Change in Undisturbed Vegetation on the Coastal Slopes of Subantarctic Macquarie Island, 1980–1995

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Abstract

The vegetation of 30 undisturbed permanent quadrats on the steep coastal slopes of subantarctic Macquarie Island was recorded in 1980–81 and 1994–95, a period in which temperatures rose briefly then declined, precipitation increased and rabbit grazing pressure decreased. Previous investigators of the plant ecology of the island have suggested a successional sequence, in the absence of disturbance, towards total dominance of the two major plant species on the coastal slopes, the tall tussock-forming grass *Poa foliosa* and the megaherb *Stilbocarpa polaris*, with a concomitant reduction in the diversity of subordinate species. Our observations demonstrate a more complex reality. Dense tall tussock grassland became more open, resulting in an increase in quadrat species richness. The more open tussock grassland on the upper slopes became more dense, with a concomitant decrease in quadrat species richness. The large herb *S. polaris* changed little in its abundance over the period, perhaps reflecting a need for disturbance for its expansion. The opening of dense stands of *P. foliosa* may be part of a previously unrecorded endogenous successional process, while the closure of open stands of *Poa* could be a response to improved growth conditions, including relief from rabbit grazing and the relatively high temperatures in the initial years of monitoring, but may also be endogenous in origin.

Introduction

Subantarctic Macquarie Island (54°30′S, 158°56′E) has a cool, moist, and windy climate, and no permanent ice or snow cover due to its position immediately north of the Antarctic Polar Front. The island is an elongated plateau rising to a maximum of 433 m, surrounded by an escarpment, or steep coastal slopes, 100–250 m in height. The main plant communities are feldmark, short grassland, herbfield, mires, and tall tussock grassland (Selkirk et al., 1990).

A substantial increase in air temperatures occurred on Macquarie Island between the late 1940s and the mid 1980s (Fig. 1; Adamson et al., 1988; Tweedie and Bergstrom, 2000), a phenomenon also noted for other subantarctic islands (e.g., Smith and Steenkamp, 1990; Chown and Smith, 1993; Frenot et al., 1997). However, both summer and annual temperatures tended to decrease on Macquarie Island after the mid 1980s high (Fig. 1). Summer temperatures show the same tendencies as annual temperatures, while having a greater variation around the mean (Fig. 1). The annual precipitation recorded for Macquarie Island has steadily increased since the 1970s (Fig. 1). This has also been the case with summer precipitation.

The introduced rabbit, *Oryctolagus cuniculus*, declined in numbers from 150,000 in 1977–78 (Copson et al., 1981) to approximately 50,000 between 1980 and 1984 with an average of between 5000 and 15,000 from 1985 to 1994 (Fig. 2; Copson and Whinam, 2001), as a result of the deliberate introduction of myxomatosis and its regular use in subsequent years to control population numbers.

The impact of these environmental changes on the vegetation of the island seems likely to have varied between vegetation types due to factors such as altitude and rabbit habitat preferences (Copson et al., 1981; Copson, 1984; Scott, 1988). Vegetation change has been documented by Scott (1985, 1995) on land slips of various ages on the steep slopes of the escarpment of the plateau, and by Copson and Whinam (1998) for the mid-altitude plateau, two of the main environments affected by rabbit grazing. Studies have also been conducted along an altitudinal gradient to simulate the effects of climatic warming (Tweedie and Bergstrom, 2000). The control permanent quadrats in the land slip succession studies of Scott (1985, 1995), monitored every few years from 1980 onwards, are used in the present paper to determine vegetation change, relatively independent of the influence of land slips, that took place on the escarpment of the plateau in the period between 1980–81 and 1994–95.

The steep coastal slope vegetation is dominated by either or both of the tall tussock grass *Poa foliosa*, and the large-leaved forb *Stilbocarpa polaris*, with smaller grasses, forbs, and bryophytes as understory (Taylor, 1955; Selkirk et al., 1990; Scott, 1995). Exceptions are recent land slips, rocky outcrops, and areas of short grassland on some slopes. Given that both *Poa foliosa* and *Stilbocarpa polaris* are eaten by rabbits and are capable of forming closed stands, previous investigators have suggested a successional sequence, in the absence of disturbance, towards dominance of these two species, or towards the ultimate dominance of *Poa foliosa* (Taylor, 1955; Ashton, 1965; Copson, 1984; Scott, 1985). The complete dominance of one or both of these species could theoretically be expected to reduce the diversity of subordinate species and thus the species richness of the vegetation at the quadrat scale (Connell, 1978).

