum durum* is confined to maritime tussock grasslands, banks, and ledges (sometimes under coastal bushes), with a distribution similar to the less common *Asplenium obtusatum*. *Blechnum* "sp. 2" is most prevalent in mesotrophic sedge swamps and shrublands. The smaller *B. penna-marina* is found in only a few mossy swamps or grazed turfs. The summer-green *Hypolepis millefolium* is rather localised in modified areas where grazing by sheep has been heavy, although it may be associated with scrub margins. These sites are mesotrophic but well drained.

Other pteridophytes include the filmy ferns (Fig. 13). These occur in mesotrophic to oligotrophic conditions, although *Hymenophyllum minimum* is generally epiphytic in dwarf forests. *Hymenophyllum multifidum* is a lowland to middle altitude species in shade or in the open meadows and bogs, whereas *H. villosum* is an essentially upland herbfield and fellfield inhabitant. Of the club mosses (Fig. 13), *Lycopodium fastigiatum* is a sporadic inhabitant of open uplands, while the even less common *L. australianum* is restricted to rocky, high altitude places. *Lycopodium varium* is a

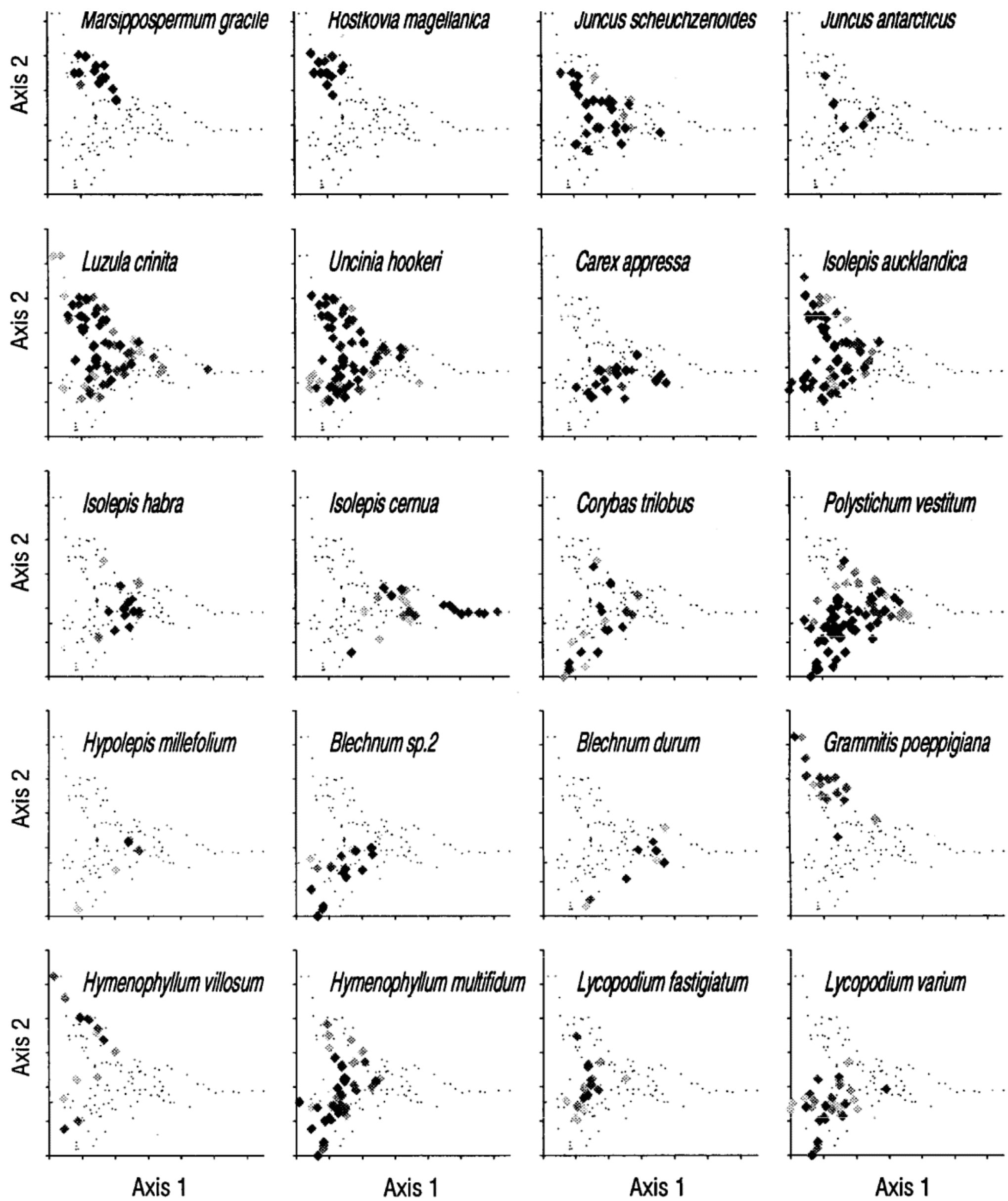


Figure 13: *Distribution and dominance of principal rush, sedge, orchid, fern and lycopod species in ecological space (Axes 1 and 2 of site ordination). Sites for which the species are absent are indicated by fine dots. The dominance of the species at each site is indicated by 5 levels of shading (black = highest level, with dominance value of 8-10 inclusive from Table 1).*

common associate of lowland forest, scrub, and bogs on both mesotrophic and acid peats.

The orchid *Corybas trilobus* is fairly widespread from lowlands to uplands, sometimes in open meadows, but more commonly under the shelter and shade of tussock grassland or scrub. It appears to prefer mesotrophic conditions.

Small asterads include *Damnamenia, Leptinella, Abrotanella, Helichrysum*, and *Lagenifera* species (Fig. 14). *Damnamenia* rosettes occur in meso-oligotrophic soils (rocks and fellfields to cushion bogs) at high elevations, but are confined to acid bogs near sealevel, where competition from taller vegetation is minimised. The plants may be small in adverse or exposed habitats and up to 15 cm diameter in more favourable conditions. The *Leptinella* species are found only in nutrient-rich sites, *L. lanata* forming mats along the littoral fringe and the taller *L. plumosa* in eutrophic, saturated, more sheltered, often animal influenced sites such as sea-elephant wallows. *Abrotanella rosulata* has tiny rosettes that in aggregate form cushions in mesotrophic summit fellfields or on cliffs and ledges down to lower levels. *Abrotanella spathulata* is a small, mesotrophic, middle altitude meadow or intertussock rosette forb. In its lower reaches on grazed, mesotrophic turfs it overlaps with *Lagenifera petiolata*. More widespread in mesotrophic habitats of low to quite high elevation is the creeping *Helichrysum bellidioides*. It too requires high light levels in grazed meadows, swamps or rocky habitats where it is generally of high frequency.

The local members of the Caryophyllaceae are inconspicuous herbs and cushions (Fig. 14). *Cardamine subcarnosa* is an associate of upland herbfields and tall turf rushlands, *C. corymbosa* is an often etiolated forb in middle elevation and maritime tussock grasslands, and *C. depressa* is an infrequent diminutive rosette of exposed maritime turfs on cliff crests. *Stellaria decipiens* has a wider range, tolerating the shade of shrublands and dense tussocks as well as occurring frequently in open, grazed turfs or meadows. None of these species stray into the poorer, acid soils of the island. *Colobanthus* is another genus with three species having clearly segregated niches. The high altitude fellfield locus is occupied by *C. hookeri*, a small cushion-former, the littoral fringe by the more robust cushion plant *C. muscoides*, and the maritime or open turfy, mesotrophic situation by *C. apetalus*. The successful adventive *Cerastium fontanum* frequents the mesotrophic middle elevations in the grazed, short tussock meadows and other disturbed or anthropogenic sites. Apart from some of the introduced grasses, this is the most successfully integrated alien plant. *Geranium microphyllum* is also mesotrophic, but with greater prominence at the upper end of its range. It is commonplace in the grazed, short tussock meadows at middle elevations and upland turf rushlands.

The rosaceous acaenas (Fig. 14) form clines and hybrid swarms, but *Acaena minor* subsp. *minor* is generally a distinct, matted forb of upland, open meadows, herbfields, and summit fellfields. *Acaena minor* subsp. *antarctica* is a more erect and robust, often bluish species typically associated with mesotrophic to maritime tussock grasslands and shrublands, tolerating a degree of shade. The possibly recently arrived *A. anserinifolia* is more or less confined to the mesotrophic, sheep-grazed turfs and meadows. Likewise *Acaena* cf. *novae-zelandiae* has recently been discovered along sheltered harbour coasts.

