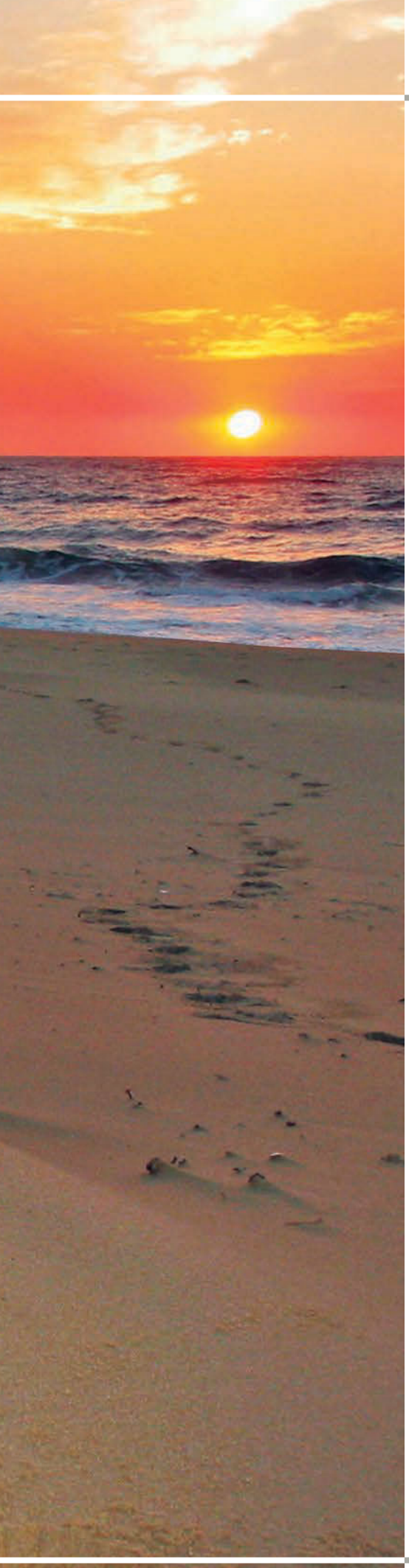

Coastal Vegetation of South Africa

14

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Figure 14.1 Evening mood with *Scaevola plumieri* (Goodeniaceae) on the coastal dunes of Maputaland (northern KwaZulu-Natal).

W.S. Matthews

List of Vegetation Units

1. Introduction: Distribution and Azonal Character of Coastal Vegetation

The vegetation of South African coasts owes its origin to two major seas—the Atlantic Ocean and Indian Ocean. These huge water masses not only shape the varied faces of the coast, but function as major factors creating the coastal climate, and indeed the climate of the subcontinent in general. Tides and salt spray are other controlling factors shaping the ecology of coastal habitats. Hence all vegetation units forming part of the coastal vegetation in this chapter and depicted by our Map are those of which the origin, structure and dynamics are a function of the sea and its immediate influence in terms of flooding by sea water, influence of salt spray, formation and re-formation of coastal sediments (beaches, dunes, old dune plumes).

The coastal vegetation of South Africa is very diverse and reflects the vastly different oceanographic and climatic conditions giving rise to a great variety of habitats occurring in this dynamic environment. These habitats result from the manifold and intricate interactions between sea and air temperature, geology and local topography, wind patterns and deposition of sand and salt, and of tidal regime. The coastal band forms a patchy series of offshore kelp 'forests' (in the west), sandy beaches, sand dunes and rocky headlands, interrupted by man-made beach fronts, harbours or estuaries. The coast extends from arid Alexander Bay (on the Northern Cape/Namibian border) on the Atlantic coast, along the semi-arid West Coast, around the famous Cape of Good Hope and Cape Agulhas (southernmost point of the African continent), further along the southern and eastern Indian Ocean seaboards as far as tropical Maputaland (northern KwaZulu-Natal) shared by South Africa and neighbouring Mozambique.

The macro-patterns of the coastal vegetation of South Africa are controlled by large-scale atmospheric systems over southern Africa and by the oceanography of the adjacent oceans. The climate is largely temperate to subtropical and is affected by two major sea currents—the cold north-flowing Benguela Current of upwelling inshore waters along the West Coast and the warm south-flowing Mozambique Current (extending southwards as the Agulhas Current) bringing equatorial waters with it and lapping the Indian Ocean coasts of South Africa (Lutjeharms 1998, Schumann 1998) (Figure 14.2). Due to its subtropical geographical position, South Africa's weather patterns are dominated by the interaction of three major pressure systems. As a result, the major winds along the coast are bidirectional and quasiparallel to the coastline. Southerly winds alternate with northwesterly winds on the West Coast, westerly with easterly winds along the South Coast, and southwesterly with northwesterly winds on the East Coast (Tinley 1985, Stone et al. 1998).

