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Terrestrial ecosystems in the Antarctic

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The composition of the terrestrial Antarctic flora and fauna and the distribution patterns of a number of species and of the principal vegetation types is now reasonably well established, at least in outline, for the Antarctic Peninsula region and the areas about McMurdo Sound as well as for some areas around the coastal ranges of East Antarctica. Detailed research at Signy Island has provided information concerning the biomass and productivity of certain vegetation types, decomposer organisms, microbivores, and invertebrate herbivores and predators. The main pathways of energy and nutrient within the terrestrial study sites can be regarded as reasonably established. Net annual production locally reaches very high levels (up to 800 g m^{-2}). Only a tiny part of this productivity is consumed by herbivores, the greater part passing to the decomposers or persisting as peat. Most of the animals are microbivores, or graze on fungi, and in turn sustain the small number of invertebrate predators.

Analysis of the range of habitats even on Signy Island indicates however that the sites for which detailed ecological information is available represent only a part of the range of environmental and ecological variation. The island is in fact characterized by a very high level of within-site diversity, some of it on a very small scale. Similarly, recent research which permits ecological comparisons with the sub-Antarctic islands of South Georgia and Macquarie, and with the McMurdo area, confirms that Signy Island displays only a small part of the very large range of diversity within the Antarctic regions as a whole. It is a reasonably representative sample of the maritime Antarctic zone in the Antarctic Peninsula region where conditions are particularly favourable for terrestrial life. Its ecological features resemble most closely those of the South Shetland Islands (except over permeable volcanic rocks) and the Palmer Archipelago on the western side of the Antarctic Peninsula. Very different plant and animal communities occur over much of the McMurdo Sound region and in the inland ranges of East Antarctica.

Some general statements can now be made about the relationships between terrestrial Antarctic eco-systems and climatic, edaphic and historical factors. There is a clearly marked attenuation of the vegetation and fauna and simplification of the ecological systems as one moves towards cold, arid continental conditions. But the biota of the maritime Antarctic and the sub-Antarctic islands is more impoverished than ecological factors alone would indicate, because of the isolation of these land habitats, many of which have only recently been deglaciated. If present environmental conditions persist, a slow increase in the complexity of these ecological systems is to be expected and in some areas, especially the subantarctic islands, this process is being accelerated by human influence.

Introduction

Ten years ago there was a Royal Society Discussion Meeting on the Terrestrial Antarctic Ecosystem (Smith 1967). In the concluding paper of that meeting an attempt was made to summarize what was then known about the marine and terrestrial ecological systems of the Antarctic zone, taken as the area south of the Antarctic Convergence (Holdgate 1967). Since then, a great deal of research has been done on almost all components of the land and freshwater systems of the Antarctic (see, for example, papers in two S.C.A.R. Symposium volumes edited by Holdgate (1970*a*) and Llano (1977)). Ecosystem processes were analysed as a component of the study of the Tundra Biome in the International Biological Programme at Signy Island (Collins, Baker & Tilbrook 1975), South Georgia (Smith & Walton 1975*a*) and Macquarie Island, north of the Convergence in the Australasian sector of the Antarctic (Jenkin 1975). These studies allow useful comparisons between maritime Antarctic and sub-Antarctic localities, and with the polar, sub-polar and alpine sites studied in the Northern Hemisphere (Rosswall & Heal 1975).

Such comparisons, however, need care if like is to be compared with like and the few sites that have been studied in detail are to be placed within the broader context of environmental variation. This is particularly important in the Antarctic, where ecosystems (in the sense of Tansley (1939)) are so fragmented that there may be hundreds of rock-soil-vegetation-herbivore-carnivore-decomposer-microbivore systems forming a 'recognizable self-contained entity' within a square kilometre.

Habitat variation in the Antarctic

Environmental variability can be examined on many scales. The great extent of the Antarctic land mass and its surrounding seas makes it inevitable that large-scale variability is analysed, and classifications of habitat groupings and regions developed, as a background to the consideration of the terrestrial ecology of the whole zone. Most detailed ecological studies have, however, been done on samples within localities a few square kilometres in extent, so that variability at this level also needs appraisal. Finally, the actual samples examined in these studies are often under 1 m^2 in extent, and variability at this third level needs consideration in order to relate them to the study areas as a whole.

Variations in habitat on the continental scale

The Antarctic Continent has a land area (including ice shelves) of about 14×10^6 km^2: the Antarctic and sub-Antarctic islands south of the Antarctic Convergence add only another few thousand square kilometres. Classifications used by biologists to subdivide this region (like that in table 1, taken from Holdgate (1970*b*)) can readily be related to latitude, distance from the sea, temperature and seasonal light régime, precipitation (and its form) and the extent of snow-free ground in summer, while altitude, slope aspect, soil and soil moisture régime are recognized as important on a smaller scale. Many of these variables are directly correlated because of the geography of the Antarctic: thus latitude, distance from the sea, altitude, temperature, precipitation and day length pattern vary together in the nearly-circular continent centred upon the Pole.

Analysis suggests that the broad pattern of variation in physical habitats over the Antarctic region can be brought out using only seven variables (table 2). These were scored for areas within 100 km of the intersections of a 500 km grid superimposed on the 1:15000000 scale map of the Antarctic, this grid being adjusted to make the South Orkney Islands one of the sample units. The data were analysed by Mr J. N. R. Jeffers to determine the variation in and correlations between these variables, and the groupings of the sites. Eight clusters were apparent (table 2*b*) and their geographical distribution is shown in figure 1. Even using such a small number of parameters and a very few points in a rapid pilot exercise of this kind, it is thus possible to demonstrate the concentration of environmental variability in the Antarctic Peninsula, and the coastal zone, to make a rough evaluation of the relative frequency of particular combinations of conditions, and to confirm the logic of the matrix classification developed, using many years experience, by the Conservation Sub-Committee of the S.C.A.R. Working Group on Biology (which is substantially that used in table 4).