Epilobium (Fig. 14) is, after *Poa*, the largest genus in the island's flora. *Epilobium pernitens* is a rather rare, upper tundra species which may grow in saturated, boggy ground. The subantarctic, endemic *E. confertifolium* is ubiquitous, and can tolerate both relatively poor and maritime soils. *Epilobium pedunculare* is also fairly versatile in middle to lower country, being able to grow both in the open meadows, mesotrophic swamps, and maritime grasslands and also in the shade of the more oligotrophic dwarf forests or shrublands. *Epilobium alsinoides* is typically an erect forb of the lowland, tall sedge swamps, whereas *E. brunnescens* is a creeping plant of flushed and higher altitude turf herbfields, often grazed. *Crassula moschata* is a loose reddish cushion prominent in the littoral fringe. It is more etiolated and green in maritime situations, associated with tussocks.

Relating the species to the ordination of Axes 3 and 4 (Fig. 15), we note that Axis 3 represents proximity to sheltered water (cf. distance from any coast), high redox potential, and high direct animal influence (grazing or mechanical) to the left, and proximity to open water (cf. open coast) and high soil conductivity to the right. Axis 4 is a weak fertility gradient with generally higher values at the base related to maritime or flushed conditions (but not near-toxic levels of salt), whereas the upper axis (or positive end) is characterised by sites marginal to or previously affected by bird nesting (with perhaps only residually slightly elevated nutrient values). These environmental relationships are displayed in Fig. 17.

The shrubs and most other physiognomically dominant species appear as an undifferentiated group in the middle of this ordination figure. Sites with vegetation of low stature due to temperature/

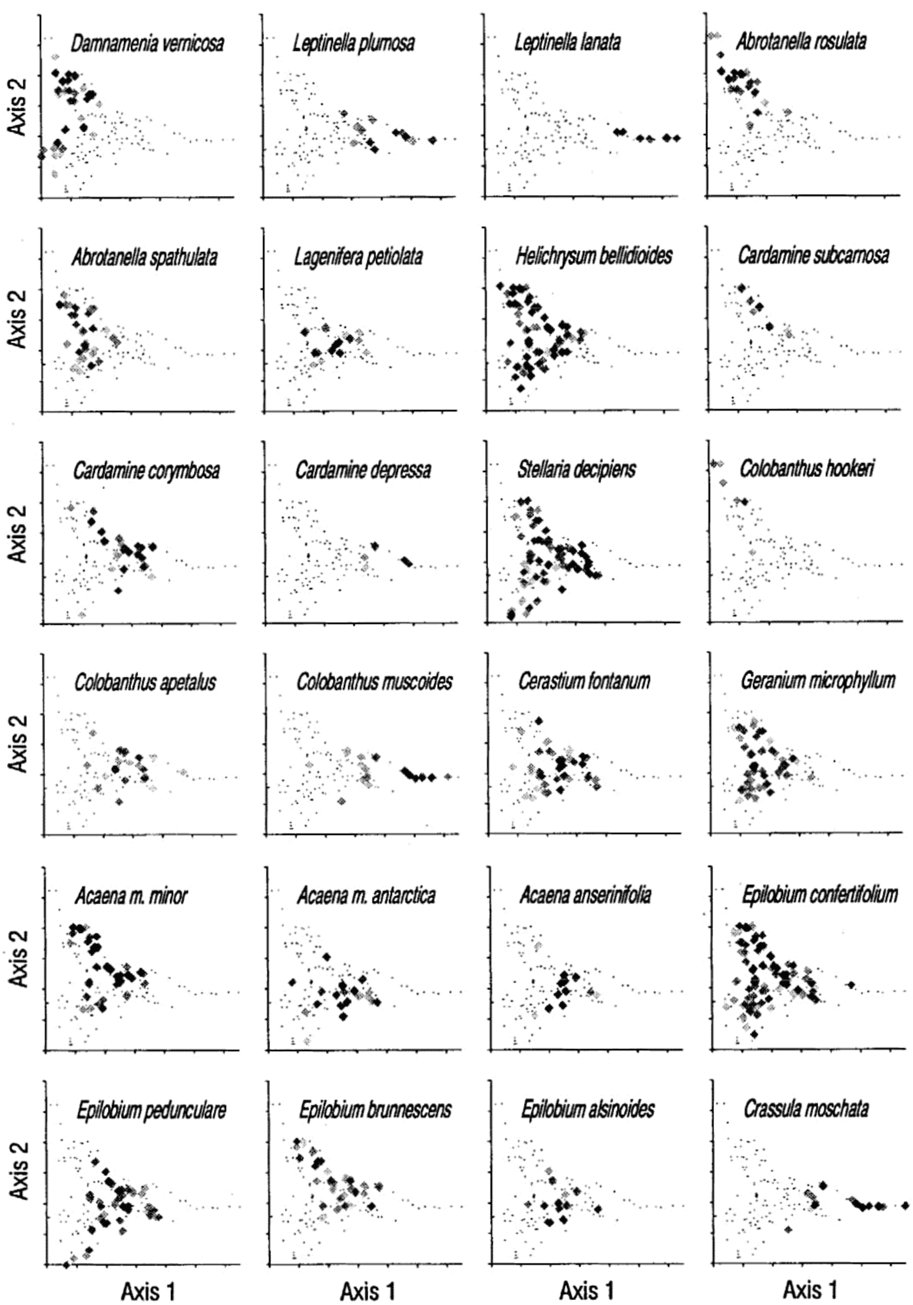


Figure 14: *Distribution and dominance of principal or matrix terrestrial forb species in ecological space (Axes 1 and 2 of site ordination). Sites for which the species are absent are indicated by fine dots. The dominance of the species at each site is indicated by 5 levels of shading (black = highest level, with dominance value of 8-10 inclusive from Table 1). Acaena m.* = A. minor.