The permanent quadrats used in the present study showed no signs of disturbance by rabbits or other agents over the period of monitoring. The research was initiated as a latitudinal study of succession on land slips, with the undisturbed quadrats being controls. There were thus no *a priori* hypotheses on the nature
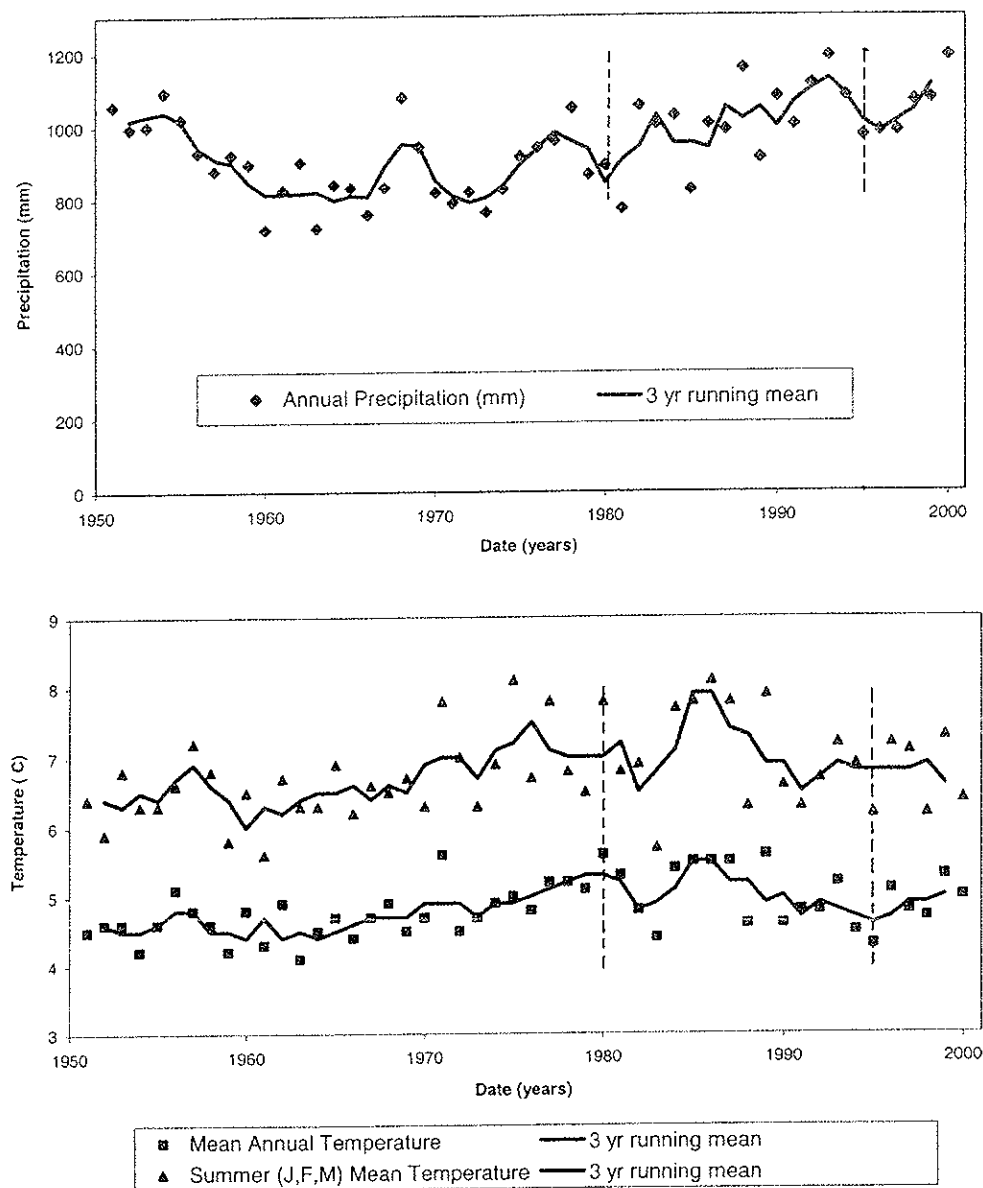
FIGURE 1. Changes in annual precipitation, mean annual temperature, and the mean temperature for January, February, and March for Macquarie Island between 1950 and 2000 (Bureau of Meteorology, unpublished). The two vegetation sampling times are shown as dashed vertical lines.

of expected vegetation change in undisturbed vegetation in the medium term. However, the following a posteriori hypotheses might have been thought appropriate at the time in the context of previous work and ecological theory: directional change in the vegetation over time, increased dominance of Poa foliosa and/or Stilbocarpa polaris, and decreased species richness at the quadrat scale.

Methods

FIELD DATA COLLECTION

In the summer of 1980–81 data from a total of 150, 1 × 1 m quadrats were collected from the undisturbed vegetation adjacent to 50 areas of disturbed vegetation in coastal slope tall tussock grassland. Quadrats were marked with wooden stakes. In the summer of 1994–95 data were collected from a subset of these quadrats. Because time of the year has an influence on the cover of some of the plants in the coastal slope vegetation, the final selection of permanant quadrats for analysis was restricted

to those from which data were recorded in summer (December–February) in both 1980–81 and 1994–95. Permanent quadrats with any signs of rabbit grazing or other disturbance during the time period were excluded. The rabbit signs included scats, burrows and/or obviously grazed plants. Other disturbances included the collapse of Poa peat pedestals and other mass movement. The number of times that quadrats were revisited between 1980–81 and 1994–95 varied, with all being visited several times between the two summers. A total of 30 permanent quadrats were chosen for the ensuing analyses (Fig. 3). The majority are at the southern end of the island, consistent with the relative lack of rabbit grazing disturbance on coastal slopes in the far south compared to elsewhere on the island during the monitoring period (Scott, 1988).