Climatic variables affect the classification used in table 1 but are not included in the analysis in table 2. Largely in consequence, the habitat groups in the latter fall in more than one region and sub-region of the former. Group 1 habitats (coastal areas with rock exposures, usually

Table 1. Regions and sub-regions in the Antarctic

region	sub-region	climatic features	biotic features	localities
sub-Antarctic	—	Oceanic climate, small temperature range, mean annual temperature above 0 °C, temperature above freezing for at least 6 months, precipitation over 100 cm.	From the southern limit of woody vegetation southwards to the southern limit of extensive closed phanerogamic vegetation: vascular plants dominate vegetation near sea level. Abundant seabird and marine mammal fauna: some land birds and many higher insects.	South Georgia, Marion and Prince Edward Islands, Iles Crozet, Archipel de Kerguelen, Macquarie Island, Heard Island.
maritime Antarctic	—	Cold maritime climate, mean monthly temperatures exceed 0 °C in midsummer, rarely fall below −15 °C, precipitation from over 100 to about 25 cm (water equivalent).	Patches of closed phanerogamic vegetation, but mainly cryptogamic vegetation, locally diverse, with rich bryophyte stands near coast. Abundant marine bird and mammal fauna: also substantial invertebrate fauna including the only higher insects (Diptera) in Antarctic.	South Sandwich, South Orkney, South Shetland Islands, Palmer Archipelago and west coast of Antarctic Peninsula to about lat. 70° S: also Bouvet and Peter I Oya.
continental Antarctic	Coastal	Cold climate, with all monthly means below 0 °C and means down to −15° to −25° C in winter but some maritime influence shown in narrowing of temperature range and precipitation above 10 and often above 15 cm water equivalent.	Bryophyte vegetation present but restricted in species and extent. Lichens and land invertebrates (notably Acarina and Collembola) numerous. Seabird colonies frequent and large: many marine mammals.	Coastal fringe of East Antarctica, and West Antarctica S of 70° S, and on E coast of Antarctic Peninsula S of *ca.* 65° S.
	Antarctic slope	Cold and more continental climate, all monthly means below −5 °C, low winter temperatures, precipitation around 10 cm water equivalent.	Mainly open lichen vegetation, some moss patches near rare snow petrel and antarctic petrel colonies. Some mites and Collembola.	Mountain and glacier zone inland from the coast, girdling the central ice plateau.
	Antarctic ice plateau	Extreme continental cold conditions, monthly mean temperatures generally below −10 °C, falling well below −25 °C in winter, slight precipitation.	No known life.	Centre of the continent.

considerable altitudinal range and no ice shelves) are especially extensive in the Maritime Antarctic region on the western flanks of the Antarctic Peninsula and in its offshore islands. The South Sandwich Islands and South Orkney Islands, including Signy Island, are the northernmost examples of this group in the Antarctic, experiencing no period of total winter darkness or summer daylight, and having the most oceanic climate with substantial rainfall and a fairly narrow temperature range. The sub-Antarctic islands, including South Georgia, contain only group 1 habitats and represent a further extension of the axis of variation with reduced ice cover, no ice shelves, milder climates (and greater biotic richness). At the other end of the scale groups 1, 2 and 3 habitats line the coastal continental sub-region, where groups 4 and 5 habitats alone occur. Habitat groups 7 and 8 are almost co-extensive with the Antarctic ice plateau sub-region.

```
1
        6 8 8 7 1
2       8 8 8 8 8
  2 5 7 7 8 8 8 6 4
  5 3 7 8 8 8 8 8 8
  3 7 8 6 8 8 8 8
    6 7 5 5 8 8 8
          4 8 8 8
            6 7 7
```

Figure 1. Print-out showing geographical distribution of habitat groups derived for Antarctica using attributes in table 2*a*.

Table 2. Habitat attributes and habitat groups in Antarctica

(*a*) habitat attributes used in analysis

minimum altitude
maximum altitude
extent of coastline
presence of ice shelf
presence of significant rock exposures
least distance from coast
extent of permanent ice and snow

(*b*) habitat groups and frequency

open coastal sites	
1. Coastal sites with rock exposures but no ice shelf	2 sites
2. Coastal sites with rock exposures and ice shelf	2 sites
3. Coastal sites with ice shelf but no rock	2 sites
ice shelf and ice shelf coasts	
4. Sites with rock exposures and ice shelves but no open coasts	2 sites
5. Sites with ice shelf but no rock exposure or open coasts	4 sites
mountain sites	
6. Rocky sites lacking coast, and ice shelf, ranging up to 2200 m	5 sites
ice cap sites	
7. Sites without rock, coast or ice shelf, below 2000 m and under about 750 km from sea	8 sites
8. Sites without coast, ice shelf and rock, minimum altitudes over 1500 m and most over 2500 m: many over 1000 km from sea	27 sites

Groups 4 and 6 more or less correspond with the Antarctic slope sub-region, but group 6, because of the wide distribution of high mountain habitats, is met with in areas with a broad spread of maritime influence from the spine of the Antarctic Peninsula and the ranges above the Victoria Land coast inland to the southernmost outcrops of the Transantarctic Range.

Biological research on land in the sub-Antarctic and Antarctic has been concentrated in a few sample areas: especially Macquarie Island, South Georgia and Signy Island (all areas of group 1 habitats at the maritime and northern extreme in the continental range of variation). There is substantial biogeographical and some ecological information for the Antarctic Peninsula, South

Sandwich Islands, South Shetland Islands, Ross Island, Cape Hallett and localities in Victoria Land, and along the coast of East Antarctica to the shores and ranges of Dronning Maud Land. It is evident that such sampling is not spread so as to sample the range of Antarctic habitats evenly either by habitat group or locality, being naturally weighted in favour of the most accessible areas of richest environment.

TABLE 3. HABITAT FEATURES AND VEGETATION FEATURES RECORDED FOR EACH 500 m GRID SQUARE ON SIGNY ISLAND

(*a*) habitat attributes	(*b*) vegetation attributes
minimum altitude	extent (%) of moss carpet subformation: continuous cover, discontinuous cover
maximum altitude	extent (%) of moss turf subformation: continuous cover, discontinuous cover
contours cut on N–S transect through middle line of square	extent (%) of lichen and moss cushion subformation: continuous cover, discontinuous cover
contours cut on E–W transect through middle line of square	extent (%) of communities of calcicolour character, e.g. dominated by species of *Tortula* or *Grimmia*
% slope facing north (i.e. between NW and NE)	extents of various mosaics:
% slope facing east	(*a*) moss carpet and moss turf mixtures: continuous cover, discontinuous cover
% slope facing south	(*b*) moss carpet and lichen/moss mixtures: continuous cover, discontinuous cover
% slope facing west	(*c*) moss turf and lichen/moss mixtures: continuous cover, discontinuous cover
% of area of square occupied by sea	presence of patches of Antarctic vascular plant vegetation in square
% of area of square occupied by lakes	
% of area of square occupied by permanent ice and snow	
% of area of square shown as rock on map by Maling *et al.*	
% of area of square shown as drift or scree	
distance from margin of square to sea to north	
distance from margin of square to sea to east	
distance from margin of square to sea to south	
distance from margin of square to sea to west	
length of streams in square	
length of coastline in square	
% of quartz-mica-schist shown on geological map	
% of amphibolites shown on map	
% of marbles shown on map	

Variations in habitat and vegetation on the local scale

All the areas subjected to intensive study are highly variable. Subjective inspection by a competent ecologist is enough to indicate broad patterns and suggest the main determinant variables but not to explore relationships or document the diversity more strictly. Inspection of the published topographic map, backed by field experience, suggested that the habitat variability on Signy Island might be described by the 22 attributes listed in table 3*a* while the categories of vegetation in table 3*b* are those mapped in unpublished field surveys in 1961–2 and 1963–4 (Holdgate 1964, and unpublished data), extended by more thorough phytosociological analysis (Longton 1967; Smith 1972). These attributes were scored for 500 × 500 m squares covering the whole island.