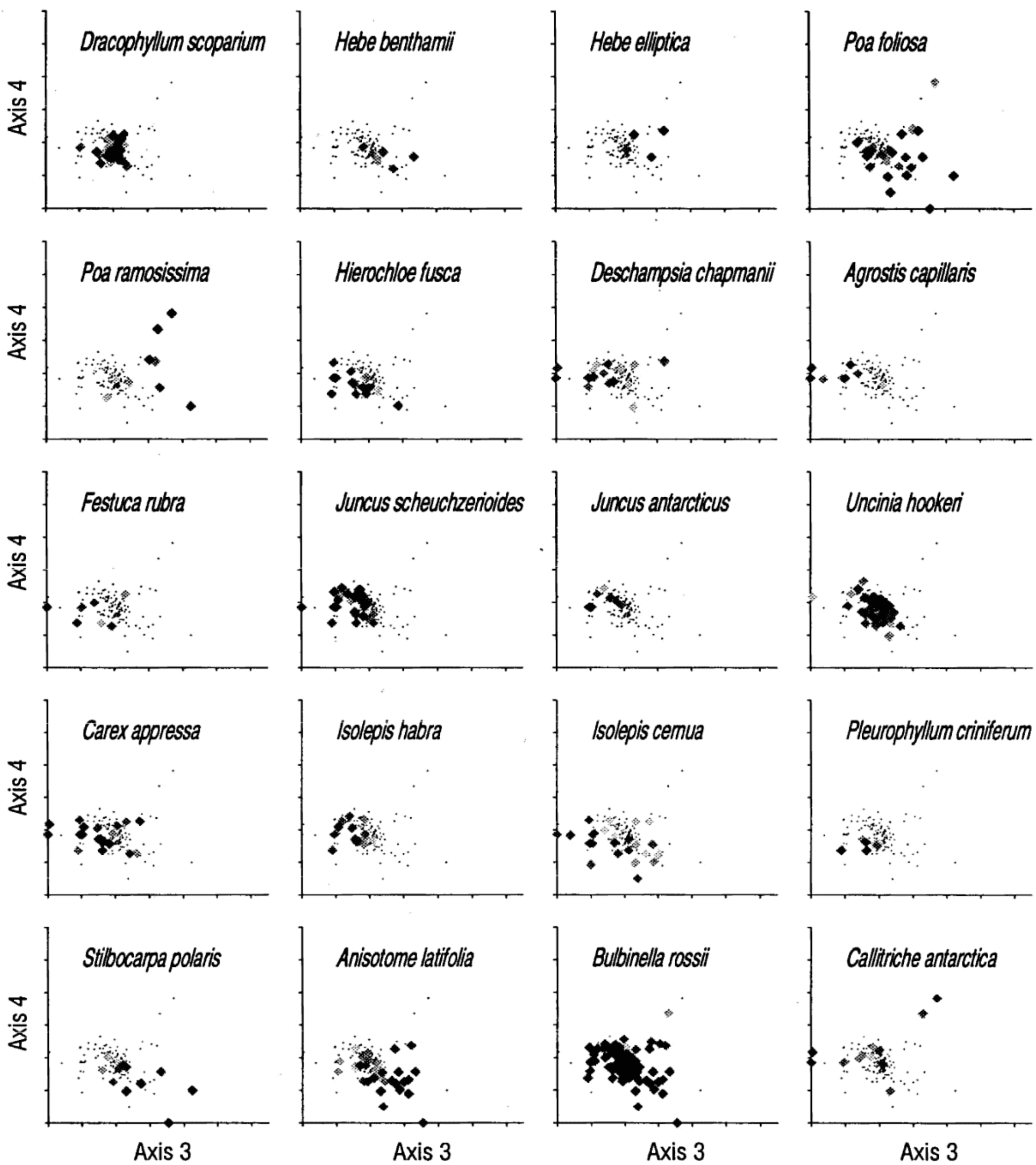


Figure 15: *Distribution and dominance of discriminating vascular species in ecological space (Axes 3 and 4 of site ordination). Sites for which the species are absent are indicated by fine dots. The dominance of the species at each site is indicated by 5 levels of shading (black = highest level, with dominance value of 8-10 inclusive from Table 1). Continued opposite. Acaena m.* = A. minor.

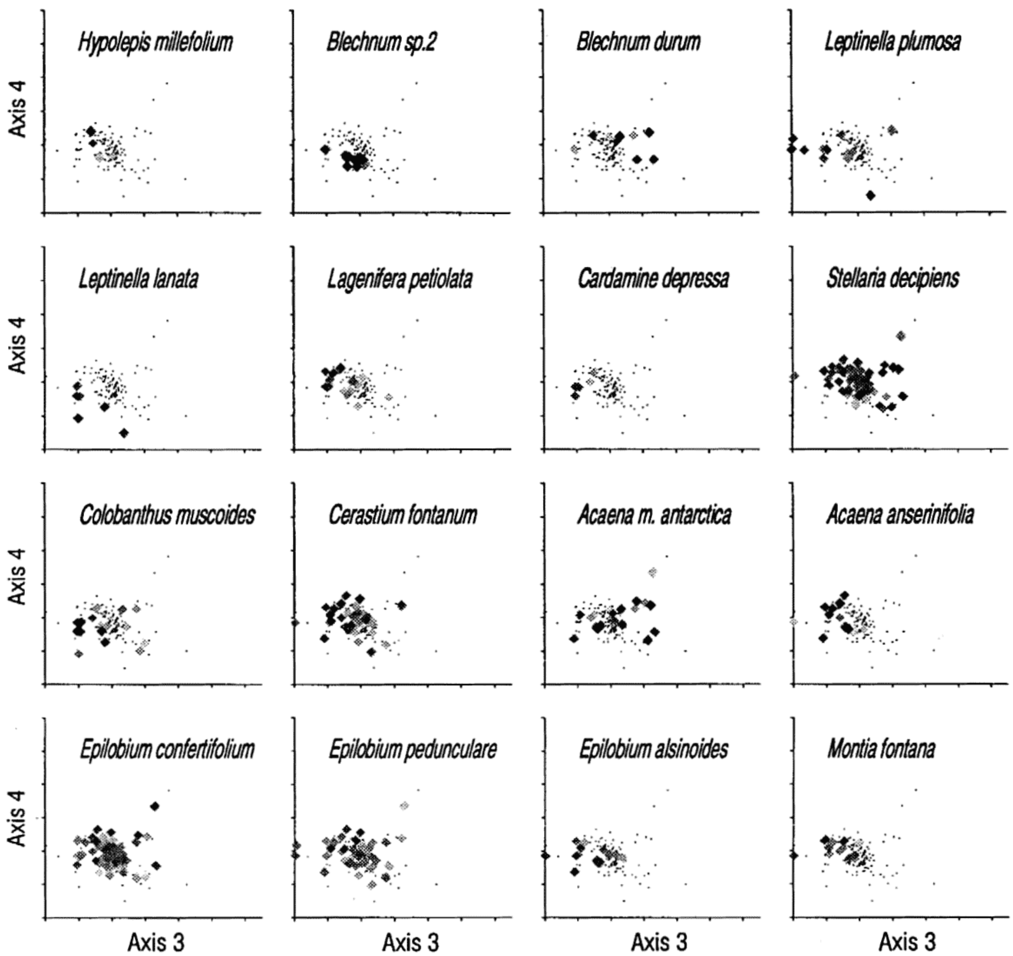


Figure 15: *Contd.*

altitude or very low fertility are likewise clustered in the centre of the diagram. This implies that all the extremities are related to suppression of biomass due to salt toxicity, grazing, trampling/wallowing, or serality, not to temperature or exposure to wind alone.

Species at the left end of Axis 3 are either lowland, swamp, and wallow inhabitants or are associated with sheep-grazed turfs and meadow. A prominent adventive element is common to both groups, and a few littoral fringe turf species (*Isolepis cernua, Leptinella lanata, Colobanthus muscoides, Cardamine depressa*) are found in grazed swards close to the coast. The swamp associates are *Carex appressa, Juncus scheuchzerioides, Isolepis habra, Pleurophyllum criniferum, Deschampsia chapmanii, Leptinella plumosa, Epilobium alsinoides, Hierochloe fusca, Blechnum* ìsp. 2î, and some local or minor species such as *Callitriche, Montia, Stellaria media, Holcus*, and *Rumex acetosella* (the latter three in Fig. 8 as centroids only). The meadow species are *Cerastium fontanum, Acaena anserinifolia, Agrostis capillaris, Festuca rubra, Epilobium pedunculare, Juncus antarcticus, Lagenifera petiolata, Hypolepis millefolium*, and to some extent *Uncinia hookeri*. Other local species represented only as centroids (Fig. 8) are