The following data were collected from each quadrat at both times by the one observer. Species abundance was noted using a visually estimated 6-point cover-abundance scale: 1 = <1%; 2 = <5%; 3 = 5–20%; 4 = 20–50%; 5 = 50–75%; 6 = >75%. Species nomenclature of vascular plants follows that of

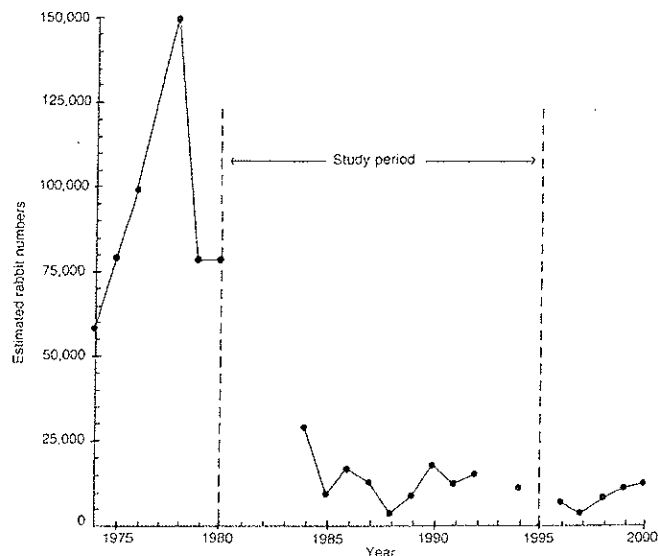J. B. KIRKPATRICK AND J. J. SCOTT / 301

FIGURE 2. Changes in estimated annual rabbit numbers on Macquarie Island 1974–2000 (Copson and Whinam, 2001). The two vegetation sampling times are shown as dashed vertical lines.

Australian Government Publishing Service (AGPS) (1990). Bryophytes were identified to species level where possible (Scott, 1995). Some bryophytes were identified to generic level only (e.g., *Metzgeria* sp.), or grouped as "spp." if there was a possibility of several species being involved (e.g., *Brachythecium* spp.). The listing of *Megaceros* sp. and *Riccardia* sp. as a single entity, "*Megaceros/Riccardia*," is an acknowledgment of inconsistent field identification of these species, which both have similar moist habitats. Only one lichen, the foliose taxon *Peltigera* sp., was recorded. The category "other mosses" included all those mosses which were not identified or were extremely rare.

Mean vegetation height was estimated and placed into the following classes: 1 = 0–5 cm; 2 = 6–10 cm; 3 = 11–30 cm; 4 = 31–70 cm; 5 = 71–100 cm. Cover estimates of bare ground and rock were made using the same 6-point scale as for the floristic data.

Data on altitude, aspect, slope, and peat depth were obtained for each quadrat in 1980–81. Altitude was measured approximately using a Thommen 2000 pocket altimeter-barometer. Aspect and slope were measured using a compass and pocket clinometer respectively. Peat depth, excluding litter, was measured by taking three depth measurements per quadrat with a 1 m peat probe and then calculating the mean. The means were placed in the following classes: 1 = 0–10 cm; 2 = 11–20 cm; 3 = 21–50 cm; 4 = 51–100 cm; 5 = >100 cm.

DATA ANALYSIS

The presence/absence floristic data for the quadrats, comprising both 1980–81 and 1994–95 recordings, were converted to an initial sorted table using the polythetic divisive procedure in TWINSPAN (Hill, 1979). Both the taxa and the quadrats were then resorted by eye, and the resulting rearrangement led to the selection of the four group classification produced by TWINSPAN. Shifts of permanent quadrats from group to group over the monitoring period were recorded.

The floristic abundance data were ordinated using nonmetric multidimensional scaling adopting the default options in DECODA (Minchin, 1991). The direction of movement of perma-
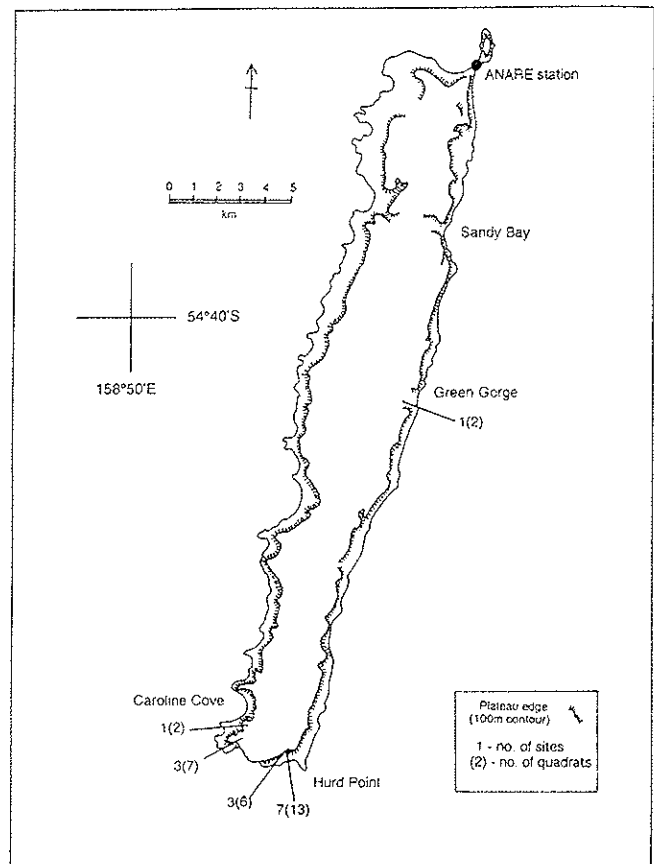

FIGURE 3. Locations of the permanent quadrats on Macquarie Island.

nent quadrats in the ordination space over the measurement period was graphed.

