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Ecological studies of a marine terrace sequence in the Waitutu Ecological District of southern New Zealand. Part 2: The bryophyte communities

R. S. Tangney*

The bryophyte communities of the Waitutu marine terrace sequence are described on the basis of quantitative sampling. Local frequency data were obtained for ground bryophytes and percent cover values for epiphytes. Patterns of quadrat and phorophyte groupings generated by Cluster Analysis are confirmed by Detrended Correspondence Analysis. The bryophyte patterns relate closely to the communities of vascular plants recognised on the terrace sequence and described by Mark *et al.* (1988).

Bryophyte diversity (as species number) on the terrace sequence is highest in the tall lowland forest and decreases with increasing altitude and deteriorating drainage of the upper sites, with its associated decreases in plant height, cover and tree basal area. It is lowest at the upper bog sites. The low diversity in the coastal turf is the result of the exposed coastal habitat.

Keywords: Waitutu Ecological District, marine terrace sequence, bryophyte communities, quantitative sampling, Cluster Analysis, Detrended Correspondence Analysis, bryophyte diversity.

INTRODUCTION

A series of at least 13 marine terraces in the Waitutu Ecological District has been described in detail by Ward (1988). Mark *et al.* (1988) have given an account of the vascular plant-soil relationships of ten of these terrace surfaces ranging in altitude from near sea-level to 630 m, and extending inland for 12 km. This study treats the bryophyte communities of the terrace sequence separately.

Relatively few quantitative studies exist on the New Zealand bryophytes. Notable previous studies are from Secretary Island, Fiordland (Scott, 1970), Mt Anglem, Stewart Island (Scott and Armstrong, 1966) and Jackson Bay, South Westland (Scott and Rowley, 1975). These studies aimed to provide a record of these "extremely abundant, but hitherto largely ignored, components of New Zealand forests." (Scott, 1970). The present study, undertaken as a complement to the description of the vascular plant communities of the terrace sequence (Mark *et al.*, 1988), adds to this record.

The Secretary Island study (Scott, 1970) showed that differences in the dominant vegetation were reflected in the associated bryophytes. The suggestion that the terrace sequence represented a soil-vegetation chronosequence was being investigated by Mark *et al.*, 1988; hence the relationship between the vascular plant and bryophyte communities was of particular interest.

METHODS

Bryophytes were sampled at the same sites as the vascular plants (Mark *et al.*, 1988), by methods following those of Scott and Rowley (1975). Ground bryophytes were sampled using a series of usually ten 0.5 m square quadrats, each subdivided into 25 dm square subunits. These quadrats were staggered along one predetermined edge of the first of the three 20 × 10 m forest quadrats at each site. Local frequency, measured as presence/absence in each of the 25 subunits, was recorded from each quadrat. Epiphytic

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bryophytes were sampled on a limited number of phorophytes encountered on the perimeter of the same 20 × 10 m quadrat. Only trees (stems > 10 cm d.b.h.) were sampled, and then only the basal 2 m of stem. Abundance of the epiphytes was estimated subjectively and each bryophyte given a numerical cover value according to the following scale adopted from Scott and Rowley (1975):

Numerical value	*"Abundance"*	*Mean Cover (%)*
1	Present/rare	< 1
2	Occasional	5
3	Frequent	15
4	Abundant	40
5	Dominant	80

The data were subjected to Cluster Analysis (City-block distance measure, flexible sorting strategy; beta = −0.25) and Detrended Correspondence Analysis (Hill and Gauch, 1980) using the Golliwog computer programme (J. B. Wilson, unpublished). For presentation of the Cluster Analysis results, the distance measure (dissimilarity) is expressed as City-block divided by the number of attributes.

Voucher specimens were made of all species recorded and these have been placed in the herbarium of the Botany Department, University of Otago (OTA).

TAXONOMY

Nomenclature follows Sainsbury (1955) and Scott and Stone (1976) for mosses; Hamlin (1972, 1973) for hepatics; and Allan (1961) for vascular plants. Where names are different from earlier studies, authorities are given in the floristic list.

The sampling methods described lessened identification errors in the field, but difficulties still existed. In the genus *Dicranoloma, D. billardierei* has been used to include all *Dicranoloma* species (except *D. menziesii* and *D. cylindropyxis*) in an attempt to avoid the effect of field identification errors. The *Riccardia/Aneura* groups provide difficulties also and identification for these must be regarded as tentative. Other areas where confusion may exist are *Macromitrium* spp., *Chiloscyphus* spp., *Lophocolea* spp., *Telaranea* spp., *Lepidozia laevifolia* and *L. concinna*.

RESULTS

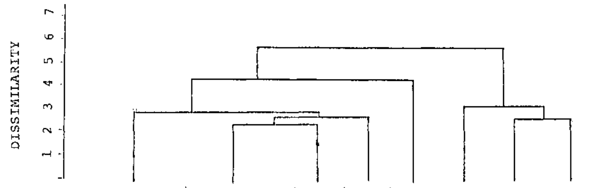
The two-way tables show the results of the Cluster Analyses: values for ground species (Fig. 1) are based on local frequency, those for epiphytes (Fig. 4) on estimated cover. Species groups (at an arbitrary 8-group level) identify dominant species as well as quadrat and phorophyte groups, which indicate the distribution of these species both within and between the sites. The dendrograms attached to the tables show the dissimilarities between both the species groups and the quadrat groups. Terrace 1 is excluded from these analyses as it was not quantitatively sampled.

Ground Species

The species groups (Fig. 1) identify several dominant species (Groups 1, 2, 4, 5, 6, 7, 8) and one large group of species of lesser and minor occurrence (Group 3).

The dendrogram shows the greatest dissimilarity between Quadrat Groups A to E and Groups F to H. The latter comprise a group from which the lowland forest sites (Nos. 2, 3, 4A-C) are excluded. These lowland sites are dominated by Groups B, C, D, E with occurrences of Sites 4A-C and 6C quadrats in Group D and a group of higher altitude sites in Group B. Low-altitude quadrats (Sites 2, 3, 4A-C) are excluded from Group A which contains quadrats from the upper terraces (Sites 10A-C, 9, 8, 7, 6A-C). By recognising on the table the positions where at least half of the quadrats from a sample site fall into one group, the relationship between the groups and their associated species, and the different sample sites emerges.

No one site has all its quadrats in the same quadrat group. Nine sites had at least