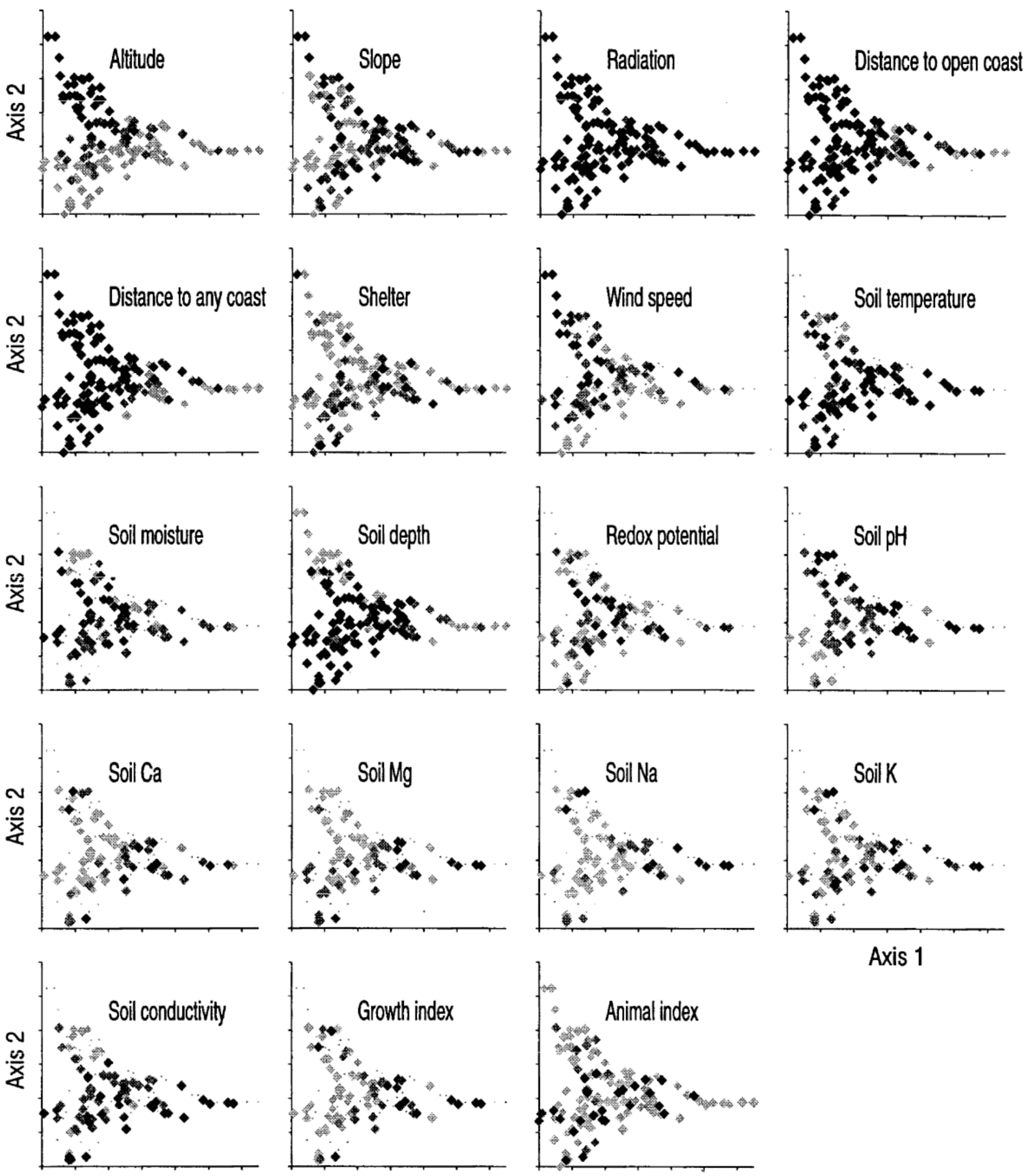


Figure 16: *Overlay of environment factors in ecological space (Axes 1 and 2). Intensity of shading represents five equal or skewed classes of magnitude within each factor. Missing values are indicated by fine dots. The environmental parameter ranges are as follows, with the 5 shading classes being equal divisions of the range except in those instances where an intermediate figure is given (this being the lower boundary of the highest of the 5 classes): altitude (0-569 m), soil temperature (5.1-12.9!), slope (0-36-78!), radiation (298-399 langleys d^{-1}), windspeed (0.1-24.5 m s^{-1}), shelter (0-29-50!), distance to open coast (-4.61 to 1.39 ln km), distance to any coast (-4.61 to 0.7 ln km), soil depth (0.01-1.5 m), soil moisture (51-1373%), soil redox potential (-410 to 97 to 575 mv), conductivity (0.13-1.61-23.0 mmho), soil pH (3.6-6.8), soil Ca (0.07-0.96-3.49 mg cm^{-3}), soil Na (0.07-0.97-3.79 mg cm^{-3}), soil Mg (0.04-0.84 mg cm^{-3}), soil K (0.01-0.24-0.43 mg cm^{-3}), growth index (0.2-3.24-5.21), animal index (0-5).*

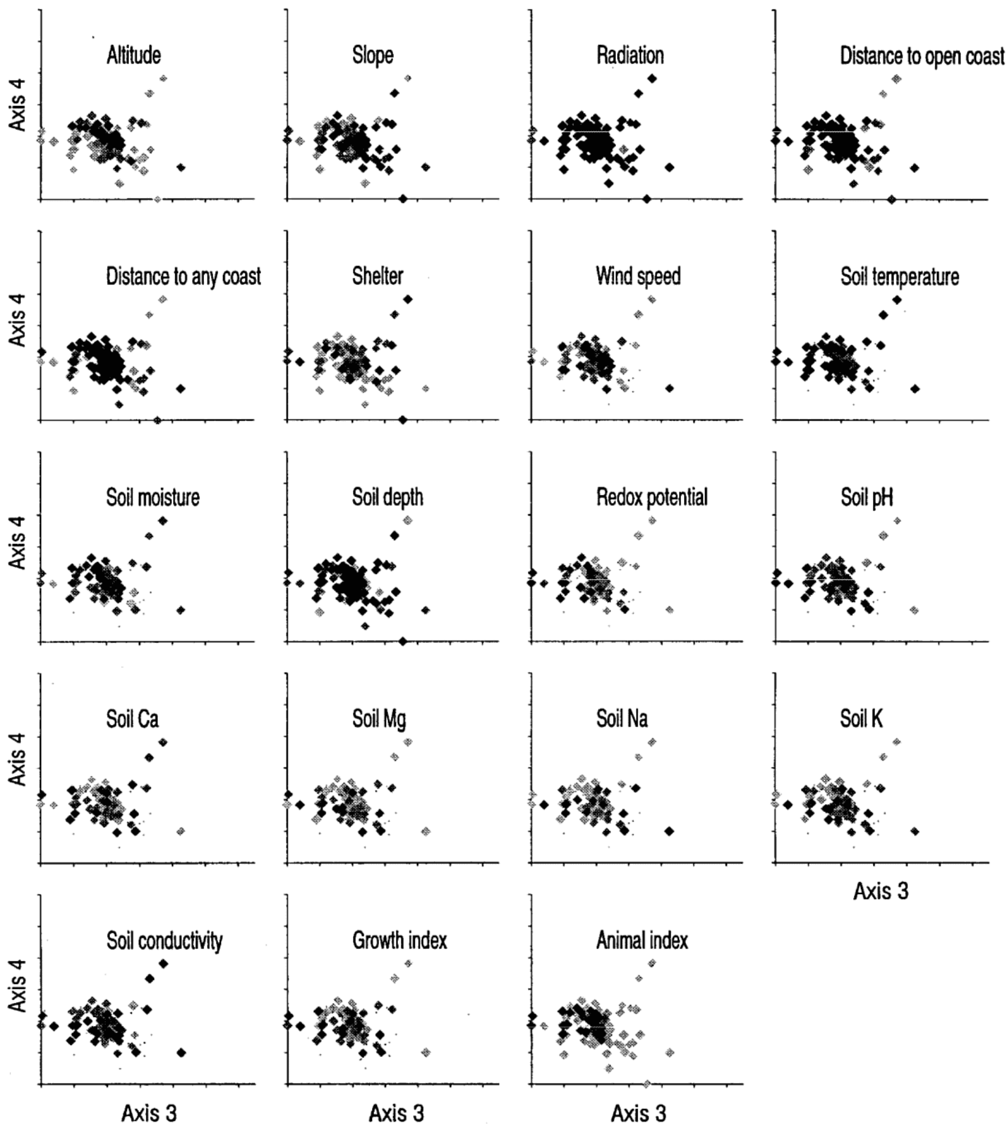


Figure 17: *Overlay of environment factors in ecological space (Axes 3 and 4). See caption to Figure 16.*

Hydrocotyle microphylla, Pratia arenaria, Poa pratensis, and *Anthoxanthum odoratum*. The meeting point of some of these swamp and grazed meadow habitat groups is along tracks where the soil is flushed or fertile owing to disturbance on a slope, and competition has been reduced.

The positive end of Axis 3 is occupied by maritime species associated with relatively tall, undisturbed, and presumably productive vegetation sometimes influenced by seabirds. This includes megaherbs (*Anisotome latifolia, Stilbocarpa)*, tall tussocks or sward grasses (*Carex trifida, Poa foliosa, P. ramosissima*), shrubs (*Hebe elliptica, H. benthamii*), and forbs (*Acaena minor* subsp. *antarctica, Blechnum durum*).

Axis 4 appears to distinguish the tall maritime (*Anisotome latifolia, Poa foliosa, Stilbocarpa*) and swamp species listed above (negative end of axis) from species associated with nest sites (*Poa ramosissima, Sagina procumbens, Epilobium confertifolium, Stellaria decipiens, Acaena minor* subsp. *antarctica, Epilobium pedunculare, Callitriche)* or which are infrequently sampled (*Isolepis praetextata, Hebe elliptica, Hypolepis* spp., *Hydrocotyle, Pratia, Carex trifida*; see Fig. 8).

The ordination diagram for Axes 3 and 4 thus illustrates how the natural vegetation (tall woody and tussock species and turfs or cushions induced by cold, exposure, and low fertility) is relegated to the centre of the diagram. The periphery reflects differing effects of disturbance, vegetation youth, or saline toxicity. The lower right quadrant reflects maritime exposure, the lower left flushed swampland, the upper left marine mammal impacts and sheep grazing, and the upper right seabird nesting.