Pearson's product moment correlation coefficient was used to test the significance of linear relationships between environmental and vegetation variables and the abundances of the more frequent taxa. Oneway ANOVA was used to determine the relationships between classificatory groups and environmental and vegetation variables.

Frequency and mean abundance for each species were calculated for the two sets of measurements, and tabulated to show direction of trends in species abundance over the period (increase, decrease, or constant). The number of taxa in each quadrat was counted. This is henceforth called species richness.

Results

VARIATION IN THE VEGETATION

Four classificatory groups were discriminated (Table 1). *Poa foliosa* and the small leafy liverwort *Lophocolea bidentata* were almost ubiquitous (Table 1). *Poa foliosa* increased in dominance through the sequence of communities, apart from Group 2 where *Stilbocarpa polaris* was codominant. Group 1 was the richest in species, and had the second lowest stature (Table 2). The most faithful and constant taxa in this community were *Sanionia uncinata*, *Thuidium furfurosum*, *Breutelia* spp., and *Epilobium pedunculare*, small understory species characteristic of drier short grassland communities (Scott and Kirkpatrick, 1994) as well as *P. foliosa*–dominated tall tussock vegetation. *Festuca contracta*, a short grass species which reflects relatively dry warm conditions in the Subantarctic, was more abundant in this

TABLE 1

Sorted table showing the time of data collection and the cover of taxa in quadrats (1 = <1%; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%; 5 = 51–75%; 6 = >75%)

Group Date[a]	1 2212221	2 11111112222i221121222	3 22212222221	4 1112111111111222222111
Hypnum sp.	------1	--------------------	-----------	----------------------
Colobanthus affinis	-1-----	------11---1-1----11	-----------	----------------------
Cotula plumosa	-------	1--1----------1------	-----------	----------------------
Pleurophyllum hookeri	-------	------33-------3---	-----------	----------------------
Poa annua	-------	-----------1---------	-----------	----------------------
Bryum argenteum	-------	2-------------------	-----------	----------------------
Megaceros/Riccardia	-------	-----1--------------	---------1	----------------------
Colobanthus muscoides	-------	-1---------1-2------	-----------	----------------------
Metzgeria sp.	------1	--211----------1---	-----------	--1---1-------------
Epilobium brunnescens	22-----	1-------------------	------3----	----------------------
Sanionia uncinata	-31-34-	1------2-----------	---------1	--1--------1-------1--
Thuidium furfurosum	-11-111	-----2-1-----------	----1-----	--1--------1-------
Festuca contracta	321-333	1---211331-1--------	----------	--1---1-------------
Agrostis magellanica	331-333	11121133234311-1211-	---11------	--1--1-------------
Acaena spp.	2212332	1-11113322-12-111-31	211-112----	-11-11-------------
Luzula crinita	3311322	1---1111222221111213	---1-11--1-	11-1--------------
other mosses	-1-1121	1-1-112------1--2-2-	1221------1	1111-1------1---------1
Epilobium pedunculare	2323322	---1--2-------1---1-	3231-132---	1122----------------
Peltigera sp.	1------	1----1-------1-1-22-	--21---1-2-	---------------------
Stilbocarpa polaris	5-----4	-5345633464441433444	---11--1--	----33--------------
Lophocolea bispinosa	21-----	2132--1222-221-21332	--222222232	----1--------1------1-
Ranunculus crassipes	2322222	41111123142321212-2	---22-21---	1121-1-111--11-----1--
Cardamine corymbosa	-111111	11111111--1111112222	22122221112	11--111-1-11--1-1---1-
Lophocolea bidentata	2113221	111-111121-2122112-1	2321113-222	111112111111122111-111
Poa foliosa	2466543	4-443134324446466545	55566656656	6666655666666666666665
Achrophyllum dentatum	------1	---------11--11-11111	11--1-2122-	11-1-11--111111-11--1-
Brachythecium spp.	-1----2	--------22----112231	33321232121	11121111212123213231-1
Bartramia papillata	3------	2-------21-1-1-11111	--11-11--21	------1----1----111
Breutelia spp.	2212221	--------------------	2-1--------	1111------1-11-11--1---
Stellaria parviflora	-------	-1------------------	------1---	--------------------11-
Marchantia berteroana	-------	2-------1------1-	----1----2	-------------------1
Ceratodon purpureus	-------	11--------1-------	---1-----1	--------------------1
Callitriche antarctica	-------	1-------------------	--------12	--1-----------------1

[a] 1 = 1980, 2 = 1995.

community than elsewhere. In Group 1 the relatively high abundance of these understory species reflects a short open *P. foliosa* canopy characteristic of higher altitude coastal slope vegetation.