	A	B	C	D	E	F	G	H	Species group
	10A 8(3) 10B 7(5) 10C(2) 6A 9(9) 6C(2)	10A 4A(3) 10B(2) 4B(2) 10C 4C(3) 7(5) 3(6) 6C(3) 2(7) 6D	4B(3) 4C(2) 2	10B 6C(4) 4B(3) 3(4)	4A(7) 4B(2) 4C(4) 2(2)	10A(6) 10B(3) 6B(8) 6D(6)	10A 10C 8(7) 6A(9)	10A(11) 10B(3) 10C(3) 6B(2) 6C 6D(3)	
Acromastigum anisostumum	+						12.9	1.4	1
Riccardia marginata	+	+			+	1.6		7.7	2
Bazzania involuta	+							+	3
Hypnum cupressiforme	+								
Plagiochila pleurata						+			
Chiloscyphus coalitus		+							
Aneura rodwayii		+							
Plagiochila baylisii		+							
Telaranea gottscheana		+							
Symphyogyna podophylla					+				
Riccardia alcicornis		+							
Lembidium nutans								+	
Rhizogonium bifarium		+							
Plagiochila fasciculata		+							
Bazzania adnexa	+				+		+		
Schistochila balfouriana	+								
Chiloscyphus tricanthus	+								
Sphagnum falcatulum		+				+			
Tetracymbaliella cymbalifera							+	+	
Wijkia extenuata	+	+	+						
Lepidolaena clavigera	+							+	
Plagiochila circinalis				+			+		
Riccardia eriocaula			+						
Megaceros sp.			+	+					
Lepidolaena taylorii		+	+				+		
Hypopterygium novae-seelandiae		+	+		+				
Chiloscyphus multispinus		+							
Dicranum aucklandicum						+			
Riccardia cochleata	+	+					+	+	
Lepicolea scolopendra	+	+					+	+	
Aneura alterniloba		+							
Telaranea tetradactyla		+			+				
Tetracymbaliella decipiens			+		+		+		
Lepidozia microphylla		+							
Dicranoloma menziesii	+	+	3.1				+		
Aneura pinnatifida		+	2.6						
Hypopterygium commutatum			5.7		+	+			
Sphagnum cristatum						+		2.1	
Kurzia calcarata						3			
Hypnodendron kerrii		1.3	+	+	+				
Achrophyllum quadrifarium	+	+	2.1	1.8	+				
Plagiochila suborbiculata		+	3.4	1.3	+				
Lepidozia concinna	1.5			+			+	1.3	
Lepidozia pendulina	1.6	+		+			2.6		
Chiloscyphus billardierei	2.2	+			+		1.4	+	
Schistochila ciliata	+	+					+		
Campylopus introflexus						3.2		2.2	
Hypnodendron comosum	1.5	+	+	8.1	+				
Ptychomnion aciculare	3.1	1.6	+	10.5	5.5	+	+	+	4
Trichocolea mollissima		4.8	+	+	4.1		+	+	5
Schistochila nobilis		+	1.9	8.9	5.7			+	6
Schistochila appendiculata		+	12.7	+	7.0				
Tylimanthus saccatus		1.4			17.8				
Bazzania novae-zelandiae	17.0	2.2	+	1.3	3.7		6.9	+	7
Dicranoloma billardieri	2.3	+		2.7		20.9	14.5	7.4	8

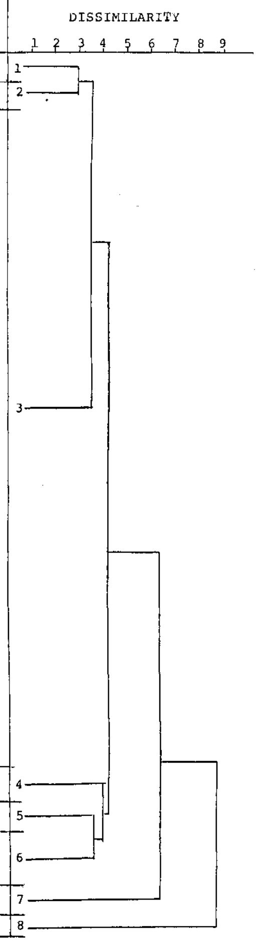


Fig. 1—Two-way nodal table showing the eight groups of bryophytic ground species (1 to 8) and eight community groups (A to H) together with their dissimilarity values based on Cluster Analysis, among the 157 quadrats and 57 species included in the analysis. Values are averages of species records per 0.5 m square quadrat within the quadrat group. + = present in that group with a mean frequency of < 1. Values in brackets refer to the number of quadrats from a particular site in each quadrat group. Other than sites 10A (20) and 10C (7) ten quadrats were sampled at each site (see text for details of analysis).

half of their quadrats in one group and one site (7) had at least half of its quadrats in two groups (A and B). Affinities between the sites that emerge are Sites 7 and 9 (Group A); 7, 2 and 3 (Group B); 4A by itself (Group E); 6D and 6B (Group F); 6A and 8 (Group G); 10A by itself (Group H).

The dendrogram for the quadrate groups (Fig. 1) shows the degree of dissimilarity between the individual groups, and allows comparison of the various sample sites. Quadrat group 7-2-3 (Group B) shows greatest similarity with quadrats from Terrace 4 and 6, as well as for the 2-3 quadrats (Groups C and D). These groups then are linked to 9-7 (Group A) and then to 4A (Group E). On the other half of the dendrogram sites 6A and 8 are seen as showing greater similarity to 10A than to 6D-6B.

The remaining sites, 10B, 10C, 6C, 4B, 4C, show no clear affinites with any one particular quadrat group; indeed quadrats from these sites are distributed throughout the quadrat groups, which means that there is greater variation within these samples than in the others. Terrace 10B quadrats associate with 10A Group, 6D-6B Group, 9-7 Group and 7-2-3 Group. Terrace 6C quadrats associate with 10A, 9-7, 7-2-3 and 3-4 quadrats in Group D. Terrace 4B-4C quadrats associate in 7-2-3 Group. The extent of the variation between the quadrats within these sites is seen in the falling of these quadrats across separations of large dissimilarities. The more uniform samples also show signs of wide internal variation, with some quadrats dispersed into widely differing groups (e.g. Terrace 9 with nine of its ten quadrats in Group A and the tenth in Group G; and Terrace 8 with seven of its ten quadrats in Group G and the other three in Group A).

Quadrat Group A (from Sites 9 and 7) is dominated by *Bazzania novae-zelandiae* with significant numbers of *Ptychomnion aciculare, Lepidozia pendulina, L. concinna, Chiloscyphus billardierei, Hypnodendron comosum* and *Dicranoloma billardierei*. Group B (from Sites 7, 2 and 3) is characterised by *Trichocolea mollissima, Ptychomnion aciculare, Bazzania novae-zelandiae* and *Tylimanthus saccatus,* associated with *Schistochila appendiculata, Hypnodendron comosum, Schistochila ciliata, Chiloscyphus billardierei, Achrophyllum quadifarium* and *Hypnodendron kerrii*. Group C (mainly Site 4 quadrats) is characterised by *Schistochila appendiculata* and *Hypopterygium commutatum* and other species include *Plagiochila suborbiculata*. Group D (quadrats from Sites 2, 3 and 4) is characterised by *Ptychomnion aciculare, Schistochila nobilis, Hypnodendron comosum, Dicranoloma billardierei* and *Bazzania novae-zealandiae* with smaller amounts of *Lepidozia pendulina, L. concinna* and *Achrophyllum quadrifarium*. Group E (Site 4A) quadrats are dominated by *Tylimanthus saccatus, Schistochila nobilis* and *Schistochila appendiculata* with significant numbers of *Ptychomnian aciculare, Trichocolea mollissima* and *Bazzania novae-zelandiae*. Minor species include *Hypnodendron comosum, Achrophyllum quadrifarium, Plagiochila suborbiculata* and *Chiloscyphyus billardierei*. Group F (Sites 6B and 6D) quadrats are dominated by *Dicranoloma billardierei* with lesser amounts of *Riccardia marginata, Campylopus introflexus* and *Kurzia calcarata*. Similarly, quadrats of Groups G (Sites 6A and 8) and H (10A) are dominated by *Dicranoloma billardierei* with Group G distinguished by the presence of *Bazzania novae-zelandiae* and especially *Acromastigum anisostomum*. Minor species here include *Campylopus introflexus, Chiloscyphus billardierei, Lepidozia pendulina* and *Tetracymbaliella decipiens* in Group G quadrats with *Campylopus introflexus, Lepidozia concinna* and *Sphagnum cristatum* in Group H quadrats.