Discussion

In contrast to most other descriptions of subantarctic vegetation, we have endeavoured here to analyse the patterns of vegetation on Campbell Island and the causal relations by standard multivariate techniques. A weakness of these is that they cannot distinguish causal from correlative phenomena. We have used as many real environmental parameters as possible, although these are generally less accurately measured than the correlated proxies. For instance, altitude is far more reliably measured than temperature (even the dampened soil temperature), given instrumental errors and corrections required for time of day. Likewise, soil chemistry assays in organic soils are highly problematic, while distance from the coast (the major influence on nutrient status) is absolutely measured. Nevertheless, wherever possible we have shown the relationship between proxy and real or causal factors. Examples are the bioassay-derived growth indices (Foggo and Meurk, 1983), the simple grazing preference experiment (Meurk, 1977), monitoring of grazing impacts on the vegetation (Meurk, 1982, 1989), which quantifies the animal influence, and finally the description of the input of nutrients from rainfall as a logarithmic regression away from the coast (Meurk *et al*., 1994)

Inevitably there are factors which confound interpretation and statistical validation of multivariate analyses. These problems are most likely to concern temporal phenomena such as dispersion, rates of succession, disruption to succession due to animal, landslide, or other catastrophic events, and environmental change such as temperature fluctuations. All these phenomena will prevent attainment of a steady state, prerequisite to a perfect correlation between vegetation and measured environmental variables. In comparison with other, less modified New Zealand subantarctic islands (e.g., Infomap 260, 1991), Campbell Island has a very complex vegetation pattern (Meurk and Given, 1990) resulting from the random patchiness of destruction during the pastoral era. On the other hand the relatively small insular flora, which in general must have good dispersal properties, the windy but relatively mesic climate, and the resilience of the vegetation will encourage the convergence of the vegetation patches towards a more easily interpreted steadystate pattern.

The present community types, derived from cluster analysis of full vascular floristic information while retaining a physiognomic (quantitative) component, can be matched tolerably well with a vegetation map produced by Meurk and Given (1990), a simplified version of which is presented as Fig. 1. The vegetation mapping units were based on ground reconnaissance and later aerial photographs. The units were subjectively derived physiognomic categories. All locations of sample sites (Fig. 1) are related to the underlying map units, except where there are inclusions too small to map. These few exceptions are Site 2 (CT18, in a maritime mapping unit), Site 107 (CT15, on the edge of a cushion lane mapping unit), and Sites 17 and 106 (CT1, on the sheltered coastal fringe within a dwarf forest unit).

The vegetation and environment of Campbell Island are very similar to those described for other subantarctic islands (Wace, 1960; Bliss, 1979; Clark and Dingwall, 1985; Smith, 1984). All are humid, windy, and dominated by maritime exposure and the influence of animals. They are floristically

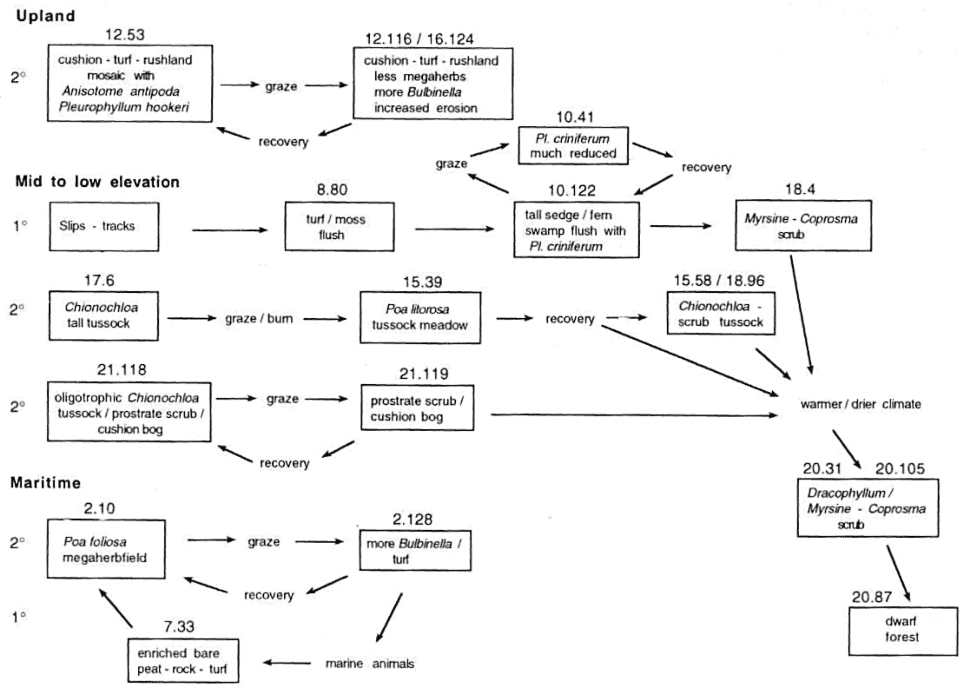


Figure 18: *Putative vegetation trajectories for both primary (1^o) and secondary (2^o) successions. Vegetation states (boxes) and agents of change are indicated. ëGrazeí includes trampling and enrichment; ëburningí was by pastoralists early this century; recovery, follows cessation of grazing/browsing/burning; marine animals include sea elephants and albatrosses. Representative sample site numbers are indicated above the boxes; thus, 12:53 = Community Type 12, sample site 53JG.*

linked by the west wind drift. The particular expression of the subantarctic ecosystem appears to be a function of latitude or base thermal climate and topographic relief (which place an upper limit on the structure of the vegetation and dictate the range of thermal regimes and hence habitat diversity) on the one hand, and the geographic area and degree of isolation from major land masses (controlling floristic relationships and species diversity) on the other. This complex of geographic factors was found to be the primary contributor to variations in the analysis of southern island environments by Smith and French (1988). Their second and third axes of variation were related to fertility, and the fourth to the contrast between animal effects and salt spray. However, their vegetation analysis produced an ordering of axes of variation similar to ours, i.e., Axis 1 of bog to coastal vegetation, Axis 2 of sheltered to exposed sites (low to high elevation), and Axis 3 of combinations of maritime, nutrient, and animal influences. The distinction between their abiotic and biotic analyses may relate to the length of the gradients. The environmental gradients are quite long, spread across 13^o of latitude. The vegetation, on the other hand, is made up of depauperate floras derived from long-distance dispersal. Accordingly the variation inherent in this vegetation is small, and that ascribed to climatic effects is less than that ascribed to localised extremes of fertility.

Meurk and Foggo (1988) found that species richness was associated with moderate environmental stress, grazing, and short vegetation (low competition). Our Axis 3 gradient shows a minor decline in species richness that corresponds to less grazing and denser vegetation.

A notable feature of southern oceanic island floras are the large herbs (megaherbs) with their strikingly coloured flowers. From our analysis it appears that both tussocks and megaherbs are strongly associated with mesotrophic to eutrophic conditions, are seral in nature, are frequently associated with and resilient to disturbance by marine animals, but are generally ill-adapted to grazing by feral mammals. This is consistent with the conjecture of Meurk *et al*. (1994) that these growth forms are equipped for nutrient harvesting from the maritime environment. Wardle (1991) has also suggested that the unusually broad leaves of some species may be designed to harvest heat from the usually diffuse radiation and short bursts of sunshine. It should be remembered that the elimination of these palatable plants from much of their potential range by grazing (Cockayne, 1904) has led observers since the 1940s to believe that their natural habitats were cliffs and ledges (Oliver and Sorensen, 1951). Removal of grazing animals has released an explosive recovery (Meurk, 1989), although the process is taking longer in areas distant from seed sources.

It has sometimes been suggested that congeners should show reduced niche overlap (e.g., Boutin and Harper, 1991). Schnitzler *et al*. (1992) suggested that such a trend could be seen in their data, although they did not attempt a test. Wilson and Lee (1994) tested for niche separation among congeners in the similar oceanic environment of montane to alpine Fiordland, New Zealand, using a unidimensional niche gradient, altitude, but found significant evidence of segregation for very few genera. However, our species ordination diagrams certainly suggest that congeners are segregating on Campbell Island quite clearly in one, two, or more resource dimensions. Notable examples are *Dracophyllum, Blechnum, Leptinella*, and *Isolepis*, primarily differentiated by nutrient status; *Agrostis, Deschampsia, Hymenophyllum, Colobanthus, Anisotome, Abrotanella, Hebe, Polystichum, Centrolepis, Hierochloe*, and *Lycopodium*, largely distinguished by altitude; and *Acaena, Epilobium, Cardamine, Coprosma, Poa*, and *Pleurophyllum*, which show mixed resource segregation and in the case of *Acaena* demonstrate a third (animal) segregating factor. This degree of differentiation is notable, given the environmentally homogenising influence of the oceanic climate and modest topographic scale discussed above.

From this work we can infer the steady state relationship between vegetation and environment and some of the dynamics or successional pathways that connect the variants. Some of these may be driven by environmental change. A conspicuous example is the spread of scrub during this century. This has been ascribed both to climatic warming and to a reduction of competition from the formerly dominant tall tussock vegetation (Rudge, 1986; Salinger, 1982). Experience over the past 20 years would suggest that in most instances release from grazing and burning will result in a rebound to something approaching the original state. Some of the more obvious pathways in a putative primary succession caused by natural peat slips and by complete stripping of the surface by marine animals, and secondary succession promulgated by burning, grazing, and/or minor animal disturbance, are mapped in Fig. 18. The trajectories of the disrupted vegetation and the extent of convergence towards semi-pristine conditions - observed as fragments on inaccessible sites of the main island, offshore islets and other subantarctic groups - may be defined by futher observation of permanent plots, which have been monitored since 1970 (Meurk, 1989).