Group 2 was next richest in species and the second tallest in stature after Group 4 (Table 2). The only largely constant and

TABLE 2

Mean characteristics of the classificatory groups, showing P values from oneway ANOVA

	Community				
	1	2	3	4	P
Altitude	89	87	57	58	0.056
Aspect (degrees)	206	257	149	142	0.000
Slope (%)	31	33	37	33	0.257
Peat depth[a]	3.0	3.3	3.5	3.7	0.033
Bare ground[a]	0.1	1.5	0.2	0.3	0.000
Rock cover[a]	0.0	0.1	0.1	0.1	0.729
Vegetation height[a]	3.7	4.1	3.5	4.7	0.000
Species richness	14	12	10	7	0.000
Ordination score axis 1	1.10	1.24	0.56	0.32	0.000
Ordination score axis 2	1.26	0.67	0.86	0.77	0.000

[a] Means of the classes described in the Methods section.

faithful species was *S. polaris* (Table 1) which codominated with *P. foliosa*. The moderate frequency of bryophytes such as *Achrophyllum dentatum* and *Brachythecium* spp. indicate a slightly moister understory environment than in Group 1. Group 3 was less rich in species and had a shorter stature than Groups 1 and 2 (Table 2). It had no constant and faithful species, but was intermediate in its composition between Groups 2 and 4. Group 3 had a slightly more open *P. foliosa* canopy and a more abundant and varied understory vegetation than Group 4. Group 4 was the least species rich of the communities with the greatest vegetation height (Table 2). It represents the closed *P. foliosa*-dominated tall tussock grassland vegetation of sheltered lower altitude slopes described by Taylor (1955) and Ashton (1965). It had no constant and faithful species (Table 1). The four groups separated well on the two axis ordination (Table 2).

ENVIRONMENTAL RELATIONSHIPS

The vegetation groups did not significantly differentiate on altitude or slope (Table 2). There was significant differentiation on aspect, with Groups 1 and 2 occurring on southwest-facing slopes and Groups 3 and 4 on southeast-facing slopes (Table 2). Peat depth was significantly differentiated between groups, steadily increasing through the sequence of communities, while

TABLE 3

Correlations between environmental variables, vegetation variables, and the most frequent taxa[a]

	alt	aspect	slope	peatd	veght	baregr	richness
Aspect	0.477	X	0.082	−0.158	−0.340	0.374	0.305
Slope	0.082	−0.156	X	−0.308	0.092	−0.117	−0.091
Peat depth	−0.158	−0.350	−0.308	X	0.399	0.061	−0.334
Vegetation height	−0.340	−0.607	0.092	0.399	X	−0.214	−0.565
Bare ground	0.374	0.581	−0.117	0.061	−0.214	X	0.206
Richness	0.305	0.455	−0.091	−0.334	−0.565	0.206	X
Acaena spp.	0.505	0.460	−0.110	−0.177	−0.558	0.294	0.580
Agrostis magellanica	0.357	0.586	−0.389	−0.270	−0.573	0.245	0.570
Cardamine corymbosa	0.208	0.068	0.304	−0.151	0.043	0.151	0.358
Epilobium pedunculare	0.152	−0.067	0.085	−0.181	−0.308	−0.242	0.338
Festuca contracta	0.129	0.383	−0.346	−0.284	−0.563	0.057	0.506
Luzula crinita	0.237	0.448	−0.254	−0.293	−0.450	0.171	0.641
Poa foliosa	−0.107	−0.428	0.360	0.172	0.593	−0.401	−0.429
Ranunculus crassipes	0.266	0.316	−0.167	−0.058	−0.278	0.189	0.557
Stilbocarpa polaris	0.243	0.688	−0.238	−0.273	−0.498	0.549	0.377
Achrophyllum dentatum	−0.243	−0.137	0.175	0.098	0.196	−0.267	−0.079
Brachythecium spp.	−0.259	−0.289	0.024	0.210	0.205	−0.393	−0.264
Lophocolea bidentata	−0.166	−0.266	0.055	0.042	0.028	−0.245	0.123
Lophocolea bispinosa	0.085	0.343	0.074	−0.082	−0.062	0.325	0.469
Other mosses	0.138	0.087	0.019	−0.220	−0.241	0.105	0.434

[a] Values in italics have a P value of less than 0.05.

vegetation height varied but was still significantly differentiated (Table 2). Bare ground was markedly greater in Group 2 than the other communities (Table 2), a characteristic which has been noted for mixed *Poa-Stilbocarpa* vegetation (Scott, 1995). Changes in floristic composition through the community sequence suggest a moisture gradient with communities becoming progressively damper from Group 1 to 4.

Altitude, bare ground, and aspect were positively intercorrelated (Table 3). Aspect was also negatively related to vegetation height and positively related to species richness (Table 3). Species richness was positively related to aspect and negatively related to vegetation height, while vegetation height was positively related to peat depth (Table 3).