The results of the Detrended Correspondence Analyses for the ground bryophytes are given in Fig. 2 (quadrats) and Fig. 3 (species). Axis 2 is not displayed. It shows that the sole record on the terrace sequence of *Riccardia alcicornis* in one of the 6D quadrats is markedly different from the pattern of the remaining species on the terrace sequence. These ordinations generally confirm the relationships between species and sample sites recognised by the Cluster Analysis (Fig. 1). Axis 1 is readily interpretable in terms of altitude. The upper terraces (6 to 10) are described by intermediate to high values of this Axis, and the sample sites from the lower terraces (2 to 4) are described by lower values of this Axis. The sample sites do not form a strict sequence from lowest to highest elevations, but rather show associations between sites, defined from species composition, that reflects habitat differences between them. Thus, the open bog sites (6B, 6D, 10A and 10B) are represented by the higher values of Axis one, while the more densely wooded upper sites (6A, 8, 7, 9, 10C, 6C) occupy that area of the ordination characterised by intermediate values of Axis 1. As a result, they are more closely associated with the tall lowland forest than are the more open sites. Site associations identified by the Cluster Analysis are recognisable in Fig. 2, and a comparison of the Detrended Correspondence Analyses reveals site-species associations that are similar to those generated by the Cluster Analysis (Fig. 1). The variation within the sites described by Axis 3 is not readily

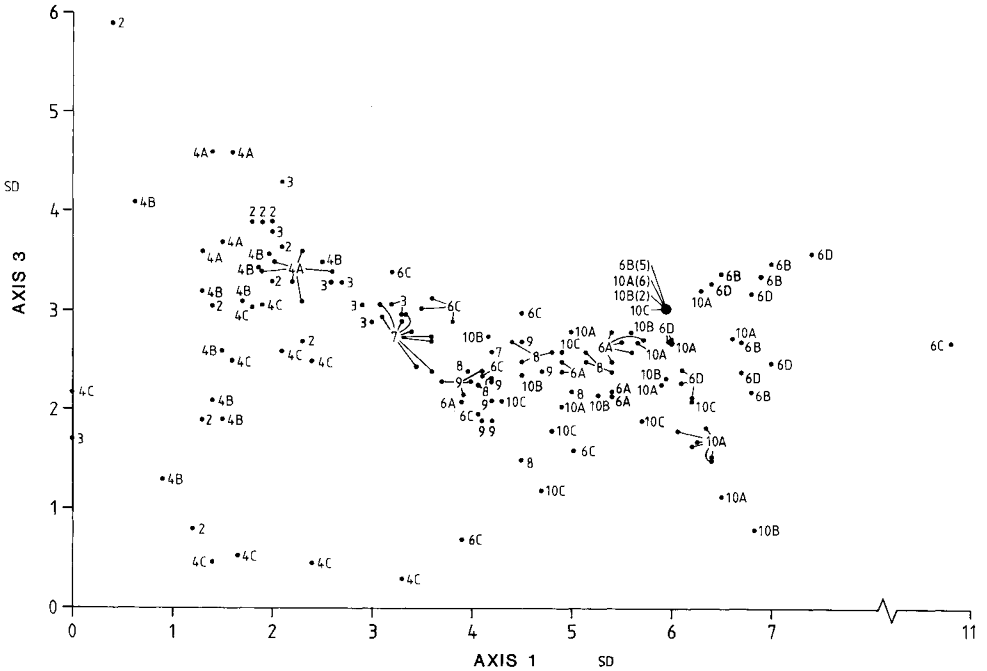


Fig. 2—Two-dimensional ordination of 157 quadrats from 15 sites (Site 1 excluded) on the Waitutu marine terrace sequence, based on a Detrended Correspondence Analysis of local frequency data of ground bryophytes.

interpretable, but is likely to be related to micro-environmental factors influencing the distribution of species within the sample sites.

Epiphytes

Fig. 4 shows the results of the Cluster Analysis for the epiphytic species. Seven species groups are distributed according to their phorophyte groupings, while the largest, Group 5, contains species of lesser and minor importance. The dendrogram of dissimilarities shows this group to be more similar to Species Groups 6, 7 and 8 than to the others.

The dendrogram of dissimilarities for the phorophytes shows them to be broadly divided into low (D, E, F, G, H) and higher altitude sites (A, B, C) with only one high site (6C phorophyte 1) among the low site groups and no low sites in the high site groups.

Group C, although in the high site group on the dendrogram of phorophytes, includes many species from both the groups associated with the upper sites (Species Groups 1, 2, 3, 4) and from those associated with the lower sites (Species Groups 6, 7, 8).

By recognising on the dendrogram where a majority of the phorophytes were recorded in one group, the relationship between the phorophyte-species groups and the sample sites can be seen. Eight of the 15 sites are associated with a phorophyte group. These are Sites 10B-6A-6C in Group B, Site 9 in Group C, Site 4C in Group D, Site 3 in Group F, Site 4A in Group G and Site 2 in Group H.

Separation of the different sample sites is not shown well by these data, especially among the upper sites; neither are the species groups associated with particular sites. However the changes in distribution of species over the altitudinal range do emerge. The dominant high altitude epiphytes are *Herberta alpina, Lepicolea scolopendra* and *Plagiochila circinalis; Macromitrium longipes* and *Holomitrium perichaetiale* are abundant to frequent; and *Dicnemon calycinum, Dicranoloma billardierei, Lepidozia concinna, Plagiochila gregaria, Wijkia extenuata, Paraschistochila tuloides* and *Bazzania novae-zelandiae* are occasional species. Dominant at the lower forest sites are *Ptychomnion aciculare, Weymouthia mollis, Plagiochila fasciculata* and

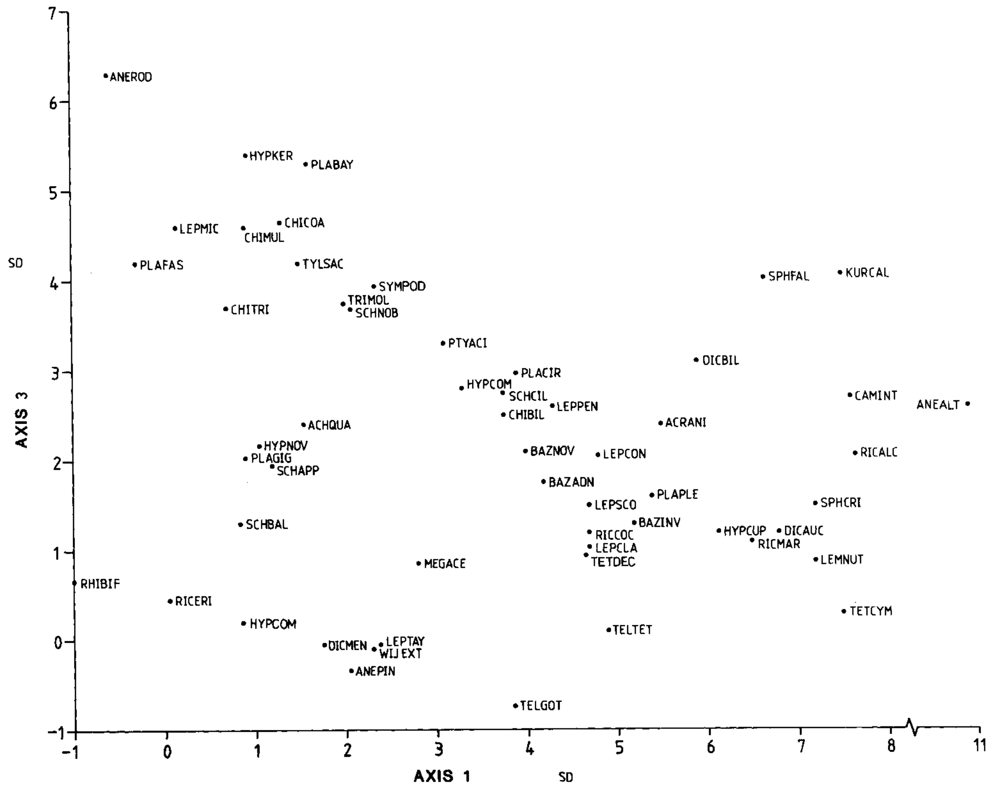
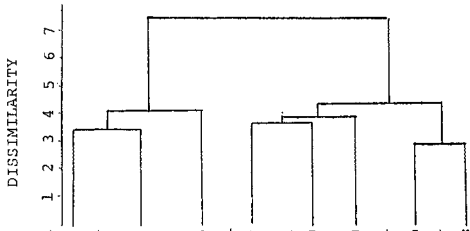


Fig. 3—Two-dimensional ordination of the 57 ground species of bryophytes recorded from 157 quadrats at 15 sites (Site 1 excluded) on the Waitutu marine terrace sequence, based on a Detrended Correspondence Analysis of local frequency data. Species names are abbreviated to the first three letters of the genus and species (complete names are given in the floristic list (Table 4)).