Conclusions

It is concluded that the primary axis of variation within the vegetation of Campbell Island is a function of the proximity of the coast, often correlated with slope, greater exposure, and decreased soil depth. It has been verified that the driving force behind this gradient of rapidly increasing and then gradually declining vegetation stature and productivity is aerosol-borne cations, derived from the sea and eluted onto the vegetation and soils (Meurk *et al.,* 1994), as has been suggested for Marion and Prince Edward islands (Huntley, 1971), Macquarie Island (Jenkin, 1975) and the Falkland Islands (Smith and Climo, 1984). The precise plant association and structure near the coast appears to represent a balance between the beneficial effects of fertigation and detrimental exposure and toxic levels of salt associated with the coastal environment. Other compromises exist between fertility and disturbance, resulting in productive but low-statured vegetation. These are associated with albatross, mollymawk, penguin, and sea elephant colonies and flushed, flooded, eroding, or trampled slopes (Foggo and Meurk, 1983). At the other extreme, on inland, old, poorly drained stable surfaces are anaerobic, acid, impoverished peats with correspondingly stunted, unproductive vegetation.

The secondary source of vegetation variation is increasing altitude (lower temperature and shorter growing season), distance from the coast, exposure, and decreasing soil depth raising the mineral and nutrient content. Altitudinal (or any) differentiation will depend on the length of the gradient. On Campbell Island the total relief amounts to only 558 m (cf. South Georgia's elevation of 2950 m - Smith and Walton, 1975), translating into an air temperature range of 4°C (Meurk and Given, 1990) and an east-west distance of only 10 km (cf. approx.

150 km for South Georgia). Summit exposure effects, wind chill and the consequences of inhibited vegetation/soil development will, in effect, increase this gradient range (cf. Meurk, 1984). On the other hand, the extreme oceanicity and windiness (Meurk and Blaschke, 1990) reduces the environmental variation across the island. This results in rather weak species' segregation (in terms of altitude) and a tendency for dominance rather than presence of species to be the distinguishing trait of the vegetation zones. Many of the species appear to be generalists. It is only when thresholds of extreme exposure, nutrient impoverishment, or toxic levels of salt are crossed that the majority of species are completely excluded.

Superimposed on these natural gradients are the residual effects of pastoralism, primarily burning and grazing of the palatable or susceptible vegetation (Wilson and Orwin, 1964; Meurk, 1977, 1989). This is weakly recognised in the 3rd and 4th DCA axes of variation. Vegetation stature and dominance were artificially reduced by pastoral management, resulting in a proliferation and probable expansion (infilling) of the natural ranges of many relatively unpalatable or preadapted native and adventive turfs, rosette plants, and mats. Local species richness was thus increased in the induced meadows (Meurk and Foggo, 1988) in the middle of the altitudinal and nutrient gradients. Now that grazing mammals have been absent since 1990, the vegetation is expected to recover within a few decades (Meurk 1982, 1989). Future vegetation analyses may fail to locate the currently extensive meadows that represent a large number of the samples in the centre of our Axes 1 and 2 ordination diagram.

The presence of an adventive flora (chiefly sward grasses and creeping forbs) does not seem to pose a great threat, since the areas where they are most vigorous are sites in which the climax native vegetation will be competitively and structurally superior. However, there are a few concerns. *Holcus lanatus, Arrhenatherum elatius* and herbaceous legumes such as *Trifolium* and *Lotus* are infiltrating the flushed swamps and grasslands, especially around the historic habitation and favoured pasture sites. *Poa pratensis* is forming localised, dense swards along the littoral fringe of Perseverance Harbour. The other exotic grasses and forbs will certainly always form a part of the successional process in and around disturbed areas such as sea-elephant wallows, tracks, and the Meteorological Station. Finally, a number of woody weeds such as gorse, broom, and blackberry could become a menace if they were to establish on the island. Fortunately, quick action has prevented this in the past.

Wider considerations of subantarctic plant ecology will be traversed once the full set of southern island data from the whole of the New Zealand sector has been evaluated. Such an analysis, incorporating information on the important bryophytes and lichens, is currently under way, and has been presented in an abbreviated form by Meurk and Foggo (1988).

Acknowledgments

Johnathon Poff, Susan Walker, and Jack Squires for preparing the ordination graphics; Julian Cone and Terry Savage for Fig. 1, Ivan Morgan for editing several figures; staff of the New Zealand Meteorological Service for helping with calibration of instruments, the former DSIR, National Film Unit, Department of Lands and Survey, and Ministry of Transport for organising expeditions and providing accommodation; the N.Z. Navy and U.S. Coast Guard for logistical support and transport; and Brian Daly of the former DSIR Soil Bureau, who assisted with the soil analyses. CDM acknowledges support for field work from the Miss E. L. Hellaby Indigenous Grasslands Research Trust, and for recent support from the New Zealand Foundation for Research, Science and Technology under Contract no. C09328. MNF thanks the CEO and Council of the Central Institute of Technology, who approved both leave of absence and travel funding on many occasions during the period of this work.

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Appendix overleaf

Appendix: *Synopsis of Campbell Island plant Community Types (CTs). Roman numbering refers to successive, normal, cluster analysis splits (see dendrogram in Fig. 2). Arabic numbers refer to the 21-group CTs (Tables 2-4) with phrases in bold being the key descriptive statement. Some clusters have been supplemented by brief descriptions of non-vascular plant communities (from other analyses), or further subdivided (a,b,c) beyond the level depicted in Fig. 2. Under each CT description (which includes the average vascular species richness in parentheses) there is, on the left, a list of constant dominant species and (in parentheses) typical but non constant dominants. On the right is a list of constant and (in parentheses) typical matrix species - including those that attain their highest ranking in that CT. Between these lists are the diagnostic species groups (guilds) with >40% representation within the CT (vascular groups with capital letters, bryophytes and lichens with lower case letters, in bold type - see Tables 2, 3). The letters following the bolded name are the vegetation mapping unit code in Meurk and Given (1990). * = Adventive. Examples of most CTs are illustrated in Figs. 3-6 and Plates 1-4.*

I Low statured vegetation, imposed by cold, wind exposure, maritime exposure, poor soils, disturbance, youth and/or shallow soils. Rockfield, fellfield, cushion, turf, meadow, sedgeland, rushland, megaherbfield, tussockland and low or scattered scrub.

II Coastal to high altitude (rockfield), eutrophic to oligotrophic, herbaceous and minor scrub vegetation.

III Maritime and exposed summit grasslands, turfs, cushion, herbfields and bare soil.

VI Maritime megaherbfields and tussock grasslands.

XIII 1 **Maritime, megaherb-tussock grassland** (with occasional shrubs) : Bm
c. pristine species-poor (11); of steep, shady, well-drained, eutrophic, coastal slopes or cliffs.

(*Anisotome latifolia, Bulbinella, Poa foliosa, Stilbocarpa, Hebe elliptica, Carex trifida, Poa litorosa*)	**ST**	(*Blechnum durum, Stellaria decipiens, Lachnagrostis, Asplenium obtusatum*)

XIII' 2 **Upper maritime, *Poa-Bulbinella* tall tussock grassland** : Pm
c. pristine, moderately rich (20); of steep well drained, mesotrophic, semi-coastal sites.

Bulbinella (*Poa litorosa, Anisotome latifolia, Polystichum vestitum, Stilbocarpa*)	**HSTW** **ls**	*Cardamine corymbosa (Cerastium*, Epilobium, Poa annua*, Acaena, Montia, Colobanthus apetalus, Deschampsia chapmanii, Stellaria media*, Cardamine depressa, Sticta variabilis, Peltigera*)

VI' Exposed, seral or biotically disturbed, species-poor, maritime and summit rockfield, bare peat, turf and mat cushionfield.

3(a) **Littoral, lichen-moss rockfield** with marine organisms : Bm [not included in the vascular plant analysis]
pristine; massive rock faces beneath vascular plant limits, occupied only by crustose black and white lichens.

Verrucaria, Pertusaria	**abh**	(*Muelleriella*)

3(b) **Littoral fringe, cushion-turf-mat-lichen field** on rock and **salt marsh turf** : Bm
pristine, species-very poor (7); of well-drained, eutrophic sites with very shallow soils.