The coastline traverses a number of climatic regions, from the hyperarid and cool-temperate climate of the southern Namib coast at Alexander Bay, the semi-arid cool-temperate climate of the coast west of Cape Agulhas, the warm-temperate climate (with various precipitation regimes) to the moist subtropical coast of KwaZulu-Natal. The coastal extremes in temperature are in general dampened by the influence of marine air, increased cloud cover, high atmospheric humidity, the cooling effect of sea breezes, and the cold and warm currents flow-

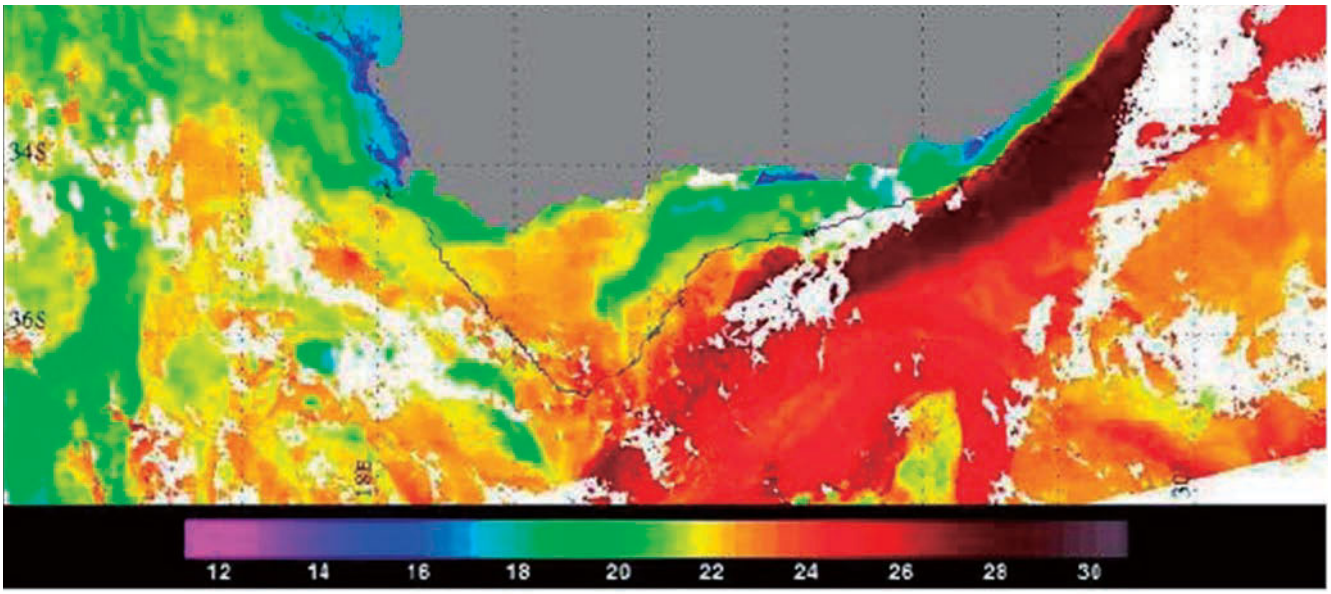

Figure 14.2 A high resolution NOAA-14 AVHRR thermal infrared composite satellite image (16-18-23 December). Colours show the sea temperatures (see the scale). The warm current along the southern and eastern coasts is the Agulhas Current, while the dark blue colour on the West Coast indicates the position of the Benguela Upwelling System. The dark line extending into the sea south of Cape Agulhas shows the edge of the continental shelf. Clouds appear white. (Courtesy of the American Meteorological Society; Rouault et al. 2002. Weather & Forecasting 17: p. 656.)

ing offshore. The West Coast is characterised by a low winter rainfall which decreases rapidly northwards, from 567 mm in Cape Town (Sea Point) to 449 mm at Koeberg (barely 25 km to the north) to 45 mm at Alexander Bay. The East Coast experiences rainfall increasing from 800 mm in the south to 1 300 mm at the border with Mozambique (compare various climate diagrams for our vegetation units: Figure 14.3).