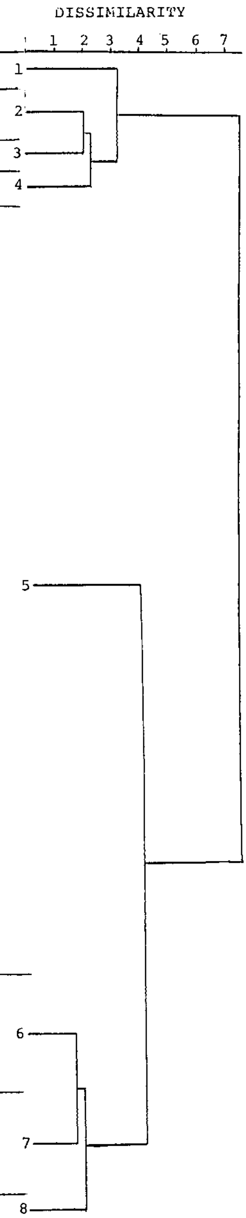
Trichocolea mollissima, with *Leucobryum candidum, Schistochila nobilis, Mastigophora flagellifera, Dicranoloma billardierei, Aneura pinnatifida, Plagiochila strombifolia, P. annotina, P. lyallii, Chiloscyphus sinuosus, Dicranum trichopodum, Bazzania adnexa* and *B. novae-zelandiae* being less important. Species recorded widely over the altitudinal range include *Dicranoloma billardierei, Radula physoloba, Bazzania involuta, Zygodon intermedius, Plagiochilion conjugatus, Ptychomnion aciculare, Chiloscyphus sinuosus* and *Bazzania novae-zelandiae*.

The results of the Detrended Correspondence Analyses for the epiphytic species are given in Figs. 5 and 6. Fig. 5 shows that the distribution of the sites on the axes is generally related to their elevation, and that these analyses reflect the distinctions shown by the Cluster Analysis of the epiphytes (Fig.4). The lowland forest sites (2-4) are well spread out over that area of the diagram described by higher values of Axis 1 and a range of Axis 2 values. In contrast the higher altitude sites (6-10) are generally described by lower values of Axis 1 and intermediate values of Axis 2 with three phorophytes, 7, 6C and 2, having lower values of Axis 2. As a result, they are not as well separated as the lower

Fig. 4—Two-way nodal table showing the eight groups of epiphytic bryophyte species (1 to 8) and eight community groups (A to H) together with their dissimilarity values based on Cluster Analysis, respectively, among the 33 phorophytes (10A1-23 as shown) and the 63 epiphytic species included in the analysis. Values are means of species occurrences (as % cover) within the phorophyte groups. + = present in that group with a mean % cover of < 1. Values in brackets refer to the number of phorophytes from a particular site in each phorophyte group. Total number of phorophytes at each site were as follows: 2 (3), 3 (3), 4A (2), 4B (2), 4C (2), 6A (2), 6B (0), 6C (3), 6D (2), 7 (2), 8 (2), 9 (3), 10A (2), 10B (4), 10C (2). (See text for details of analysis.)



	A	B	C	D	E	F	G	H
	10A 8 6C	10A 7 10B(4) 8 10C(2) 9	9(2) 7 6C	6C 4B 4C(2) 2	4B	3(3)	4A(2)	2(2)
Herberta alpina	11.7	9.6	5.0					
Macromitrium longipes	2.0	+	+					
Holomitrium perichaetiale	2.0	+		+			+	
Lepicolea scolopendra		+	1.2	2.0				
Plagiochila circinalis	3.3	+	6.2					
Isopterygium pulchellum	1.7							
Plagiochila radiculosa	1.7							
Hypnodendron comosum	+		+	+				
Hypnodendron kerrii			+	+				
Schistochila appendiculata				+			+	
Lepidozia microphylla				+				
Dicnemon calycinum		+						
Radula physoloba	+	+					+	
Lepidozia laevifolia			+					
Lophocolea semiteres		+						
Plagiochila fruticosa	+							
Telaranea herzogii				+				
Achrophyllum dentatum						+		
Acrocladium cuspidatum		+						
Ditrichum brevirostre		+						
Acromastigum anisostomum	+		+					
Schlotheimia cf. campbelliana	+							+
Plagiochila pleurata								+
Dicnemon semicryptum	+							
Leucobryum candidum						+		
Schistochila nobilis				+			+	
Hypopterygium novae-seelandiae							+	+
Achrophyllum quadrifarium							+	
Weymouthia cochlearifolia							+	
Plagiochila suborbiculata						+	+	
Hypnum cupressiforme				+		+		
Dicranoloma menziesii					+			
Dicranoloma cylindropyxis					+			
Glyphothecium sciuroides					+	+		
Lepidolaena taylorii				+	+			
Mastigophora flagellifera				+	1.0			
Lepidozia glaucophylla					1.0			
Dicranoloma billardierei	1.0	+	+	+	5.0	1.7		
Aneura pinnatifida	1.7		+	+				
Plagiochila gregaria		+	+					
Bazzania involuta		+	+		1			
Lepidozia concinna	+	+	+					
Plagiochila strombifolia		+		+		+		
Zygodon intermedius		+	1.2	+	+	+		
Plagiochilion conjugatus		+	+	+	+			
Chiloscyphus normalis		+	+			+		
Schistochila ciliata		+						
Wijkia extenuata	+		+					
Chiloscyphus billardierei		+	+		+			
Paraschistochila tuloides		+	+	+				
Plagiochila fasciculata		+	+	+			22.5	3.0
Lepidolaena clavigera	+					1.7		7.5
Trichocolea mollissima				+			1.0	1.0
Tylimanthus saccatus							+	3.0
Plagiochila lyallii								3.0
Plagiochila annotina				9				2.5
Ptychomnion aciculare		+	+	+	1.0	3.3	1.0	1.0
Weymouthia mollis				+	1.0	1.0	1.0	1.0
Chiloscyphus sinuosus	+		+			2.0		
Dicranum trichopodum						5.0		+
Bazzania adnexa			1.7			1.0	+	+
Bazzania novae-zealandiae	+		1.8	2.2		1.7	7.5	5.0



sites, a feature shown also by the Cluster Analysis (Fig. 4). Amongst the lower terraces individual sample sites are more distinctive, e.g. on Terraces 2, 3 and to a lesser extent on Terrace 4. Some of the phorophytes show close association with those from other terraces (e.g. 6C phorophytes) with the exception perhaps of Site 4A. These distinctions also confirm the results of the Cluster Analysis (Fig. 4).