Leptinella (*Colobanthus muscoides, Crassula, Isolepis cernua, Puccinellia*)	**A** **h**	(*Cardamine depressa, Muelleriella*)

4(a) **Upper maritime, biotic disclimax, trailing turf grassland** : Bm
pristine, species-very poor (7); of sheltered, moderately well-drained, acid, high conductivity, meso- to oligotrophic sites among mollymawk colonies.

Poa ramosissima (*P. litorosa, P. foliosa, Bulbinella, Polystichum vestitum*)	**DT** **s**	*(Callitriche, Acaena minor* subsp. *antarctica, Epilobium confertifolium, Stellaria decipiens, Marchantia*)

4(b) **Mid altitude, biotic-seral, mat-turf herbfield** : P
pristine, species-poor (10); of **abandoned albatross nests** in *Poa* meadow, on deep, wet, acid, infertile peats.

Poa litorosa, Marchantia, Luzula, Acaena (Bulbinella, Cerastium)*	**TW** **p**	*Epilobium confertifolium, Stellaria decipiens (E. pedunculare, Sagina*, Ceratodon, Cladia aggregata, Campylopus, Bryum billardierei)*

5(a) **Moderate altitude**, exposed, **short turf peatland** : B
species-very poor (6); of sheep damaged (?), **wind-deflated peat scars** on gentle, wet, acid, infertile, deep peats.

Juncus scheuchzerioides, Bulbinella, peat	**TX** **ps**	*Luzula, Isolepis aucklandica,* yellow agaric (*Stellaria decipiens, Marchantia, Cladia aggregata*)

5(b) **Moderate altitude**, moderately exposed, **rush-sedge-moss turf** : B and M
species-very poor (7), of **tarn margins** on gentle, wet, moderately acid, infertile deep peats.

Juncus scheuchzeriodes, Isolepis aucklandica (Drepanocladus)	**XY** **qtu**	*Breutelia elongata, Epilobium brunnescens, Stellaria decipiens (Sphagnum)*

6(a) Exposed, **summit cryptogam rockfield** : RY : M [not included in the vascular plant analysis]
pristine, with only crustose and cushion crytogams on massive rock.

	dno	

6(b) **High altitude talus** : M
pristine, species-poor (13); of steep well-drained, high pH, infertile, shallow mineral soils.

gravel	**GW** **o**	*Grammitis poeppigiana, Stellaria decipiens, "Dicranum", Placopsis, "Stereocaulon ramulosum"*

6(c) **Moderately-high altitude grass-herbfield** of rock **crevices** and **ledges** : M and P
pristine, species-very poor (9); of well-drained, high pH, infertile thin peats.

Stereocaulon, Rhizocarpon, Grammitis poeppigiana, Pseudocyphellaria glabra (Macromitrium)	(**GW**) **cnos**	(*Abrotanella rosulata, Colobanthus hookeri, Luzula, Menegazzia*)

III' Mainly inland, sheltered, seral and disclimax (biotic), meso- to eutrophic, often flushed turf-mat grassland, and tall sedgeland with ferns and shrubs.

VII IX XIV 7 **Harbourside, turf-mat-forb grassland** of **sea-elephant wallow** banks : Bm
disclimax, species-poor (15); of gentle sheltered and shady sites on meso- to eutrophic, shallow peats, formerly sheep-grazed.
Agrostis capillaris, Callitriche, Rumex acetosella*, Poa annua*, Carex appressa (Poa pratensis*, Juncus scheuchzerioides)*
EVX
pq
Leptinella plumosa, Deschampsia chapmanii, Epilobium pedunculare, Ceratodon, Marchantia (Montia)

XIV' 8(a) **Low-moderate altitude, turf-mat-forb-grassland** of disturbed, flushed sites : S
seral, species-very rich (26); sheltered, warm, wet, mesotrophic fresh **slips, riparian mires** and **walking tracks**.
Agrostis magellanica, Helichrysum, Juncus scheuchzeriodes, Breutelia pendula (Hierochloe fusca, Poa litorosa)
STVWXY
opstu
(*Marchantia, Anthoceros, Isolepis aucklandica, Epilobium confertifolium, Poa breviglumis, I. habra, E. pedunculare, Luzula, Lachnagrostis, Deschampsia chapmanii, Juncus antarcticus*)

8(b) Other **riparian/waterfall saturated banks** of semi-aquatic **bryophytes** : [not in the vascular plant analysis]

IX' 9 **Moderate altitude, *Bulbinella*/turf-mat grassland** : B
disclimax, species-very rich (30); of warm sunny, eutrophic, sheep-grazed sites.
Bulbinella, Acaena anserinifolia, Poa breviglumis, Ptychomnion (Poa litorosa, Agrostis capillaris, Hypolepis millefolium*)
FHIPTWY
lps
Cerastium, Epilobium pedunculare, Poa annua*, E. brunnescens, Montia, Hydrocotyle, Lagenifera, Acaena minor* subsp. *minor, Stellaria decipiens, Helichrysum, Geranium, Polystichum vestitum, Marchantia*, hepatics (*Colobathus apetalus, Thuidium, Achrophyllum, Acrocladium, Pseudocyphellaria glabra, Breutelia pendula, Sphagnum*)

VII' 10 **Low - moderate altitude, divaricate shrub-forb-tall fern-sedgeland** : Sw
c. pristine species-very rich (26); of moderately acid fertile **swamps** on sunny, exposed, gentle flushed slopes.
Carex appressa, Coprosma shrubs, *Polystichum vestitum, Bulbinella, Poa litorosa (Hierochloe fusca, Blechnum* "sp.*2", Pleurophyllum criniferum, Hypolepis amaurorachis)*
FTVWX'ZA'
lps
Acaena, Cerastium, Epilobium alsiniodes, Peltigera (Isolepis habra, Helichrysum, Juncus scheuchzerioides, E. pedunculare, Corybas, E. confertifolium, Ranunculus subscaposus, Holcus*, Acrocladium, Achrophyllum, "Brachythecium", Ptychomnion, Marchantia,* hepatics)

II' Moderate to high altitude, meso- to oligotrophic, short tussock, turf, rushland, herbfield, fellfield.

IV Herbfields, tall rushlands and fellfields of the summit tundra zone.

X 11 **High altitude, turf-meadow with megaherbs** and minor shrubs on **rock ledges** : M
pristine, species-very rich (51); of very sheltered, sunny, but cool, gentle slopes, with shallow, well drained, high pH, infertile mineral peats.
Pleurophyllum speciosum, Anisotome antipoda, *Bulbinella, Marsippospermum, Polystichum vestitum*
CFGHLSTWXYZ
jlort
Plagiochila, Damnamenia, Trisetum, Ranunculus pinguis, Polystichum cystostegia, Acaena minor subsp. *minor, Poa breviglumis, Agrostis magellanica, Uncinia hookeri, Lepicolea scolopendra, Sticta latifrons*

X' XII 12 **Moderately high altitude, *Marsippospermum* tall turf rushland** with megaherbs : M-B
ca. pristine, species-very rich (27); of fairly exposed cool, zonal slopes with wet infertile, thin peat soils.
Marsippospermum, Pleurophyllum speciosum, Bulbinella, Poa litorosa, Helichrysum (Pleurophyllum hookeri, Anisotome antipoda, Stilbocarpa, Polystichum vestitum)
CNTWY
lst
Epilobium brunnescens, E. confertifolium, Acaena, Poa breviglumis, Geranium, Stellaria decipiens, Uncinia hookeri, Pseudocyphellaria glabra, Breutelia pendula, hepatics *(Hierochloe brunonis, Luzula, Cardamine subcarnosa, C. corymbosa, Ranunculus subantarcticus, Damnamenia, Deschampsia gracillima, Acaena minor* subsp. *minor)*

XII' 13 **High altitude *Marsippospermum-Bulbinella* tall turf rushland** : M
lightly browsed, species-rich (24); of very exposed, cold zonal slopes with shallow, well-drained, high pH, mesotrophic, stony peats.
Marsippospermum, Bulbinella, Luzula, Hierochloe brunonis (Rostkovia)
GNTW
lrst
Abrotanella rosulata, Poa aucklandica, Acaena minor subsp. *minor, Epilobium confertifolium, Stellaria decipiens, Uncinia hookeri, Acrocladium, Breutelia elongata (Deschampsia gracillima, Grammitis poeppigiana, Helichrysum, Trisetum, Hymenophyllum villosum, Dicranum)*

14 **High altitude *Bulbinella*/turf-forb-cryptogam fellfield/talus** : M
c. pristine, species-very rich (27); of very exposed, cold summits on shallow, well-drained, high pH, mesotrophic stony peats.
Bulbinella, Deschampsia gracillima, Agrostis subulata (Stereocaulon ramulosum)
GLTWYZ
dnort
Uncinia hookeri, Acaena minor subsp. *minor, Helichrysum, Abrotanella rosulata, Anisotome antipoda, Ranunculus pinguis, Grammitis poeppigiana, Poa aucklandica, Trisetum, Epilobium confertifolium, Luzula, Coprosma perpusilla, Gentiana, Phyllachne, Usnea, Cladia aggregata, Pseudocyphellaria glabra, Placopsis, Breutelia elongata (Damnamenia, Hymenophyllum villosum, Colobanthus hookeri, Craspedia, Myosotis antarctica, Rhacocarpus, Lycopodium australianum)*

IV' Mid-altitude, meso- to oligotrophic short turf rushlands, cushion bogs and induced short tussock meadow.