The concept of azonality of coastal vegetation follows the same principles of zonality of vegetation as discussed in Chapter 13. Although the influence of (macro)climate is undeniable in shaping the biogeographical patterns within coastal vegetation, the ecological factors delimiting this vegetation from the zonal vegetation of the neighbouring biomes prevail. Tidal regime (combined with salt stress and inoxia resulting from submergence in water) is the major complex factor controlling the vegetation of salt marshes. On the rocky headlands the major habitat conditions are the lack of, or extremely impeded, soil development, combined with air-borne salt deposition, and disturbance brought about by frequent and strong desiccating winds. The dunes can be seen as an azonal substrate subject to heavy desiccation due to fast drainage (with good water storage properties but at depths beyond many plants on the often mobile substrate), relentless desiccating coastal winds, and extreme exposure to sun irradiation due to the high albedo associated with low biomass cover and light-coloured sand. The soils are rich in deposited marine salt, buried decomposing animal bodies and plant debris, and a high content of alkaline substances due to concentration of hard body skeletons of marine organisms (macroshells of marine molluscs, microcysts of dinoflagellates, etc.).

Strictly speaking, the concepts of zonality as defined by Walter (1964, 1973; see Chapter 13 in this book) should not apply to marine vegetation (such as seaweed and seagrass communities). The global patterns of marine vegetation are directly controlled rather by temperatures of the sea (to a large extent still under the influence of the local and regional climate) and salt concentration (Den Hartog 1970, 2003, Breeman 1988, Bolton & Anderson 1997) than by climatic parameters such as air temperature, precipitation seasonality and the like.

2. Origins of South African Coastal Features

The coasts of South Africa are as old as the African continent itself—logically their origin roots in the split of Africa from the southern supercontinent Gondwanaland (started 130 mya and fully accomplished around 60 mya). Changes in sea level along the South African coast during the Cenozoic (ca. 65–2 mya) reflect global levels and geological timescales closely. Transgressions, stillstands and regressions can therefore be dated internationally. The record of changes in sea level differs regionally because of, for instance, more complex geological conditions along the South Coast as compared to the West Coast, but coincides according to vertebrate and invertebrate fossil finds. The greatest differences between the current and palaeo-coastlines (dated back to around 5 mya) are found in the broad surrounds of Cape Town, around the present Cape Agulhas, and in Maputaland. Along most of the more steeply sloping coastal zones of the southern and eastern Cape with their incised river valleys, these features are less prominent (Marker 1988). In the Langebaan region four well-defined higher Cenozoic shorelines can be distinguished from the Late Tertiary, chronologically arranged at approximately 30 m (Late Miocene), 90 m, 50 m and 20 m (Late Pliocene) above current MSL.

The high sea level (about 25 m higher than today) of two important marine transgressions 5 mya and 1.5 mya led to the isolation of the Cape Peninsula and its split into two islands separated from the mainland by the broad Cape Flats Seaway and a narrow Fish Hoek Channel (Compton 2004). During the LGM (about 20 000 BP) the sea level was more than an estimated 125 m lower than today (due to much of the planet's freshwater stock locked in polar ice caps). As a result, the coastline of the southwestern Cape migrated up to 100 km seawards, exposing broad dryland benches around Cape Point, draining False Bay and exposing the continental shelf southwards beyond the present Agulhas Plain. The fossil canyon of the Breede River has been traced for some 70 km across the present sub-