Analysis of the data (kindly undertaken by Mr J. N. R. Jeffers) revealed seven main clusters, and four anomalous squares, referred to three different groups: their pattern of distribution over the island is shown in figure 2. The axis accounting for the greatest part of the variability was related to maximum altitude and the extent of ice and snow (these being naturally correlated) contrasted with the extent of sea and of coastline in the square. The second main axis of variability was related to the proportion of west-facing slopes and of drift and scree, while the third was associated with the percentage of rock (and of quartz mica-schist as the dominant rock type). Altitude, maritime influence, slope aspect and substratum thus emerge, not unexpectedly, as dominant variables.

The habitat groups or clusters would not, however, have been predicted in the form produced by the analysis. Group 1 is clearly an assemblage of lowland sites (most, but not all, coastal) predominantly on the west side of the main hill axis of the island. This group appears closest in affinity to Group 4, a series of extreme coastal, rock sites which may be partly an artefact of the grid system since it brought together squares with over 75% sea. Group 5 is also coastal, but predominantly on east and south coasts. Groups 2 and 3 are upland squares with relatively low snow cover: group 7 is the central ice plateau in the south of the island. Group 6 (which would not have been predicted subjectively) is a series of squares with high, rocky, mainly north and west-facing slopes on the edge of the central uplands.

```
          1 1                    A B
          1 2 1                  B A A
        1 1 3 1                B B A A
      4 1 3 3 5 5            C C A A A A
      4 1 3 2 2 5            B A A A A A
    4 1 1 2 2 2 4          C B A A A A C
    1 6 6 7 2 5 4          B C A A A A C
    1 8 6 7 2 5 4          B A A A A A A
  4 6 6 7 7 7 1 5 5      B C C A A A B D E
5 9 6 7 7 7 7 3 5 5 4  A B B A A A A C A A E
  9 6 7 7 7 7 3 5        A A A A A A A A
  5 1 6 7 7 7 7 5 5      E A A C A A C E E
5 6 6 6 7 7 7 5 5 5 5  A A A A A A A F E E A
4 5 6 7 7 5 5 4 5 5 5  A E A A A A A A D A A
    6X*5                   B A A
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FIGURE 2. Print-out of distribution of habitat and vegetation groups on Signy Island, derived from analysis of variables listed in table 3. Numbers denote habitat groups and letters vegetation groups. *X equals group 10.

A parallel analysis of the vegetation data yielded six clusters, varying greatly in extent (figure 2). The relationship with habitat groups was fairly complex. Vegetation group A, by far the most extensive, included 69 squares over the whole central upland region embracing all those in habitat group 2 and most of those in groups 3 and 7. This vegetation group was characterized by low proportions of moss carpet, moss turf and calcicole communities and a predominance of discontinuous lichen and moss cushion communities. The other vegetation categories covered the coastal belt on the west, north and east sides of the island and the differences between them were related to subtle variations in the proportions of moss turf, moss carpet, calcicole communities and mosaics. Vegetation groups D, E and F were closely associated with habitat group 5: they were relatively high in continuous carpet and turf and showed varying impact from seabirds and seals. Vegetation group B, particularly associated with the lowlands in the north-west of the island and with habitat group 1, was another category with substantial moss turf and moss carpet but may differ from groups D and E in having a smaller proportion of calcicole communities. The value of such analysis, especially when undertaken after primary survey or sketch-map examination of an area (a stage reached at Signy Island in 1964), is that it may lead to hypotheses that can be tested in the field, structure more detailed investigations and ensure that field sampling is designed to take full account of the ranges of variation in habitat and broad biological patterns. Further detailed analysis is given by Jeffers & Holdgate (1976).

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Habitat groups 1, 4 and 5 have the most diverse vegetation and it is not surprising that a high proportion of the stands recorded in the phytosociological survey of Signy Island by Smith (1972) was located in these groups (35, 14 and 73 samples respectively). On the other hand, Smith examined only one stand in habitat group 6 and one in group 7 – both with relatively restricted vegetation. The uplands in the north and east in groups 2 and 3 were better sampled (18 and 12 samples). Even within the groups that were sampled intensively, Smith's stands were concentrated in the north and east of the island, although their selection followed an extensive exploration of the whole island (Smith, personal communication). This survey, like the intensive studies of ecological processes reported in a later section, was not intended as a statistical analysis of the frequency of distribution of vegetation or faunal types, but had it been possible to precede it by habitat classification like that described here as a stratification, it might have been easier to place the examples chosen in the field of variation.

Variations in habitat on the smallest scales

Inspection is enough to show the striking small-scale variability in vegetation (over distances of 1 m or less), commonly correlated with exposure, stability or drainage features, in a place like Signy Island. Some examples have been published as sketch maps by Smith (1972). The result is that biomass, productivity, faunal abundance and decomposer activity show substantial difference from point to point, making general statements impossible unless sampling is very carefully designed: this has generally not been done.

Biological variation in the Antarctic

Variations in species distribution and performance

Although there has been no systematic sampling programme (despite the coordinating efforts of the S.C.A.R. Working Group on Biology), examination of the biogeographical data summarized by Greene and others (1967), Gressitt (1967), Lamb (1970), Tilbrook (1970) and others allows some broad relationships between biological groups and habitat types to be defined (table 4).

Even the sub-Antarctic islands composed of continental-type rocks have impoverished and disharmonic biotas resembling those of oceanic volcanic islands, perhaps because few species were able to survive cool conditions at glacial maximum. On Macquarie Island the flora contains some 40 vascular plants (3 alien), 50 mosses, 30 liverworts and 55 lichens. Only two vascular plants, *Deschampsia antarctica* and *Colobanthus quitensis*, are native to the Antarctic, both being confined to group 1 habitats in the maritime Antarctic, on the islands of the Scotia Ridge and along the west side of the Antarctic Peninsula (Greene & Holtom 1971). The only persistent alien vascular plant, the grass *Poa annua*, was recorded near the former whaling station on Deception Island, also in this zone (Longton 1966). *D. antarctica* and *C. quitensis* are most abundant in the northern peninsular region and the South Shetland Islands, where the most favourable environments occur, and in the South Orkney Islands (which appear slightly less favourable). However, they are everywhere local in occurrence, their performance varying with microclimatic, edaphic, and topographic features (Holdgate 1964; Holtom & Greene 1967; Edwards 1972). Edwards (1974) points out that in the South Orkney Islands, where both species are present, they are likely to complete their reproductive cycles only irregularly: in the South Sandwich Islands, where only *Deschampsia antarctica* occurs, conditions appear even harsher