15 **Mid altitude *Poa litorosa-Bulbinella* short tussock meadow**; with ferns, shrubs and reinvading *Chionochloa* : P + P + P/cu
induced, species-rich (23); of exposed, gentle sites on deep wet, acid, oligotrophic peats.

Poa litorosa, Bulbinella, Polystichum vestitum, Coprosma shrubs, *Uncinia hookeri (Chionochloa, Dracophyllum)*	**TUWYZ'ZA'** **irsu**	*Epilobium confertifolium, Gentiana, Isolepis aucklandica, Geranium, Coprosma perpusilla, Sphaerophorus tener, Pseudocyphellaria glabra, Cladia aggregata*, hepatics *(Hymenophyllum multifidum, Luzula, Abrotanella spathulata, Phyllachne, Lycopodium fastigiatum, Dicranum robustum, Sphagnum)*

16(a) **High altitude, *Rostkovia-(Juncus)-Bulbinella*-sedge short turf rushland** : M
c. pristine, species-moderate (20); of exposed, cold, semi-flushed slopes with mesotrophic wet, thin, stony peat soils.

Rostkovia or *Juncus scheuchzerioides, Bulbinella (Polytrichum, Pleurophyllum hookeri)*	**TWXYZ** **orstu**	*Isolepis aucklandica, Coprosma perpusilla, Gentiana, Breutelia elongata, Uncinia hookeri, Pseudocyphellaria glabra (Epilobium confertifolium, Geranium, Helichrysum, Abrotanella spathulata, Phyllachne, Sphagnum, Grammitis givenii, Damnamenia, Dicranum robustum, Luzula)*

16(b) **High altitude *Centrolepis pallida* cushion bog** : M
pristine species-poor (16), of very exposed, cool-sunny, gentle slopes with very wet, moderately acid, oligotrophic infertile, thin peats.

Centrolepis pallida, Bulbinella, Damnamenia, Isolepis aucklandica	**TYZ** **stu**	*Luzula, Coprosma perpusilla, Gentiana, Phyllachne, Breutelia elongata, Dicranum robustum (Rostkovia, Rhacocarpus, Sphagnum, Epilobium pernitens, Helichrysum)*

I' Low altitude, oligo-mesotrophic, tall tussock, dwarf forest, scrub and tussock/shrubland/cushion bog.

V Tall tussock-shrubland, scrub and dwarf forest.

VIII XI 17 **Mid altitude *Chionochloa*-divaricating shrub-fern tussock grassland** : Ch
c. pristine, species-rich (22); of steep, shaded zonal remnants on thin, acid, oligotrophic peats.

Chionochloa, Poa litorosa, Bulbinella, Coprosma shrubs, *Polystichum vestitum, Myrsine (Dracophyllum)*	**STUW'ZA'** **s**	*Pseudocyphellaria glabra (Anisotome latifolia, Helichrysum, Luzula)*

XI' 18 **Low-mid altitude *Coprosma*-fern-*Myrsine* divaricating shrubland** : Co
c. pristine, species-very rich (25); of sunny gentle slopes on deep, acid (slightly flushed?), mesotrophic peats.

Coprosma shrubs, *Myrsine, Polystichum vestitum, Poa litorosa, Bulbinella, Dracophyllum, Uncinia hookeri (Carex appressa, Blechnum* "sp.2", *Hierochloe fusca, Pleurophyllum criniferum)*	**OTUVWXY'ZA'** **lmrsu**	*Epilobium confertifolium, Ptychomnion, Pseudocyphellaria glabra (Isolepis aucklandica, Gentiana, Chiloglottis, Anthoxanthum*, Pratia, Geranium, Helichrysum, Frullania, Cladia aggregata,* hepatics)

VIII' XV 19 **Sheltered-maritime *Hebe elliptica*-mixed tussock-scrub** : Pm-D
c. pristine, species-rich (24); of sheltered, warm, harbour-side coasts on acid, mesotrophic thin peats.

Dracophyllum, Hebe elliptica, Poa litorosa, Polystichum vestitum, Coprosma shrubs, *Bulbinella (Carex trifida, Myrsine*)	**ABTV'ZA'** **fgms**	*Macromitrium, Acaena minor* subsp. *antarctica, Blechnum durum, Eriopus, Collema, Metzgeria,* hepatics

XV' 20(a) **Low to mid altitude *Dracophyllum* meadow scrub** : D and D-P
partly grazed, species-moderate (20); on sunny slopes with moderately deep, moderately wet, acid, oligotrophic peats.

Dracophyllum, *Poa litorosa, Bulbinella, Uncinia hookeri, Coprosma* shrubs, *Polystichum vestitum, Myrsine (Chionochloa)*	**TWY'ZA'** **mrs**	*Hymenophyllum multifidum, Pseudocyphellaria (Lycopodium varium, Isolepis aucklandica, Frullania, Psoroma, Hypnum, Sphaerophorus tener,* hepatics)

20(b) **Low altitude *Dracophyllum* tall scrub and dwarf forest** : D
c. pristine, species-poor (14); on sunny, very sheltered, gentle slopes with deep, dry, acid mesotrophic peats.

Dracophyllum, Myrsine, Polystichum vestitum Coprosma shrubs *(Histiopteris, Blechnum* "sp.2")	**Q'ZA'** **gkms**	(*Corybas, Uncinia aucklandica, Metzgeria, Megalospora, Menegazzia, Usnea, Psoroma, Macromitrium, Pseudocyphellaria,* hepatics, *Stellaria decipiens, Lycopodium varium, Chiloglottis, Hymenophyllum multifidum, H. minimum, Grammitis magellanica, Bryum billardierei, Achrophyllum, "Brachythecium", Coccotrema, Lejeunea)*

V' Tussock/prostrate shrub/cushion (turf or pillow) bog.

21 **Low altitude, *Chionochloa* tall tussock/*Dracophyllum* prostrate shrub/cushion-turf-(pillow) bog** : CuD, P/cu
c. pristine, species-moderate (18); of warm, but very exposed convex plateaux on deep, wet, very acid, oligotrophic peats.

Chionochloa, Coprosma cuneata, Myrsine, Dracophyllum scoparium (Bulbinella, Blechnum procerum)	**RTUY'ZA'** **rsu**	*Damnamenia, Coprosma perpusilla, Gentiana, Isolepis aucklandica, Riccardia cochleata, Dicranum robustum, Sphaerophorus tener (Lycopodium varium, Astelia, Oreobolus, Phyllachne, Hypnum, Pseudocyphellaria glabra, Centrolepis ciliata, Lyperanthus, Aporostylis, Drosera, Schizaea, Gonocarpus)*

Key
A=*Acaena minor* subsp. *antarctica*, B=*Anisotome latifolia*, C=*Anthoxanthum odoratum*, D=*Chionochloa antarctica*, E=*Colobanthus apetalus*, F=*Epilobium alsinoides*, G=*Epilobium confertifolium*, H=*Epilobium pedunculare*, I=*Festuca rubra*, J=*Holcus lanatus*, K=*Hymenophyllum multifidum*, L=*Isolepis habra*, M=*Pratia arenaria*, N=*Ranunculus subantarcticus*, O=*Ranunculus pinguis*, P=*Ranunculus subscaposus*, Q=*Rostkovia magellanica*, R=*Rumes acetosella*, S=*Sagina procumbens*.

Key
A=*Abrotanella rosulata*, B=*Agrostis subulata*, C=*Anisotome antipoda*, D=*Astelia subulata*, E=*Coprosma cuneata*, F=*Epilobium brunnescens*, G=*Hecrochloe brunonis*, H=*Hymenophyllum multifidum*, I=*Oreobolus pectinatus*, J=*Phyllachne clavigera*, K=*Polystichum cystostegia*.