Significant correlations between the more abundant taxa and environmental variables (Table 3) are as follows. Only one of the more abundant taxa, *Acaena* spp., was significantly correlated with altitude, occurring preferentially at higher elevations (Table 3). *Acaena* spp., *Agrostis magellanica, Festuca contracta, Luzula crinita,* and *Stilbocarpa polaris* were positively associated with aspect, occurring more on southwesterly slopes, while *Poa foliosa* had the reverse relationship, occurring more on southeasterly slopes. *Poa foliosa* occurred more abundantly on steeper slopes, while *A. magellanica* preferred shallower slopes. *Poa foliosa* and *Brachythecium* spp. were negatively correlated with bare ground, while *S. polaris* was positively correlated. None of the more abundant taxa had a significant relationship

TABLE 4

Transitions between classificatory groups 1980–1995

Group (1994–1995)	Group (1980–1981)			
	1	2	3	4
1	1	1	—	3
2	1	7	—	1
3	—	2	—	7
4	—	1	2	4

with peat depth. Vegetation height was positively correlated with *Poa foliosa* abundance, and negatively correlated with *Acaena* spp., *A. magellanica, F. contracta, L. crinita,* and *S. polaris* abundances. Species richness was negatively correlated with *P. foliosa* abundance and positively correlated with abundance of *Acaena* spp., *A. magellanica, Cardamine corymbosa, F. contracta, Lophocolea bispinosa, L. crinita,* other mosses, *Ranunculus crassipes,* and *S. polaris.*

TIME AND VEGETATION VARIATION

Groups 2 and 4 had more 1980–81 quadrats than 1994–95 quadrats, while Groups 1 and 3 had only two 1980–81 quadrats each (Table 1), signifying a shift in vegetation community characteristics towards the latter two communities. The transition matrix (Table 4) shows that most of the change in community composition resulted from 11 quadrats in Group 4 shifting to Groups 1, 2, and 3 in 1995, mainly to Group 3. Overall, 12 quadrats shifted in the direction of Group 1, or towards the drier end of the vegetation continuum, while 6 quadrats shifted in the other direction towards Group 4, or the moister end of the continuum (Table 4).

Of the 11 quadrats that moved from Group 4, nine had increased species richness in 1994–95, one was constant, and only one had decreased species richness. This contrasts with the general situation, in which 12 of the permanent quadrats decreased in species richness over the monitoring period and 18 were constant or increased. In only three of the quadrats that shifted from Group 4 did the major dominant *Poa foliosa* increase or maintain its cover. In eight quadrats its cover decreased. Concomitant with this decline in abundance of *P. foliosa,* there were consistent increases in the cover of *Acaena* spp., *Cardamine corymbosa, Epilobium pedunculare, Luzula crinita, Brachythecium* spp., *Lophocolea bidentata, L. bispinosa,* and other mosses.

Poa foliosa increased or maintained its cover in 19 of the 30 quadrats and decreased in abundance in 11 quadrats over the 15-yr period. In 9 of these 11 quadrats species richness increased

Changes in percentage frequency (f) and mean abundance scores (a) for taxa 1980–81 and 1994–95, showing direction of change

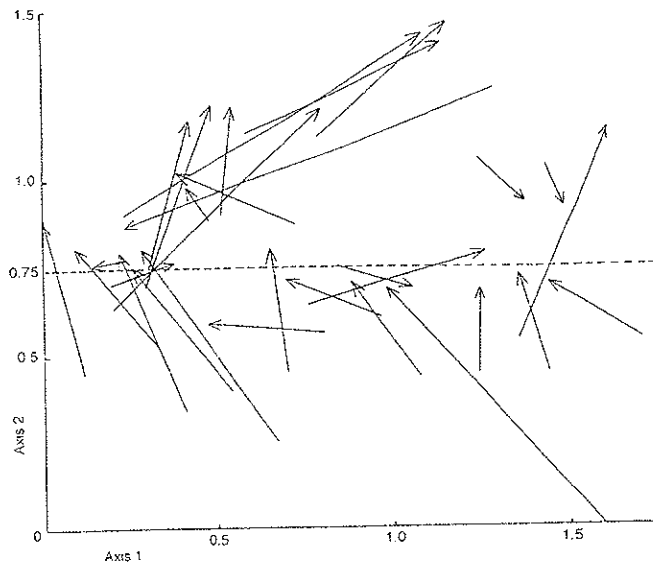|	f 1980	a 1980	f 1995	a 1995	f	a
Bryum argenteum	3.3	0.1	0.0	0.0	–	–
Poa annua	3.3	0.0	0.0	0.0	–	–
Pleurophyllum hookeri	3.3	0.1	6.7	0.2	+	+
Epilobium brunnescens	3.3	0.0	10.0	0.2	+	+
Hypnum sp.	3.3	0.0	0.0	0.0	–	–
Megaceros/Riccardia	3.3	0.0	0.0	0.0	–	–
Stellaria parviflora	3.3	0.0	3.3	0.0	=	=
Colobanthus affinis	6.7	0.1	16.7	0.2	+	+
Callitriche antarctica	10.0	0.1	6.7	0.1	–	–
Cotula plumosa	10.0	0.1	0.0	0.0	–	–
Colobanthus muscoides	10.0	0.1	3.3	0.0	–	–
Marchantia berteroana	13.3	0.2	10.0	0.1	–	–
Peltigera sp.	13.3	0.1	23.3	0.4	+	+
Cerastium fontanum	16.7	0.2	3.3	0.0	–	–
Ceratodon purpureus	16.7	0.2	3.3	0.0	–	–
Thuidium furfurosum	16.7	0.2	16.7	0.2	=	=
Sanionia uncinata	20.0	0.2	13.3	0.4	–	+
Festuca contracta	20.0	0.3	26.7	0.6	+	+
Metzgeria sp.	23.3	0.3	0.0	0.0	–	–
Breutelia sp.	26.7	0.3	36.7	0.6	+	+
Epilobium pedunculare	30.0	0.4	43.3	1.0	+	+
Bartramia papillata	30.0	0.3	43.3	0.6	+	+
Lophocolea bispinosa	36.7	0.4	63.3	1.3	+	+
Achrophyllum dentatum	40.0	0.4	63.3	0.7	+	+
Stilbocarpa polaris	43.3	1.6	43.3	1.5	=	–
Luzula crinita	43.3	0.5	60.0	1.1	–	+
Acaena spp.	46.7	0.6	63.3	1.2	–	+
Agrostis magellanica	50.0	0.8	43.3	1.0	–	+
Other mosses	53.3	0.6	30.0	0.4	–	–
Brachythecium spp.	63.3	0.8	76.7	1.6	+	+
Ranunculus crassipes	76.7	1.1	60.0	1.2	–	+
Cardamine corymbosa	80.0	0.9	73.3	1.0	–	+
Lophocolea bidentata	93.3	1.1	90.0	1.5	–	+
Poa foliosa	96.7	4.9	100.0	5.0	+	+