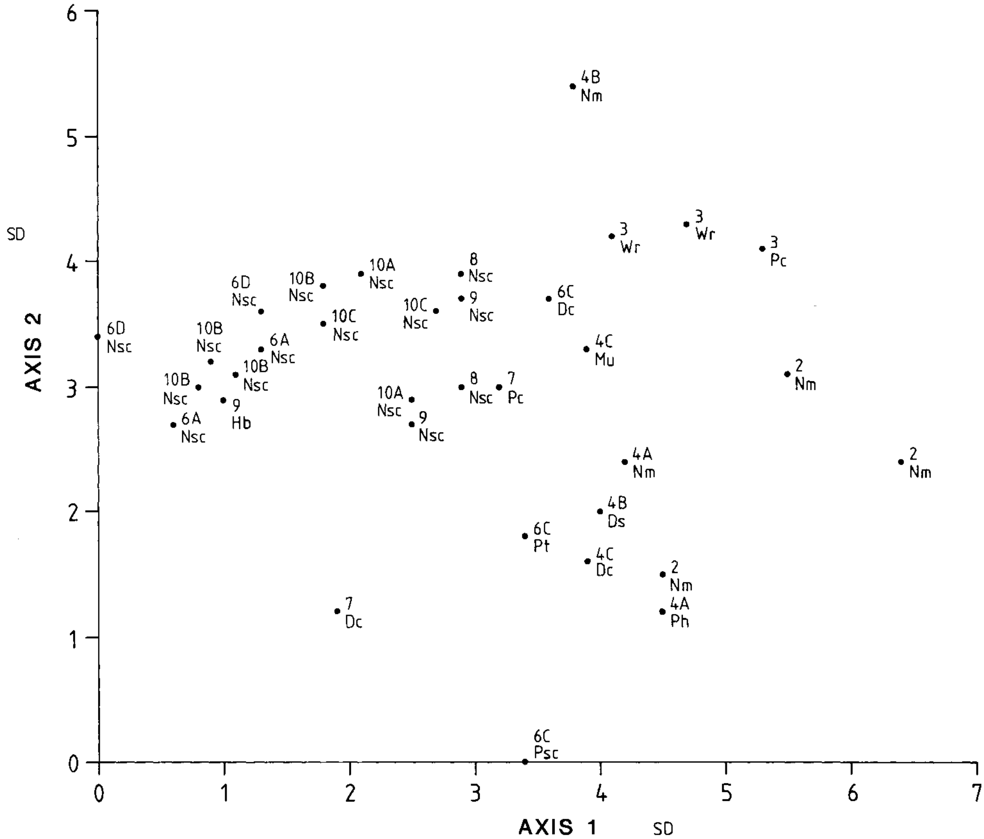
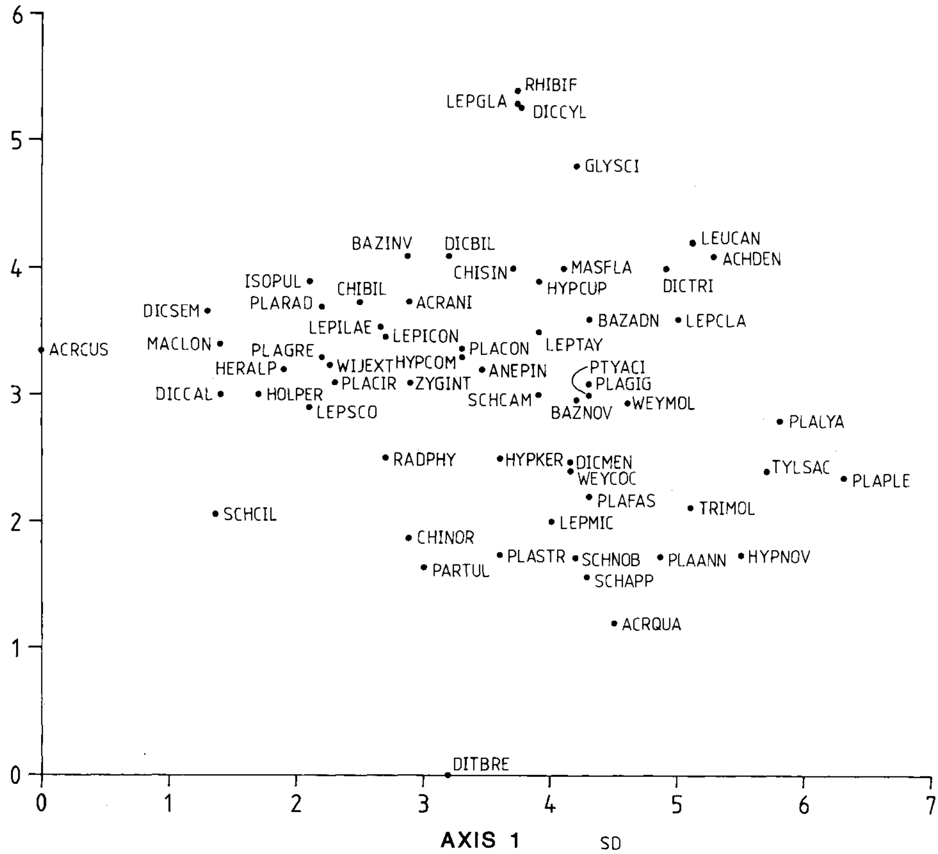


Fig. 5—Two-dimensional ordination of 33 phorophytes from 15 sites (Site 1 excluded) on the Waitutu marine terrace sequence, based on a Detrended Correspondence Analysis of estimated cover data of bryophytes.
P.f. = *Prumnopitys ferruginea*; N.m. = *Nothofagus menziesii*; M.u. = *Metrosideros umbellata*; W.r. = *Weinmannia racemosa*; D.s. = *Dicksonia squarrosa*; P.h. = *Podocarpus hallii*; Ps.c. = *Pseudopanax crassifolius*; N.c. = *Nothofagus solandri* var. *cliffortioides*; H.b. = *Halocarpus biformis*; D.c. = *Dacrydium cupressinum*.

As the phorophytes sampled were not all of the same species, their names were attached to the ordination diagram (Fig. 5) to determine whether this factor explained some of the observed variation. *Nothofagus solandri* var. *cliffortioides* tends to fall in the middle left of the ordination diagram, with only *Halocarpus biformis* associated with it. *Nothofagus menziesii* falls to the right of the diagram but its distribution is rather scattered and is interspersed with several other species, notably *Dacrydium cupressinum, Podocarpus hallii* and *Weinmannia racemosa*. The similarities of the two quadrat ordinations (Figs. 2 and 5), in terms of the general distinctions between the sample site groups, indicate that the positions of the phorophytes on the ordination diagram (Fig. 5) are largely a function of the site's altitude to the extent that any possible phorophyte effect is obscured.

The results of the Detrended Correspondence Analysis of species for the epiphytic bryophytes are shown in Fig. 6. This ordination, when compared with the Detrended Correspondence Analysis of quadrats, yields species-phorophyte associations in agreement



g. 6—Two-dimensional ordination of the 63 epiphytic bryophyte species recorded from 33 ıorophytes at 15 sites (Site 1 excluded) on the Waitutu marine terrace sequence, based on a ɜtrended Correspondence Analysis of estimated cover data. Species names are abbreviated ɔmplete names are given in the floristic list (Table 4)).

ith the Cluster Analysis (Fig. 4). It also shows that the widely dispersed phorophytes ne from each of Sites 4B, 6C and 6D) are separated on the presence or absence of rtain species of minor importance, e.g. *Rhizogonium bifarium, Lepidozia glaucophylla, icranoloma cylindopyxis* and *Glyphothecium sciuroides* (Site 4B), *Ditrichum brevirostre* (Site 6B) ıd *Acrocladium cuspidatum* (Site 6D).

The present coastal terrace (Terrace 1) was not quantitatively sampled. Few bryophytes ɜre observed growing on the coastal turf. *Marchantia berteroana* had an estimated cover 8-10%, and *Bryum laevigatum* was found in scattered clumps of negligible total cover.

Epiphytes were collected from the few logs and tree stumps present. Species collected ɜre: *Bryum billardierei, Holomitrium perichaetiale, Hypnum cuppressiforme, Lepidolaena clavigera, ıphocolea lenta, Bazzania adnexa, Schlotheimia c.f. campbelliana, Macromitrium gracile, Campylopus ɪroflexus, Ptychomnion aciculare, Cyathophorum bulbosum.*

ISCUSSION

In the analyses of the vascular plants (Mark *et al.*, 1988), four main community groups ɜre recognised: (1) coastal terrace; (2) tall forest on the three terraces below 150m 'erraces 2, 3, 4; Groups H and I); (3) mixed woodland above 250m (Groups C, D, ; (4) more or less open shrubland bog sites of impeded drainage above 250m (Groups and B).

These community groups are also recognisable in the analyses of the bryophytes. Among

Table 1 – Quantitative data on the 22 more important ground species of bryophytes at 15 sites sampled on the Waitutu terrace sequence (coastal Terrace 1 excluded). Data are presented as the average occurrence, in 25 subunits of a 0.5 m square quadrat, at each sample site. The 15 sites are arranged as in Mark *et al.*, (1988).