(Longton & Holdgate 1976). The gradient of increasing environmental severity southwards down the west coast of the peninsula is also reflected in the cryptogamic flora. Almost all the antarctic hepatics are restricted to the maritime region in the peninsular sector, where bryophyte peat formation alone occurs and the mosses have their greatest diversity. (One hepatic, *Cephaloziella sp.*, is present at Ablation Point, Alexander Island (71 ° S) and on the continental coast at Cape Hallett.) Greene and others (1967) state that the diverse peninsular moss flora extends south to about 68 ° S: Smith & Corner (1973) however indicate a diminution in its richness around 65° S where several species reach their limit and *Polytrichum alpestre* replaces *Chorisodontium aciphyllum* as the main turf peat former. The bryophyte flora is relatively attenuated on the east side of the peninsula, in group 2 and 4 habitats abutting on the Larsen Ice Shelf,

TABLE 4. MATRIX SHOWING MAIN BIOGEOGRAPHICAL FEATURES AND HABITAT TYPES IN THE ANTARCTIC. DIVERSITY BROADLY INDICATED BY THE NUMBER OF CROSSES. NUMBERS REFER TO HABITAT GROUPS

	Maritime region	Coastal	Continental region		Antarctic Slope	Ice cap	
	1. Open rocky coastal	1, 2. Open rocky coastal, some with ice shelf	3. Rocky margins of ice shelf	4, 5. Ice shelf and ice coast	6. Rocky inland valley and mountain	7. Lower levels, under 500 km from sea	8. High interior, over 500 km from sea
flora							
vascular plants	+						
hepatics	++	+	+				
mosses	++++	++	+		+		
lichens	++++	+++	++		++		
snow algae[a]	+	+	+	+			
fauna							
Diptera	+						
Enchytraeida	+						
Nematoda	++	+					
Arthropoda	+++	++	+		+		
marine faunal influence							
marine mammals[b]	+++	++		+			
seabirds	++++	+++	+	+	+		

a Snow algae are typical of the maritime fringe of the Antarctic and probably do not penetrate far inland in the Continental region.

b Seal carcases are well known from sites in the Victoria Land dry valleys well away from the sea, but environmental conditions at the time the animals arrived there are not known.

and only about 20–25 species penetrate to the coastal and Antarctic slope regions of the continental Antarctic zone and to habitats of group 6 in the interior mountains. Reproductive performance in mosses, as in vascular plants, falls off before limits of distribution are reached: on Signy Island only some 17 out of 75 mosses produce sporophytes (Webb 1973). The timing and efficiency of sexual reproduction in mosses may be critically related to temperature in the surface layer of the turf, and hence microclimatic factors are likely to be important in this group as in vascular plants (Longton 1972). There is some evidence of correlation between the extremes of bryophyte distribution and the limits of seabird (*Thalassoica antarctica* and *Pagodroma nivea*) breeding colonies in the mountains up to 250 km from the sea (e.g. Bowra, Holdgate & Tilbrook 1966; Brook & Beck 1972). Schofield & Ahmadjian (1972) suggested that one of the mosses found in such situations, *Sarconeurum glaciale*, might be nitrophilous; however, this species extends to within 6° latitude of the South Pole in the mountains above the Dufek Coast (Greene *et al.* 1967), where seabird enrichment seems unlikely, and has recently been discovered as an epiphyte on *Nothofagus antarctica* in western Patagonia (Greene 1975, and personal communication). The lichen flora likewise displays a distinctive maritime Antarctic/peninsular west coast element. Of the continental total of 350–400 species, about 100 are restricted to this region. Only 20% or so of the total peninsula lichen flora traverses the mountain spine to grow in the colder, drier groups 2 and 4 habitats along the Larsen Ice Shelf (Greene *et al.* 1967). Although bryophyte diversity at Ablation Point and at other favoured continental coastal habitats is as great as at about 68° S on the peninsula (Smith, personal communication) sites in the continental region support predominantly lichen floras (Llano 1965; Greene *et al.* 1967; Lamb 1970). These floras contain a distinctive range of species, many of them restricted to the coastal sub-region. There are relatively few species in common between the peninsular sector and the main land mass of East Antarctica, suggesting biogeographical separation in the past.

The terrestrial fauna displays a similar pattern. The two Diptera native to the Antarctic are confined to the peninsula and South Shetland Islands and are not recorded even from the South Orkney Islands. Although their status is doubtful, it is in this maritime Antarctic sector also that Coleoptera and other probably alien arthropods have been recorded (Balfour Browne & Tilbrook 1966) and where vagrant American land birds have been seen. Enchytraeidae are similarly restricted to the northern part of the peninsula and the islands of the Scotia Ridge. The Protozoa (Smith 1974), Nematoda (Spaull 1973*a*), and Arthropoda (Gressitt 1967; Tilbrook 1967) show clear gradients of declining diversity southwards and eastwards from the South Shetland Islands, which clearly emerge as the richest biologically and most favoured ecologically of antarctic areas. In this, fauna and flora show a parallel trend, for many bryophytes and both vascular plants have a higher reproductive success in the South Shetland Islands than in the South Orkney Islands, and some bryophyte species do not extend to the latter group. The Arthropoda also parallel the lichens in showing substantial differences in the genera and species present in the peninsular region (where sub-Antarctic and South American genera predominate) and the Victoria Land/East Antarctic land mass: according to Gressitt (1967) and Greene and others (1967) only 2 or 3 free-living species are common to the two. It is interesting to speculate how far these biogeographical differences are attributable to ecological factors (including climate), how far they result from the recent re-colonization of the peninsula and islands from South America following ice retreat, and how far they may reflect the different histories of the two main parts of Antarctica and include relicts from pre-glacial Gondwanaland (cf. Brundin 1970). The ready dispersion of many bryophytes across sea barriers is indicated by the rich moss communities around fumaroles in the youthful South Sandwich Islands (Longton & Holdgate 1977), and the discovery around fumaroles formed during the recent eruptions on Deception Island of fruiting moss belonging to a genus previously unrecorded in the maritime Antarctic (Collins 1969). These observations may suggest that ecological factors are especially important in limiting bryophyte distributions. Callaghan, Smith & Walton (1976) suggest however that the impoverished vascular flora of South Georgia is chiefly due to geographical isolation. Arguments based on endemicity are difficult to rely on until the floras and faunas of southern temperate lands (especially in South America) are better known, as the recent discovery there of *Sarconeurum glaciale*, previously believed endemic to Antarctica, emphasizes (Greene 1975). In this connection it is pertinent to note that the soil and litter fauna of the Magellanic zone of South America are still very poorly known.

Variations in biomass and productivity

The localities studied