FIGURE 4. Movement of permanent quadrats in floristic ordination space. The arrows extend from the 1980 location to the 1995 location, which is marked by their head. The line at 0.75 on axis 2 marks the upper value at which all permanent quadrats share the same direction.

over the measurement period. The one quadrat in which species richness decreased was one of only two quadrats in which Stilbocarpa polaris increased its cover over the time period. Species richness decreased or remained constant over the time period in 12 of the 19 quadrats in which P. foliosa increased or maintained its cover. Mean quadrat species richness increased from 9.0 to 12.2 where P. foliosa decreased in cover, while it decreased from 10.5 to 9.2 in those quadrats in which P. foliosa maintained or increased its cover. In the three quadrats in which S. polaris decreased in cover over the time period species richness increased, from a mean of 8.7 to a mean of 11.3. Where S. polaris remained constant (eight quadrats) or increased in cover (two quadrats), there was a decline in species richness in five quadrats and constancy or increase in five quadrats. The mean quadrat species richness for quadrats with S. polaris declined from 12.1 in 1980 to 11.5 in 1995.

While overall mean quadrat species richness increased from 9.97 to 10.27 in the period 1980–81 to 1994–95, the total number of species recorded in all quadrats declined from 33 to 27 (Table 5). Taxa which disappeared were Bryum argenteum and Poa annua (both commonly associated with bare ground and disturbance), Hypnum sp., Megaceros/Riccardia, Cotula plumosa, and Metzgeria sp.

Sixteen of the 18 permanent quadrats with scores of 0.75

or less on axis 2 in 1980 had higher scores in 1995 than 1980 (Fig. 4), indicating strong directional change over time in this sector. Seven of the 12 permanent quadrats with scores greater than 0.75 on axis 2 in 1980 also had higher scores in 1995 (Fig. 4).

The vascular plants that increased most dramatically in both mean cover and frequency between the two measuring times were Colobanthus affinis, Festuca contracta, L. crinita, Epilobium pedunculare, E. brunnescens, and Acaena spp. (Table 5). In addition, 6 of the 14 nonvascular taxa (Peltigera sp., Breutelia sp., Bartramia papillata, L. bispinosa, Achrophyllum dentatum, and Brachythecium spp.) showed strong increases (Table 5). The introduced Cerastium fontanum was the only vascular plant species to decrease markedly in both cover and frequency (Table 5). One nonvascular plant, Metzgeria sp., exhibited a similarly marked decrease (Table 5). The prevailing dominant, P. foliosa, slightly increased both its frequency and cover, in contrast to the other major dominant of the coastal slopes, S. polaris, which maintained its frequency but slightly decreased in cover (Table 5).

Discussion

Environmental variation has a strong relationship with variation in the species composition and structure of the escarpment vegetation sampled in this study. The association of peat depth with floristic composition and vegetation height is particularly strong (Tables 2, and 3). The independence of peat depth from the other measured environmental variables (Table 3) indicates that the vegetation responses might partly reflect long term factors of slope stability such as different periods since the last land slip. Land slips are frequent on the steep vegetated slopes as a result of seismic activity and heavy rainfall events (Scott, 1988). Slope instability may be inevitable in this environment given progressive peat accumulation (Selkirk et al., 1990). The nature of the vegetation change with increasing peat depth is consistent with the successional sequence on land slips documented by Scott (1985). The relatively high cover of bare ground in the

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species-rich Group 2 (Table 2) and in quadrats in which *Stilbocarpa polaris* was present (Table 3), and the low levels of bare ground where *Poa foliosa* was most abundant (Table 3), is also consistent with this posited successional sequence. The statistically strong role of aspect in influencing vegetation variation is likely to be an artifact of the locations of the permanent quadrats.