	SITE NUMBER														
	2	3	4B	4A	4C	7	6C	9	8	6A	10C	10A	6D	6B	10B
Kurzia calcarata	–	–	–	–	–	–	–	–	–	–	–	–	–	4.5	–
Campylopus introflexus	–	–	–	–	–	–	–	–	–	–	–	0.9	7.1	3.2	0.4
Sphagnum cristatum	–	–	–	–	–	–	–	–	–	–	–	1.4	–	2.2	–
Dicranoloma billardierei	–	–	–	0.2	–	1.2	3.6	4.7	8.8	10.1	5.0	11.3	15.0	17.1	9.6
Acromastigum anisostomum	–	–	–	–	–	–	–	0.4	6.5	14.0	–	2.2	–	–	–
Riccardia marginata	–	–	–	–	–	–	0.6	–	1.3	–	2.8	6.9	3.8	–	2.2
Lepidozia concinna	–	–	–	–	–	0.3	0.6	2.2	–	0.8	1.9	0.8	–	–	–
Lepidozia pendulina	–	–	–	–	–	0.8	1.2	0.2	7.1	0.3	–	–	–	–	–
Schistochila ciliata	–	–	–	–	–	3.9	–	–	1.8	–	–	–	–	–	–
Chiloscyphus billardierei	–	–	–	–	1.4	4.8	0.4	0.8	2.9	–	–	–	–	–	–
Bazzania novae-zelandiae	0.4	0.3	1.5	3.2	4.1	13.5	4.4	19.5	12.7	2.7	7.2	0.6	–	–	1.2
Hypnodendron comosum	1.2	8.3	–	0.3	–	2.1	1.0	3.3	–	–	–	–	–	–	2.2
Ptychomnion aciculare	1.6	5.7	3.6	3.7	1.6	8.8	7.4	1.2	0.8	–	–	–	–	–	–
Schistochila nobilis	–	–	9.6	3.9	2.9	–	4.7	–	–	–	–	–	–	–	–
Achrophyllum quadrifarium	0.1	0.7	4.7	0.9	0.7	0.1	–	–	–	–	–	–	–	–	–
Trichocolea mollissima	5.4	1.9	4.7	3.2	2.6	5.6	–	–	0.1	–	–	–	–	–	–
Tylimanthus saccatus	4.5	–	5.5	13.5	8.1	–	–	–	–	–	–	–	–	–	–
Schistochila appendiculata	1.5	–	4.8	2.4	13.1	–	–	–	–	–	–	–	–	–	–
Plagiochila suborbiculata	1.6	–	5.0	0.6	0.8	–	–	–	–	–	–	–	–	–	–
Hypnodendron kerrii	0.9	0.3	0.3	5.1	0.3	–	–	–	–	–	–	–	–	–	–
Hypopterygium setigerum	0.4	–	2.1	–	1.7	–	–	–	–	–	–	–	–	–	–
Hypopterygium novae-seelandia	0.6	–	0.4	–	0.1	–	–	–	–	–	–	–	–	–	–

the ground species (Cluster Analysis, Fig. 1), the distinct Groups F, G, H are recognised as containing the more open bog/shrubland sites (Groups F and H) while Group G contains sites from the mixed woodland community. The remaining groups can be recognised as relatively tall lowland forest (Groups C, D, E) and mixed woodland (Group A). Group B contains a mixture of both lowland forest and mixed woodland quadrats.

The distribution of the ground bryophytes is well correlated with the vascular plant communities (Table 1); some species are restricted to, or closely associated with, particular vascular plant communities. Characteristic of the permanantly wet open sites are *Sphagnum cristatum, Kurzia calcarata, Campylopus introflexus* and *Dicranoloma billardierei. D. billardierei* also extends significantly on to the better drained sites on the upper terraces (Sites 10A, 10C, 6A, 8) where there is an increase in cover, height and diversity of the woody species (Mark *et al.*, 1988). Other bryophytes living on these sites are *Acromastigum anisostomum, Riccardia marginata, Lepidozia concinna* and *Bazzania novae-zelandiae*. All these species extend into another community group characterised by the absence of typical bog vascular species and an increase in vegetation height, tree density and canopy cover associated with improved drainage (Terrace 9) and decreasing altitutde (Terrace Site 6C, Terrace 7). *Bazzania novae-zelandiae* is found throughout the terrace sequence, but is notably absent from very open bog sites (6B and 6D), though well represented in the mixed woodland sites. Also living here are *Lepidozia pendulina, Chiloscyphus billardierei, Schistochila ciliata, Hypnodendron comosum, Ptychomnion aciculare* and *Trichocolea mollissima*. These last two species are here represented at the upper limit of their distribution on the terrace sequence while they also extend down to the lower altitude forest (Terraces 2, 3, 4) where they are conspicuous components of the bryophyte cover. Also notable in the lowland forest are the umbrella mosses *Hypopterygium commutatum* and *Hypnodendron kerrii*, together with the robust liverwort *Schistochila appendiculata* in association with *S. nobilis, Tylimanthus saccatus, Plagiochila suborbiculata, Achrophyllum quadrifarium* and *Hypopterygium novae-seelandia*. Several of the latter species are restricted to the lower terraces.

Table 2 shows the performance of the epiphytic bryophytes over the terrace sequence, with the sites arranged to show the relationships with the vascular plant communities. In comparison with the ground bryophytes, the epiphytes do not show distinctions between the recognised vascular plant communities. While the individual performances of the epiphytic species show the general effect of altitude (i.e. broad separation of the lowland species from those of the upper terraces—6-10), the higher altitude species are not readily identifiable with the vascular plant communities. As a result, this table is largely a reiteration of the altitudinal distributions for the epiphytic species, already discussed.

The distribution pattern of bryophytes on the terrace sequence is reinforced by their diversity in relation to the vascular plant communities. Table 3 shows that bryophyte diversity (as species number) is well correlated with the vascular plant communities and is related to the nature of the vegetative cover, as described by Mark *et al.* (1988). In the open bog sites with permanent water (Sites 6B, 6D, 10B) bryophyte diversity is low (e.g., only 5 at Site 6B with no epiphytes); it increases at the sites of improved drainage (8, 6A, 10C, 10A), although the number of vascular plant species is not significantly different. With the further improvement in drainage (Sites 7, 6C, 9) and decrease in altitude there is a further increase in the number of bryophyte species, culminating in the tall lowland forest (Sites 2, 3, 4). The coastal turf (Terrace 1), however, has a low bryophyte species diversity, similar to that of the upper, more open bog sites.

Bryophyte species number on the terrace sequence increases with decreasing altitude and with improved drainage. Both altitude and drainage are associated with increases in complexity of the vascular plant community (reflected by increased height, canopy cover and tree basal area) and, on the upper terraces, with a decreasing herb layer of vascular plants. At the open wetland sites the herb layer of vascular plants is well developed, and it persists on to the sites of increased drainage; but with further improvement in drainage and some decrease in altitude the herb layer disappears (e.g. Sites 6C, 7, 9). It should be noted, however, that epiphytic bryophyte species also increase in number with decreasing herbaceous cover, emphasising the predominant effect of increasing canopy height and canopy cover in influencing bryophyte diversity. In the

Table 2 – Quantitative data on the 25 more important epiphytic species of bryophytes at 15 sites sampled on the Waitutu terrace sequence (coastal Terrace 1 excluded). Data are presented as the average percent cover estimated at each sample site. The 15 sites are arranged as in Mark *et al.*, (1988).