Detailed information about the three I.B.P. sites on Macquarie Island, South Georgia and Signy Island appears in Rosswall & Heal (1975) as summaries by Jenkin (1975), Smith & Walton (1975 *a*) and Collins *et al.* (1975) respectively. All these islands have more or less oceanic climates (table 5) and on Macquarie Island and South Georgia, peat formation is extensive. All three islands have relatively impoverished biotas, lacking native land mammals, but support very large seabird and marine mammal populations (the former somewhat reduced on Macquarie by introduced predators – cats and rats – while seals were formerly reduced on all the islands by sealers). The islands show marked marine influence, with sea spray as the main source of sodium, magnesium, and probably chloride, and seabirds and seals bringing nitrogen and phosphorus. This last feature also holds for many coastal sites on Continental Antarctica, including Cape Hallett and localities on Ross Island, and for localities where seabirds breed in the inland mountains.

Only a small part of the total area of these localities has been subjected to intensive study although all have been covered by primary survey. At Macquarie, research has concentrated on two (tussock grassland and herbfield) out of the five main vegetation formations (the others being bog, fen and fell-field). On South Georgia the I.B.P. study area of *ca.* 2 km^2 was at King Edward Cove, an atypical area in having been deglacierized for longer than much of the island and having an unusually favourable climate (Smith & Walton 1975 *a*). The study area contained seven main community types; dry meadow (dominated by *Festuca contracta*), mesic meadow (*Deschampsia antarctica*), oligotrophic mire (*Rostkovia magellanica*), eutrophic mire (*Tortula robusta* and *Juncus scheuchzerioides*), dwarf shrub heath (*Acaena magellanica*), tussock grassland (*Poa flabellata*) and fell-field: in addition there were special communities of rock faces and crevices. The vegetation pattern appeared most closely related to soil water régime, which in turn reflected topography and drainage systems. Detailed measurements of biomass and productivity were made in *Festuca contracta* meadow, *Acaena magellanica* dwarf shrub heath and *Poa flabellata* tussock grassland (a community very similar to the tall coastal grassland of *P. foliosa* examined at Macquarie).

At Signy Island, work concentrated on three of the 10 subformations recognized by Smith (1972) – the moss turf subformation dominated by *Chorisodontium aciphyllum* and *Polytrichum alpestre*, the moss carpet subformation (*Drepanocladus uncinatus*, *Calliergon sarmentosum* and *Callergidium austro-stramineum*) and the grass and cushion chamaephyte subformation (*Deschampsia antarctica* and *Colobanthus quitensis*). Reference sites have now been established in the two former subformations (Tilbrook 1973) as focal points for study, and their Protozoa (Smith 1973 *a*, *b*), Nematoda (Spaull 1973 *b*), Tardigrada (Jennings 1975), Arthropoda (Goddard, in press), and soil algae (Broady, in press) have been examined so far: work on bacteria is in progress and microclimates are being recorded. The main purpose of these sites is to serve as samples of relatively simple ecosystems which can be studied in depth, as an aid in reaching a greater understanding of functional relationships. They are not intended to cover the full range of environmental or biological variability (Tilbrook, personal communication).

On Ross Island in the continental coastal sub-region, Longton (1973) described examples of the moss hummock, fruticose lichen and moss cushion and crustose lichen subformations, while much ground is covered with gravel with no visible vegetation (the chalikosystem of Janetschek

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Table 5. Climatic features of some Subantarctic and Antarctic stations

site	lat.	long.	region	mean temp. (year)/°C	mean temp./°C Dec./Feb.	mean temp./°C June/Aug.	precipitation mm	rel. humidity	sunshine h.
Macquarie Island	54° 30′ S	158° 57′ E	Subantarctic	+4.7	+6.2	+3.0	926	89.2	814
South Georgia	54°–55° S	36°–38° W	Subantarctic	+1.8	+4.4	−1.5	1405	75	1236
Signy Island	60° S	45° W	Maritime Antarctic	−3.3	+0.1	−9.6	*ca.* 400	86	518
Cape Hallett	72° 18′ S	170° 19′ E	Coastal Continental Antarctic	−15.5	−2.4	−25.3	118	65	—
McMurdo, Ross Island	77° 51′ S	166° 37′ E	Coastal Continental Antarctic	−17.6	−5.6	−25.9	119	57	—

Table 6. Plant biomass and primary production at some Subantarctic and Antarctic sites

	standing crop/(g m^{-2})						production/(g m^{-2} a^{-1})			
	above ground			standing dead total (including litter)	below ground (all)		below ground	above ground		
site	vascular	bryophytes	lichens		alive	dead		vascular	bryophytes	lichens
Macquarie grassland (site M1)[a]	912	6	0	2693	1690	3110	3670	1890	21	0
Macquarie herbfield (site M3)[b]	139	393	9	266	670	1250	550	314	146	4
South Georgia *Acaena* dwarf shrub	1300	221	0	521	7536		*ca.* 500	855	250	0
South Georgia *Festuca contracta* meadow	425	*ca.* 500	12	1738	1642		*ca.* 350	340	150	2
South Georgia *Poa flabellata* grassland	7525	0	0	5255	5000		*ca.* 1000	5020[h]	0	0
Signy Island closed *Deschampsia* sward	327[c]	136[c]–233[d]	0	215[c]–651[d]	75[c] 131[e]	1602[c] 1913[e]	131	390	85	0
Moss turf *Chorisodontium*	0	400–600[f]	?	?	45000 (to 1 m)[g]		0	0	342–551	?
Moss carpet *Drepanocladus/Calliergon*	0	200–900	0	?	2000–5000		0	0	275–893	?
Ross Island *B. antarcticum*	0	1012–1108[j]	0	?	?		?	0		
B. argenteum	0	241–602[j]		?	?		?	0	*ca.* 100 g m^{-2} a^{-1}[k]	

a, b Two tussock grassland and two herbfield sites at different altitudes were studied on Macquarie. The best documented examples in each case are quoted here. The figures are the mean of many harvests.
c March figures. d November figures. e February figures.
f Green shoots. g Brown shoots.
h This very high value was based on an individual tussock with a large proportion of overwintering green foliage. True values for the tussock community might be only 50 % or less of this figure.
j Longton (1974) points out, however, that these patches of very high biomass cover only about 2 % even of favourable areas: overall *ca.* 5–20 g m^{-2} is a more likely figure.
k Longton (1974) calculated a production of 252 g carbon m^{-2} a^{-1} by extrapolation from climatic and published physiological data but considered this too high, suggesting 96 g C m^{-2} a^{-1} for the richest moss patches and only 5 g C m^{-2} a^{-1} as an average value.

1970). The figures summarized in table 6 come from isolated moss patches belonging to the *Bryum* association (Longton 1974) which exemplify the richest extreme in the 'bryosystem' of Janetschek (1970).

Primary production

None of these localities has been studied sufficiently to provide figures for the biomass and productivity of all the chief components of the ecosystem. Plant biomass and primary production figures are available from four localities (table 6). They are not directly comparable for several reasons. Biomass varies seasonally (see, for example, Walton 1973). As Walton, Greene & Callaghan (1975) have stressed, different methods have been used and give results that are known to vary, while some of the figures come from small patches of unusually productive vegetation, like the single *Poa flabellata* tussock yielding the exceptionally high production value for South Georgia or the patches of *Bryum* studied on Ross Island by Longton (1974). There are thus two statistical problems: the reliability and inter-comparability of the methods, and the relationship of the sample sites to the regions in which they occur. Until the variability in biomass and production within the sites is better documented such figures are difficult to compare meaningfully: they do show, however, that the plant standing crops and production *can* be remarkably high in the most favourable subantarctic and Antarctic situations. Collins *et al.* (1975) attempt to place the Signy Island values in context by estimating that average net annual production over the snow and ice-free areas there may be at most about 100 g m^{-2} a^{-1}. Longton (1974) similarly indicated that biomass of *ca.* 20 g m^{-2} and annual production of *ca.* 5 g carbon m^{-2} a^{-1} were much more representative of the sparse and discontinuous moss vegetation even in the favourable habitats of coastal Antarctica that he studied.