The shift in floristic composition of permanent quadrats on axis 2 in the ordination space (Fig. 4) indicates highly consistent directional variation in the vegetation between 1980–81 and 1994–95, particularly in the sector of axis 2 below 0.75, which includes Groups 2 and 4 (Fig. 4). This directional change occurs in all parts of the environmentally related continuum, which is reflected roughly by scores on axis 1. Nevertheless, the degree and nature of the change varied between those permanent quadrats that were relatively species rich in 1980 and contained *S. polaris* (mostly Group 2), and those that were relatively species poor in 1980 and were dominated almost totally by *P. foliosa* (mostly Group 4). The former group of quadrats experienced a lesser degree of change than the latter, many of which shifted markedly in the vegetation continuum (Table 4), with a decline in the abundance of *P. foliosa* and an associated increase in species richness.

The ecological dominance of *P. foliosa* and *S. polaris* is apparent in the strong increases in the richness of other species with a decline in either or both of their abundances, compared to a mean decrease in species richness in quadrats in which they remained constant or increased in cover.

The expected increase in cover of *P. foliosa* was somewhat subdued (Table 5). Increases in abundance which occurred where it had relatively low cover were almost compensated for by some decreases in abundance where it had relatively high cover. Some of the opening out of the *P. foliosa* tussock grassland may result from the senescence of long-established individuals, uncompensated by establishment of new seedlings or rhizomatous spread. Seedlings of *P. foliosa* have not been recorded in long-undisturbed vegetation, although they have been noted from revegetating land slips (Scott, 1995).

Like *P. foliosa*, *S. polaris* failed to increase in dominance, a superficially surprising result given its known positive response to exclusion from grazing by fencing (Scott, 1995; Copson and Whinam, 1998). However, the criteria for selection of undisturbed sites in 1980 implied that the vegetation included in the present study was not in the early successional stages after disturbance. The lack of response of *S. polaris* to environmental change in later successional stages suggests that soil disturbance may be a prerequisite for its establishment (Scott, 1995), that it is not highly competitive with *P. foliosa* in closed communities, and that *P. foliosa* is not highly competitive with it. There is little evidence of the posited cyclic succession between *P. foliosa* and *S. polaris* (Ashton, 1965) in the data from the permanent quadrats. In only 1 of the 10 quadrats in which there was a decrease in cover of *Poa foliosa* was there an associated increase of cover in *S. polaris*. In no quadrat was there an increase of *P. foliosa* with a decrease in *S. polaris*.

Thus, of our hypotheses, we can confirm only directional change in the vegetation with time. Increased dominance of *P. foliosa* and/or *S. polaris*, and decreased species richness at the quadrat scale either did not occur or occurred in only a subset of the quadrats. In reality *S. polaris* changed minimally and two sets of quadrats behaved very differently. Those with initial low cover of *P. foliosa* gained more cover of the species, with a concomitant tendency towards a reduction in species richness, while those with an initially high cover of *Poa foliosa* lost cover of the species, with a concomitant increase in species richness.

There is widespread and justifiable concern that the nature and distribution of terrestrial subantarctic ecosystems is changing with global warming (e.g., Tweedie and Bergstrom, 2000). However, climatic change is not strongly indicated as a cause of most of the vegetation changes we have documented. Temperatures on Macquarie Island in the late 1980s and early 1990s were similar to those recorded in the 1960s (Fig. 1). However, the historically very high summer and annual temperatures recorded for the mid 1980s (Fig. 1) might have been partially responsible for increases in the cover of *P. foliosa* in the subset of quadrats in which it did increase in cover. It is difficult to relate this warm period to the decrease in cover of *P. foliosa* in the other subset. The steady increase in annual precipitation from the early 1970s to the early 1990s (Fig. 1) seems unlikely to have markedly influenced the changes given that the shifts in floristic composition were weighted towards the drier end of the vegetation continuum, unless there was a decline in peat depth caused by increased rainfall. Increased erosion seems unlikely given the drizzly nature of Macquarie Island precipitation and was not observed. Any increase in peat breakdown rates as a consequence of possibly higher levels of cyclic salts seems likely to have been more than compensated for by reduced breakdown rates as a consequence of lower temperatures.

There seems little doubt that a reduction in rabbit grazing pressure has resulted in increases in cover of *P. foliosa* and *S. polaris*, where previously sparse, on parts of Macquarie Island (Copson and Whinam, 1998), but this relationship cannot explain the observed reduction in the cover of *P. foliosa* where it was initially high in cover, and the constancy in cover of *S. polaris*. There is also a possibility that those escarpment sites with no rabbit grazing between 1980–81 and 1994–95, may also have been ignored by rabbits in earlier years (Scott, 1988).

Our observations strongly suggest the existence of a previously unrecorded late successional stage on the escarpment, involving a reduction in *P. foliosa* cover and stagnation in the cover of *S. polaris*. This change may reflect senescence of the *P. foliosa* tussocks and the absence of its regeneration, and lack of regeneration of *S. polaris*, without disturbance. The increase in *P. foliosa* cover where it was initially relatively low was an expected part of the succession, which may have been influenced in its rate by either, or both of, a reduction in rabbit grazing pressure, and initially high temperatures during the monitoring period.

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