	SITE NUMBER														
	2	3	4B	4A	4C	7	6C	9	8	6A	10C	10A	6D	6B	10B
Herberta alpina	–	–	–	–	–	5.0	–	11.6	10.0	10.0	18.3	15.0	2.5	–	15.0
Plagiochila circinalis	–	–	–	–	–	2.5	1.6	1.6	5.0	2.5	13.3	–	5.0	–	1.3
Lepicolea scolopendra	–	–	–	–	7.5	–	5.0	6.6	–	2.5	3.3	–	2.5	–	2.5
Holomitrium perichaetiale	–	–	–	2.5	–	–	–	–	–	–	–	2.5	5.0	–	2.5
Macromitrium longipes	–	–	–	–	–	–	–	1.6	–	–	–	1.6	5.0	–	–
Chiloscyphus normalis	–	–	–	–	–	7.5	–	–	–	–	–	–	–	–	–
Ptychomnion aciculare	–	–	–	–	2.5	–	–	–	1.0	1.0	–	–	–	–	–
Lepidozia concinna	–	–	–	–	–	–	–	–	–	–	6.6	–	–	–	–
Schistochila ciliata	–	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–
Zygodon intermedius	–	–	–	–	–	7.5	1.6	–	–	–	1.6	1.6	–	–	–
Plagiochla fasciculata	2.5	–	–	25.0	–	–	–	–	–	–	–	2.5	–	–	–
Bazzania novae-zelandiae	5.0	1.6	–	13.2	2.5	–	6.6	1.6	–	–	3.3	–	–	–	–
Dicranoloma billardierei	–	13.3	7.5	–	–	–	1.6	–	2.5	–	13.3	2.5	–	–	–
Chiloscyphus billardierei	–	–	–	–	–	–	–	–	–	1.0	–	–	–	–	–
Bazzania involuta	–	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–
Plagiochilion conjugatus	–	–	–	–	2.5	2.5	–	–	–	–	–	–	–	–	–
Paraschistochila tuloides	–	–	–	–	–	2.5	1.6	–	–	–	–	–	–	–	–
Lepidolaena clavigera	5.0	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–
Bazzania adnexa	–	1.0	–	–	–	–	1.6	–	–	–	–	–	–	–	–
Plagiochila strombifolia	–	2.5	2.5	–	1.6	–	10	–	–	–	–	–	–	–	–
Weymouthia mollis	5.0	5.0	5.0	5.0	5.0	–	–	–	–	–	–	–	–	–	–
Trichocolea mollissima	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	–
Tylimanthus saccatus	5.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dicranum trichopodum	–	5.0	–	–	–	–	–	–	–	–	–	–	–	–	–
Plagiochila lyallii	2.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 3 — Number of bryophyte species recorded at each terrace sample site. Sites are ordered, as in Mark *et al.* (1988) to show the relationship between bryophyte number and the vascular plant communities.

Vascular Plant Community	Coastal Turf	Tall Lowland Forest					Mixed Woodland above 250 m							Open Bog		
Sample Site No	1	2	3	4B	4A	4C	7	6C	9	8	6A	10C	10A	6D	6B	10B
Moss species	9	9	13	13	12	11	9	6	10	7	5	2	10	8	3	6
Hepatic species	5	20	9	20	13	19	19	16	18	14	11	13	14	8	2	11
Total Bryophyte species	14	31	22	33	25	30	28	22	28	21	16	15	24	16	5	17
Hepatic/Moss ratio	0.55			1.40						2.10					1.24	

Table 4 — Floristic list of bryophytes recorded from 16 sites on nine marine terraces (numbers 1-4 and 6-10) in the Waitutu Ecological District (see Mark *et al.*, 1988, Fig. 1 for approximate locations). X = recorded from that site quantitatively. + = recorded from that site but not included in analyses.

Terrace site number	OTA No.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
MUSCI																	
Sphagnales																	
Sphagnaceae																	
Sphagnum cristatum Hamp.	042714				+			+	X						X	+	
S. falcatulum Besch.	042692															X	
Bryales																	
Amblystegiaceae																	
Acrocladium cuspidatum (Hedw.) Lindb.											X						
Bartramiaceae																	
Breutelia elongata (Hook.f.& Wils.) Mitt.	042700												+				
Bryaceae																	
Bryum billardierei Schwaegr.		+															
B. laevigatum Hook.f.& Wils.	042715	+															
Dicnemonaceae																	
Dicnemon calycinum (Hook.) Schwaegr.	042515							X						X	X		

(continued)

Table 4 continued.

Terrace site number	OTA No.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
D. semicryptum (C.Muell.) Hedw.	042728										X						
Dicranaceae																	
Campylopus introflexus (Hedw.) Brid.	042729	+							X		X				X	X	
Dicranoloma billardierei (Brid.) Par.	041282			X		X		X	X	X	X	X	X	X	X	X	X
D. cylindropyxis Dix.	042566				+	X											
D. menziesii (Tayl.) Par.	042730				X		X					X	X				
Dicranum aucklandicum Dix.	042731														X		
D. trichopodum Mitt.			X	X			+							+			
Holomitrium perichaetiale (Hook.) Brid.	042178	+			X			X		X	X	X		X	X	X	
Leucobryum candidum (P. Beauv.) Wils.	024733			X													
Ditrichaceae																	
Ditrichum brevirostre (R.Br.ter.) Broth	042734									X							
Hookeriaceae																	
Achrophyllum dentatum (Hook.f.& W.) Vitt & Crosby	042735			X													
A.quadrifarium (Hook.) Vitt & Crosby	042736		X	X	X	X	X					X					
Hypnaceae																	
Hypnum cupressiforme Hedw.	042518	+			X	X									X		
Hypnodendraceae																	
Hypnodendron comosum (Labill.) Mitt.	042183		X	X	X	X	+			X		X		X	X	X	
H. kerrii (Mitt.) Par.	042737		X	X	X	X	X					X		X			
Hypopterygiaceae																	
Cyathophorum bulbosum (Hedw.) C. Muell	042738		+														
Hypopterygium novae-seelandiae C. Muell	042739		X		X	X	X										
H. novae-seelandiae var. *glaucum* (Sull.) Dix.	042739					+											
H. commutatum C. Muell.	042690		X			X	X										
Meteoraceae																	
Weymouthia cochlearifolia (Schwaegr.) Dix.	042749				X												
W. mollis (Hedw.) Broth	042741		X	X	X	X	X										

(continued)

Table 4 continued.

Terrace site number	OTA No.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
Orthotrichaceae																	
Macromitrium gracile (Hook.) Schwaegr.	042179	+		+								+					
M. longipes (Hook.) Schwaegr.	042180							X			X		X	X	X		
Schlotheimia c.f. *campbelliana* C.Muell.	042184	+	X								X	+					
Zygodon intermedius B.S.G.	042181			X						X		X	X	X			X
Plagiotheciaceae																	
Isopterygium pulchellum (Hedw.) Jaeg.	042712														X		
Ptychomniaceae																	
Cladomnion ericoides (Hook.) Hook.f.& W.	042742						+										
Glyphothecium sciuroides (Hook.) Hampe.	042743			X		X											
Ptychomnion aciculare (Brid.) Mitt.	042501	+	X	X	X	X	X			X		X	X	X			
Rhizogoniaceae																	
Rhizogonium bifarium (Hook.) Schimp.	042744			X		X											
Sematophyllaceae																	
Wijkia extenuata (Brid.) Crum	042701						X				X	X		X			
HEPATICAE																	
Jungermanniales																	
Acrobolbaceae																	
Tylimanthus saccatus (Hook.) Mitt.	042745		X		X	X	X										
Geocalycaceae																	
Chiloscyphus billardierei (Schwaegr.) Nees	042524						X			X		X	X	X			
C. coalitus (Hook.) Nees	042746		X														
C. multispinus Hodgs. & Allis.	042589		X		X	X											
C. normalis (Steph.) Hodgs.	042544										X	X		X			
C. sinuosus (Hook.) Nees	042747			X									X	X			X
C. tricanthus (Hook.f. & Tayl.) Steph.	042748		X														

(continued)

Table 4 continued.