Herbivory

Holdgate (1967) speculated that herbivory was unimportant in the Antarctic – at least in bryophyte vegetation. This view is broadly supported by the more recent data. In the sub-Antarctic islands there are no native mammalian herbivores. On Macquarie Island, introduced rabbits (*Oryctolagus cuniculus*) are abundant and on South Georgia there are reindeer (*Rangifer tarandus*), and both have caused major changes in vegetation and local erosion. On South Georgia the native pipit *Anthus antarcticus* takes seeds and two duck species consume aquatic and stream-side plants. Jenkin (1975) considers invertebrate herbivory unimportant at Macquarie: at South Georgia some Coleoptera graze bryophytes and vascular plants and one mollusc inhabits moss cushions on rock faces (Smith & Walton 1975*a*), while on Signy Island some mites feed on crustose lichens (Collins *et al.* 1975). Tardigrades, rotifers and enchytraeids are abundant in moist bryophyte vegetation at South Georgia and the two former occupy this habitat on Signy Island, but their biomass and impact as herbivores are judged to be negligible. Herbivory in continental Antarctic situations is likely to be similarly unimportant.

Decomposers

On all sites, the bulk of the plant production either passes to peat, is physically removed by wind or water, or is consumed via the decomposers. The decomposer system has not been studied at Macquarie (although bacteria and saprophytic and parasitic fungi are abundant). The activity of the system is indicated by the fact that the first year mass losses for dead material of three grassland species ranged from 51–90% (Jenkin 1975). On wet ground, however, especially on the uplands and on gentle slopes, peat accumulates.

At South Georgia the bacterial microflora varies in abundance with season, reaching a peak of 2.09×10^6 individuals per gram in litter and 0.03×10^6 g^{-1} in soil: the corresponding biomasses have been calculated as 0.63 and 0.04 μg g^{-1} (Smith & Walton 1975*a*). Decomposition rates here, as at Macquarie, are variable: deep peat accumulates under anaerobic conditions beneath some vegetation types while in others, like *Acaena magellanica*, over 90% dry mass loss has been recorded in 14 weeks. Standing dead material of *Poa flabellata* lost from 12 to 30% according to exposure.

Table 7. Signy Island: biomass of decomposers and invertebrates
(From Collins *et al.* 1975)

Organism	mineral soils: young moraine	mineral soils: old moraine	habitat: crustose lichen	habitat: moss turf	habitat: moss carpet	habitat: grass and cushion plants	habitat: fruticose lichen and moss cushion
micro-organisms (μg wet mass per gram of soil or peat)							
bacteria	2	3	—	1	—	12	—
yeasts	—	—	—	179	—	—	—
moulds	32	665	—	40600	—	2610	—
flagellates	—	—	—	3	—	—	—
Testacea	—	—	—	115	150	59	—
non-carnivorous invertebrates (mean annual: mg wet mass m^{-2})							
Nematoda	—	—	—	296	1329	4097	1580
Collembola	—	—	100	350	7200	4100	675
Acari	—	—	2408	9	<1	4	2
carnivorous invertebrates (mg wet mass m^{-2})							
Nematoda	—	—	—	2	350	32	12
Acari	—	—	27	11	49	144	38

At Signy Island bacteria, yeasts, moulds and testate amoebae were abundant at the study sites (table 7). The annual production of bacteria was calculated at around 7.5 mg dry mass m^{-2} at 1–2 cm depth, a rate that is negligible compared with primary production. The microfungi, with their higher standing crop, may have a substantially higher production. Decomposition rates of organic material are variable but generally slow, and between 75% and 98% of the production may persist into the following season. Frozen deep peat accumulates especially under moss turf and extrapolation from one radiocarbon dated site gives a minimal increment of about 1 mm a^{-1} (Holdgate 1967). Peat does not accumulate under moss carpets, despite their greater waterlogging. Decomposition is more rapid under carpets (Collins 1973), and removal of dead plant matter may be influenced by growth form (Gimingham & Smith 1971) and water percolation, which may remove some of the organic matter. Carpets may also be relatively short lived, developing and declining with changing water régime (Collins 1976).

In Victoria Land, bacterial counts from the Dry Valley area (impoverished compared with coastal habitats) only exceeded 10^5 g^{-1} at one place studied by Cameron (1972): algae were also present here but moulds, coliforms, streptomycetes and thermophiles were not recorded. The driest and most saline soils in these regions were virtually sterile.

The saprovore and microbivore system

The invertebrate fauna of Macquarie Island soils and litter is not well known, but nematodes are present and said to be mainly microbivores, and earthworms occur. At South Georgia the soil fauna has been studied more fully and it is clear that some groups are abundant, with substantial variation from habitat to habitat. Acarina and Collembola formed the bulk of the biomass and numbers ranged from 6440 to 32380 m^{-2} and from 5590 to 56000 m^{-2} respectively. Enchytraeids were numerous (110–3110 m^{-2}): Coleoptera larvae and adults, commonest in grasslands, ranged from 0 to 3060 m^{-2} and Diptera from 60 to 230 m^{-2}. On Signy Island the principal microbivores are Nematoda, Collembola and Acari, with less abundant Rotifera and Tardigrada (table 7). Spaull (1973*b*) recorded this habit in 58% of the nematodes at reference site 1 and 41% at site 2, with fungal feeders also important at the former and omnivores at the latter. The biomass varies with habitat for reasons not entirely clear: Spaull (1973*c*) indicated, for example, that a relatively low nematode abundance at reference site 2 might be due to waterlogging and oxygen lack under the moss carpet while Smith (1974) related interesting differences in the Protozoa inhabiting the carpet-forming moss *Drepanocladus* in the South Orkney Islands to nutrient status. Invertebrate respiration rates likewise vary from site to site and give an indication of production, which has not been measured directly: for many groups the annual production is likely to be of the same order as the standing crop. Janetschek (1970) gives some figures for numbers of arthropods from the Victoria Land area, ranging up to 100 individuals m^{-2} in the coastal bryosystem: inland chalikosystem sites were sparser with Collembolan numbers closer to 10 m^{-2} at many sites.

Predation

The chief native predators within the terrestrial ecosystems of the subantarctic and antarctic sites are invertebrates. On Macquarie these have not been thoroughly studied: at South Georgia there are spiders and carnivorous Coleoptera and some Acarina, Collembola and Diptera are said to be 'scavenging carnivores'. Land birds on both islands also take some invertebrates: on South Georgia the endemic pipit *Anthus antarcticus* and the two ducks *Anas georgicus* and *A. flavirostris* do so. On Signy Island one species of tardigrade, nematode and mite are carnivorous: the total carnivore biomass is low (table 7). Predatory seabirds (e.g. great skua, *Catharacta skua*, giant petrel, *Macronectes giganteus* and on the Atlantic islands, sheathbill, *Chionis alba*) are numerous, but depend on the marine system for food. Mammalian predators have been introduced to Macquarie (cats, rats) and South Georgia (rats): on the former island the seabird colonies have been affected severely.

Comparison of biomass and production

The gradient of impoverishment in the species composition of flora and fauna southwards from maritime to continental Antarctic is accompanied by a marked diminution in the extent of macrophytic vegetation and therefore of net biomass of comparable areas. Table 6 indicates that these trends are accompanied by a rather less marked diminution in the biomass and production of the best developed systems. Even the *Bryum* patches on Ross Island, certainly a severe habitat compared with Signy Island or South Georgia, have maximum standing crops and

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productivities little less than some samples from those places. Table 8 similarly indicates that those invertebrates that occur on both South Georgia and Signy Island show comparable abundance in the two places. Wider comparisons extend this conclusion: Heal (1965) long ago pointed out that the abundance and biomass of testate amoebae in Signy Island grassland soils was comparable with that in some upland situations in northern England and various authors in Rosswall & Heal (1975) reinforce the point. Walton (1973) suggested that the total biomass in *Acaena decumbens* sward at South Georgia might be as great as that recorded at any I.B.P. northern tundra site. Walton *et al.* (1975) have shown that *Festuca contracta* grassland at South Georgia is comparable in end of season biomass with grasslands in Saskatchewan and the Taimyr Peninsula and suggest that the island is less severe as a habitat than many Arctic tundra sites, and more comparable with alpine localities. Callaghan *et al.* (1976) emphasized the high productivity of dominant communities on South Georgia compared with other tundra areas. Another approach to such comparative assessments is to use crop plants as 'phytometers': Lewis & Greene (1970) did this and suggested that environmental conditions were more favourable to growth in southern Greenland than South Georgia. Smith & Walton (1975*b*), in a more extensive study, showed greater variation with time of season than between sites, but also considerable within-site variation at South Georgia and stressed the care needed in such experiments.

TABLE 8. COMPARATIVE BACTERIAL BIOMASS AND INVERTEBRATE ABUNDANCE: SOUTH GEORGIA AND SIGNY ISLAND (From Rosswall & Heal 1975)

(All figures except bacterial biomass are numbers per square metre, the Signy data being annual means.)

	South Georgia	Signy Island
Bacteria	0.04–0.63 μg g^{-1}	2—12 μg g^{-1}
Enchytraeidae	110–3110	present on island: not significant in study area
Acarina	6440–32380	< 1000–40000
Collembola	5590–56500	4000–670000
Coleoptera (adults and larvae)	0–3060	absent
Diptera	60–230	absent
Nematoda	n.d.	576000–6027000

The sustained performance among species that do penetrate deep into the Antarctic might reflect temperature adaptation. Holdgate (1967) suggested that the terrestrial Antarctic biota contained many organisms tolerating low temperatures, but few that were active below 0 °C. Stanley & Rose (1967) indicated temperature optima around 10–15 °C for micro-organisms, and these values are often attained in soil and moss warmed by radiation in summer (Longton & Holdgate 1967). Baker (1974) determined optima for five psycrophilic bacteria from Signy Island to be around 25 °C, a finding that differs from Latter & Heal's (1971) statement that most isolates grew better at 13 °C than 1 °C or 25 °C. Most soil bacteria are likely, on this evidence, to be growing at suboptimal temperatures. Decomposition processes were said by Heal, Bailey & Latter (1967) to proceed at about a third the rate in upland Britain, but as Collins *et al.* (1975) point out, climatic conditions alone cannot account for the slow rate of breakdown of moss like *Chorisodontium* when litter of the grass *Deschampsia antarctica* in the same area is rapidly removed despite its high production rate and the absence of macro-invertebrates like millipedes and earthworms. Invertebrate activity is said by some to be curtailed or stopped below 0 °C (Pryor 1962, for Collembola) or perhaps at temperatures well below zero in mites (Dalenius & Wilson 1958): current studies of respiration are slowly providing more reliable data. As Janetschek (1970) emphasized, the determinant factor for many arthropod species distributions is capacity to complete the life cycle under prevailing conditions.

Rather similarly, Lange & Kappen (1972) have shown that antarctic lichen species have optima for photosynthesis below 15 °C, but high CO_2 uptakes near 0 °C and a capacity for some assimilation down to −12.5 or −18 °C. This, coupled with extreme cold resistance (to −196 °C in some species) is held to explain the success of lichens in inland habitats. Rastorfer (1972) indicated higher optima in some bryophytes (10–20 °C, with a possible photosynthetic cut-off at about −5 °C). Longton & Holdgate (1967) and Greene & Longton (1970) both indicated how bryophyte communities can readily be warmed by radiation into this optimum range. Collins *et al.* (1975) record that high rates of photosynthesis are maintained in *Polytrichum alpestre* and *Drepanocladus uncinatus* from Signy Island at 0 °C while at this temperature the vascular species *Deschampsia antarctica* and *Colobanthus quitensis* have rates 40 and 30% respectively of their maxima. Within the areas of tolerance, however, other factors are also likely to be of importance as determinants of vegetation patterns, and Schofield & Ahmadjian (1972) have studied the type of available nitrogen and the concentration of water soluble salts. They point out that some plants (e.g. the lichen *Lecanora tephroecta* and the algae *Prasiola crispa* and *Phormidium autumnale*) grow best on reduced (ammonia) nitrogen or uric acid, hence explaining their association with bird and seal colonies, while others (like *Bryum algens*) grow well on all nitrogen compounds.

This sustained production by tolerant species does not mean (as uncritical inspection of table 6 might suggest) that overall biomass and production are comparable at all the sites examined. The progressive reduction in the flora and fauna leads to loss, at the margin of the maritime Antarctic zone, of those vascular plants accounting for much of the biomass and production in the sub-Antarctic, along with the larger soil animals that dominate the biomass in this habitat in temperate regions. At the southward margin of the continental coastal sub-region the bryophytes that sustain biomass and production figures in the maritime Antarctic, reach their limits causing another marked drop in both values. Accompanying this attenuation is a marked reduction in the area occupied by vegetation of high biomass and production (full analysis of how the net biomass and production of comparable areas in the various regions differ awaits further sampling). The present figures also show (eg. table 7) that the within-site variation at all the localities examined is very great – greater than the between-site differences in the production and standing crop of the most productive comparable organisms

Discussion

As knowledge of Antarctic biology has increased, so the variability in the terrestrial ecological systems of the region has become more apparent. Over the continent and adjacent oceanic zone as a whole, the bulk of land plants and animals are clearly concentrated on the oceanic fringe, where the climate is least extreme, precipitation highest, stable snow-free ground most extensive in summer and seabird and marine mammals – important sources of nutrient – most abundant.

This biogeographical pattern probably has both ecological and historical causes. Not only are the most favourable habitats for the land biota and for seabird colonies concentrated on the west coast and fringing archipelagoes of the Antarctic Peninsula, but this area is closest to cool-temperate South America, which may well have been an important source of colonists in the period since ice retreat. These maritime Antarctic regions, like the sub-Antarctic islands, are

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still biologically impoverished, with disharmonic floras and faunas and transplant experiments suggest that more species might succeed there if they were able to disperse across the oceanic barriers (see, for example, Longton & Holdgate 1967; Greene & Longton 1970; Edwards & Greene 1973).