Terrace site number	OTA No.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
Lophocolea lenta (Hook.f. & Tayl.) Tayl.		+															
L. semiteres (Lehm.) Mitt.	042750															+	
Tetracymbaliella cymbalifera (Hook.f.& Tayl.) Grolle	042520															X	
T. decipiens (Gott.) Grolle	042582				X		X	X									
Herbertaceae																	
Herberta alpina (Steph.) Hodgs.	042522							X			X	X	X	X	X	X	X
Jubulaceae																	
Radula physoloba Mont.	042708				X			X						X	X		
Jungermanniaceae																	
Anastrophyllum schismoides (Mont.) Steph.	042521							+						+			
Lepicoleaceae																	
Lepicolea scolopendra (Hook.) Dum. ex Trev.	042695						X	X		X	X	X		X	X	X	X
Lepidolaenaceae																	
Lepidolaena clavigera (Hook.) Dum. ex Trev.	042751	+	X	X								+			X		X
L. taylorii (Gott.) Trev.	042523					X	X										
Lepidoziaceae																	
Acromastigum anisostomum (Lehm. & Lindenb.) Evans	042516							X					X	X	X		X
Bazzania adnexa (Lehm. & Lindenb.) Trev.	042581	+	X	X	X			X		X		X					
B. involuta (Mont.) Trev.	042519					X				X				X	X	X	X
B. novae-zelandiae (Mitt.) Besch. & Massal.	042524		X	X	X	X	X	X	X	X		X	X	X	X	X	X
B. tayloriana (Mitt.) O. Kuntze	042527						+										
Kurzia calcarata (Steph.) Grolle	042585								X								
Lembidium nutans (Hook.f. & Tayl.) Mitt.	042752																X
Lepidozia concinna Col.	042697									X		X	X	X	X	X	X
L. glaucophylla (Hook.f. & Tayl.) Tayl.	042753					X											

(continued)

Table 4 continued.

Terrace site number	OTA No.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
L. laevifolia (Hook.f. & Tayl.) Tayl.	042754													+			X
L. microphylla (Hook.) Lindenb.	042586				X	X											
L. pendulina (Hook.) Lindenb.	042583							X		X		X	X	X			
Telaranea gottscheana (Lindenb.) Hodgs.	042504									X							
T. herzogii (Hodgs.) Hodgs.						+											
T. tetradactyla (Hook.f. & Tayl.) Hodgs.	042693						X									X	
Zoopsis leitgebiana (Carrington. & Pears.) Bast.	042519											+					
Plagiochilaceae																	
Plagiochila annotina (Menzies) Lindenb.	042756		X				X										
P. banksiana Gott.	042757			+			+					+					
P. baylisii Inoue & Schust.	042758			X													
P. circinalis (Lehm. & Lindenb.) Lehm. & Lindenb.	042503		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X•
P. fasciculata Lindenb.	042706		X		X	X				X		X			X		
P. fruticella (Hook.f. & Tayl.) Hook.f. & Tayl.	042759												+				
P. gregaria (Hook.f. & Tayl.) Hook.f. & Tayl.	042696														X	X	X
P. lyallii Mitt.	042725		X														
P. pleurata (Tayl.) Hook.f. & Tayl.	042761		X														
P. radiculosa Mitt.	042762														X		
P. strombifolia Tayl.	042763			X	X		X				X						
P. suborbiculata Col.	042764		X	X	X	X	X										
Plagiochilion conjugatus (Hook.) Schust.	042765	+				X	X					X	X	X			
Porellaceae																	
Porella elegantula (Mont.) Hodgs.	042766											+					
Ptilidiaceae																	
Mastigophora flagellifera (Hook.) Steph.	042767			X		X											
Schistochilaceae																	
Paraschistochila tuloides (Hook.f. & Tayl.) Schust	042544		X							X		X	X	X			

(continued)

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Table 4 continued.

Terrace site number	OTA No.	1	2	3	4A	4B	4C	6A	6B	6C	6D	7	8	9	10A	10B	10C
Schistochila appendiculata (Hook.) Dum. ex Trev.	042768		X		X	X	X										
S. balfouriana (Hook.f. & Tayl.) Steph.	042691		X				X										
S. ciliata (Mitt.) Steph.	042699						+	X				X	+				
S. nobilis (Hook.) Trev.	042501				X	X	X			X		+					
Trichocoleaceae																	
Trichocolea mollissima (Hook.f. & Tayl.) Gott.	042524		X		X	X	X					X	X				
Metzgeriales																	
Aneuraceae																	
Aneura alternilobata var. *alternilobata* (Hook.f. Tayl.) Hewson	042502									X	X						
A. pinnatifida (Nees) Nees	042769		X							X							
A. rodwayi Hewson	042770		X														
Riccardia alcicornis (Hook.f. & Tayl.) Trev.	042569										X						
R. cochleata (Hook.f. & Tayl.) O. Kuntze	042528												X	X	X		X
R. eriocaula (Hook.) Besch. & Massal.	042771					X											
R. marginata (Col.) Pears.	042568									X	X		X	X	X	X	X
Hymenophytaceae																	
Symphyogyna podophylla (Thunb.) Mont. & Nees	042772						X										
Marchantiales																	
Marchantiaceae																	
Marchantia berteroana Lehm. & Lindenb.	042773	+															
Anthocerotales																	
Anthocerotaceae																	
Megaceros sp.	042774					X											

lowland forest, where a herb tier is best developed, bryophyte diversity is high, presumably in response to the associated lower light levels and higher humidity.

On the coastal terrace, terrace 1, the low number of bryophytes is also associated with an extensive vascular plant herb layer. However, the effect of the herb layer is seen as being less important in reducing bryophyte diversity than is the probable effect of high salinity in the exposed coastal habitat.

The findings of this study are in general agreement with those of Scott (1970), who found that the bryophyte communities on Secretary Island in adjacent Fiordland were well correlated with those of the dominant vegetation. He considered this to be a response to the distribution of microenvironments.

In the present study the average number of ground species per quadrat (0.5 m square) is 3.75 from a total of 57 species (Table 4). These figures are similar to those of Scott (average 4.38 species from a total of 55 species) from lowland forest sites. (< 50 m. elevation) on Secretary Island. The slightly lower average for Waitutu probably is due to the presence of open boggy sites of generally low species diversity.

The data used for the computer analyses were not pooled and, as a result, the variation within sample sites is not suppressed. Quadrats and phorophytes are grouped together on species composition (itself determined by a variety of factors) and it is expected that the data should reflect some of this variation. When the data for the sample sites are pooled and related to the recognised vascular plant communities (Figs. 3, 4, 5) close agreement is observed, and much of the variation within sites shown in the computer analyses can be explained in terms of the vascular plant communities.

The hepatic/moss ratio for the total floristic list is 1.7, but Table 3 shows that the ratio varies considerably between the respective communities. The highest value is for the mixed woodland above 250 m (2.1) and the lowest for the coastal turf (0.55). This generally confirms the findings of previous studies. For example, Scott (1970) found a value of 1.7 for Secretary Island while, Scott and Rowley (1975) found a value of 2.2 for the lowland climax forest at Jackson Bay. Similar variation of this ratio between communites over an altitudinal sequence has also been shown for Stewart Island by Scott and Armstrong (1966); the highest values were recorded in the montane *Leptospermum/Dracophyllum* tall scrub at 390 m (2.5/5.25, for ground and epiphytic species respectively) and subalpine *Olearia colensoi* tall scrub at 490 m (3.6/2.2).

CONCLUSIONS

Patterns of quadrat groupings generated by Cluster Analysis are confirmed by Detrended Correspondence Analysis. The observed distribution of bryophytes is closely related to the recognised communities of vascular plants.

Bryophyte diversity (as species number) on the terrace sequence is highest in the tall lowland forest and decreases with increasing altitude and deteriorating drainage at the upper sites, with its associated decreases in plant height, cover and tree basal area, and is lowest at the upper bog sites. Bryophyte diversity is low at the coastal turf due to the exposed coastal habitat.

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