Habitat conditions in the Antarctic are highly variable at the macro-, meso- and micro-scales. Over the zone as a whole, three major regions (sub-Antarctic, maritime Antarctic and continental Antarctic) are now widely recognized: the last of them, which is by far the greatest in extent can be subdivided into coastal, Antarctic slope and central ice desert sub-regions. These well established units accord well with eight habitat groups defined by a preliminary analysis of altitude, distance from open sea, extent of rock exposure, extent of inland snow and ice cover and of ice shelf. There is a broad relation between biological diversity and floristic and faunistic composition and the habitat groups and regions, and this is well established despite the lack of objective sampling to bring out precise correlations. On the meso-scale (illustrated by Signy Island) analysis of a wider range of topographic variables allows definition of seven main habitat groups mainly related to altitude, coastal influence and substrate. There is also very marked diversity on the micro-scale, over distances of a few metres. Biological variability accompanies, and is related to, this habitat diversity in a way that has yet to be established quantitatively.

Since 1967 there has been a great increase in information about species, biomass and production rates in samples of the biota on certain sub-Antarctic, maritime and coastal continental Antarctic sites. Along a southward gradient, and from maritime to continental conditions, there is a diminution in species richness and in the extent of the best developed macrophyte vegetation, but a less marked decline in the biomass and primary production rates of the best developed comparable vegetation types. Probably this indicates the high order of adaptation in antarctic bryophyte and lichen species, able to maintain physiological efficiency even at very low ambient temperatures.

Holdgate (1967) suggested a low level of herbivory in the land fauna of the maritime Antarctic and this has been confirmed (Collins *et al.* 1975). The same generalization can be extended to coastal continental Antarctic bryophyte vegetation, but applies less completely in the sub-Antarctic, where there are native invertebrate herbivores, although even here a very small proportion of the plant standing crop is likely to be consumed. Introduced vertebrates are, however, making major inroads on some plant communities on both South Georgia and Macquarie Island, as on other subantarctic and southern temperate oceanic sites. The bulk of the production in the examples studied passes either to peat or to the decomposers, which are abundant in all examples studied and in turn sustain microbivore and carnivore invertebrates. All these components of the ecosystem, like the plants, diminish in species diversity southwards faster than they diminish in productivity. Native 'higher' insects, except for two Diptera, penetrate no further south than the sub-Antarctic.

The fauna in the sub-Antarctic and Antarctic thus lacks important components. Heal (personal communication) points out that taking the model developed by Heal & MacLean (1975), with a primary production of 400 g m^{-2} a^{-1} (which is not unusual at the sites listed in table 6), the expected production rates in the herbivore system would be (all figures in g m^{-2} a^{-1})

vertebrate herbivores	1.00	vertebrate carnivores	0.01
invertebrate herbivores	2.56	invertebrate carnivores	0.16

and in the saprovore system:

invertebrate saprovores	4.84	microbial saprovores	218.20
invertebrate microbivores	5.23	invertebrate carnivores	0.62

Actual data reviewed above indicate the total absence of native vertebrates and negligible biomass of invertebrate herbivores. Heal suggests that the total standing crop of all invertebrates in moss and grass habitats on Signy Island is up to 8.5 g wet mass m^{-2} (i.e. 2.1 g m^{-2} dry mass) while on South Georgia the figures may be twice this allowing for the Coleoptera and Diptera larvae. This contrasts with calculated invertebrate production of the order of 10 g m^{-2} a^{-1} for moss areas and 10 g m^{-2} a^{-1} for grass areas on Signy and up to the order of 100 g m^{-2} a^{-1} in the most productive small areas on South Georgia. If, with an annual life cycle, production and standing crop are assumed to be about the same, the discrepancies are apparent, suggesting that these habitats produce less invertebrate material than they should: the implication is that these ecosystems may be functioning differently from those from which the model was derived and that invertebrates in the Antarctic and sub-Antarctic are not as efficient as those in lower latitudes, or in the Arctic, in contrast to the plants, which are relatively productive.

Part of this discrepancy emphasized by Heal may be an island effect. The lack of vertebrates and impoverished native invertebrate faunas would almost certainly give comparable results for even the luxuriant vegetation of Gough Island and other parts of the Tristan da Cunha group. It may be that oceanic islands generally have a shortfall in invertebrate production, just as they lack vertebrates. This, moreover, may help to explain the dramatic changes in these island systems when alien vertebrates and invertebrates are imported and begin to crop vegetation which is not adapted to sustained herbivory. These issues cannot be examined further here, but they suggest that the reasons why antarctic and subantarctic ecosystems appear to function differently from those in temperate lands may not be elucidated until the relative influences of biogeographical isolation and impoverishment and of the harshness of the polar environment are disentangled.

To an extent that is probably misleading, the different components of Antarctic ecosystems appear to function as independent variables. The biomass and production of plants appears to be largely governed by physicochemical environmental factors – temperature, water and nitrogen and other nutrient availability: the latter does depend to a considerable degree on input from seabirds and marine mammals, establishing one definite biological dependence in the system. There is presumably some relation between plant production and decomposer abundance, but it is far from direct, being strongly influenced by temperature and water régime, just as microbivore numbers appear to fluctuate almost independently of plant production. More work is still needed before the interrelationship within the ecosystems, and rates of energy flow, can be defined and variation from place to place explained. The establishment of the Signy Island reference sites is a step in the right direction, but these need to be replicated and placed within the wider field of ecological and environmental variation. In future, before such sites are set up, objective survey and analysis of the range of variation in Antarctic environmental features, with which biological performance may be related, should be undertaken to provide stratification. In the last decade a great amount of information has been gathered although sizeable gaps remain. We are nearing the point at which preliminary models can be constructed for some terrestrial Antarctic ecosystems even if others remain almost unknown. The work already done is enough to establish the value of ecological studies in the Antarctic, and we can

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predict that the relationship between patterns and processes in terrestrial communities there and in other parts of the world, and the reasons for apparent differences, will be a major theme in coming years.

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