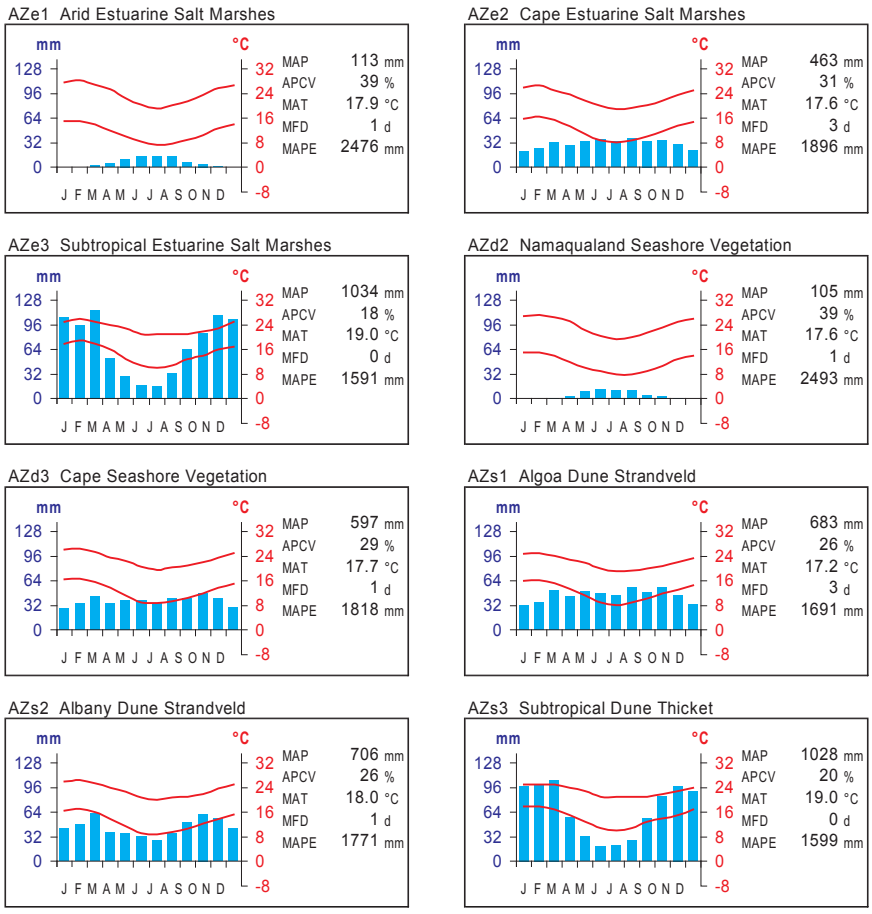

Figure 14.3 Climate diagrams of the coastal vegetation units (excluding AZd 1 Namib Seashore Vegetation due to lack of data, but see Figure 6.2 for climate diagram of Alexander Bay). Blue bars show the median monthly precipitation. The upper and lower red lines show the mean daily maximum and minimum temperatures, respectively. MAP: Mean Annual Precipitation; APCV: Annual Precipitation Coefficient of Variation; MAT: Mean Annual Temperature; MFD: Mean Frost Days (days when screen temperature was below 0°C); MAPE: Mean Annual Potential Evaporation.

merged Agulhas Shelf and similar canyons have been mapped for the larger rivers such as the Gamtoos on the East Coast (Marker 1988).

The coastal plains of Maputaland have also been witness to numerous marine transgressions and regressions which have recurrently altered the shape of these coasts. For instance, during the Last Interglacial (Eemian, also known as oxygen-isotope stage 5e) with sea level being approximately 5 m higher than today, an offshore barrier archipelago evolved which isolated a back-barrier environment comprising intertidal sand-flats, reefs and tidal channels. The last 9 000 years witnessed numerous changes in sea level in Maputaland shaping the current lagoon systems such as Kosi Bay and St Lucia and turning original salt-water lakes into freshwater bodies such as Lake Sibaya (Wright et al. 2000). As can be expected, estuarine landforms are essentially features that develop along transgressive shorelines following a rise in sea level because of the higher energy wave action depositing sediments and building sand bars across river mouths. These geomorphic processes were paralleled in similar fashion in the shaping of the Wilderness lake system and by development of other lagoons along the southern and western coasts (Reddering & Rust 1990).

Throughout the Cenozoic, the southeastern coast of southern Africa has been characterised by a long series of marine transgressions and regressions, induced both by continental uplift (see Partridge et al. 1995 for an exhaustive summary), seaward marginal tilting of the subcontinent (De Wit 1993) and glacio-eustatic sea level movements. These increases and decreases occurred in response to accumulation and melting of ice caps (Maud & Botha 2000). Of all the marine transgressions revealed after the Mid-Miocene, the Early Pliocene transgression reached the maximum elevation of 80–90 m (Haq et al. 1987). In the Langebaan region a major Middle to Late Miocene transgression formed a 30 m palaeo-shoreline along which the phosphatic layers were deposited in the inundated valleys along the coastline that preserved the fossils at the Langebaan Fossil Park. The later regression that produced the maximum 90 m shoreline left present hilltops as isolated islands and the mouth of the Berg River entering the sea near present-day Langebaan, only to shift northwards with the rising sea level (Erasmus 2005).

The current South African coasts are a mosaic of various geologies—a chronicle of geological history of the subcontinent. There are hard rocky coasts built of sandstone and hard mudstones (Silurian-Devonian Table Mountain Group, Silurian Natal Group), granites (mostly Cape), Malmesbury shales and Beaufort sandstones and mudstones (see for instance Marker 1988, Boucher & Le Roux 1993, Taylor & Boucher 1993, Weisser & Cooper 1993 for regional accounts of coastal geology). These older geological formations are contrasted, however, by much younger unconsolidated Cenozoic sediments of Tertiary age deposited in the coastal lowlands as sands of littoral marine, estuarine, lacustrine and aeolian origin and reaching prominence along the western and southern Cape and Maputaland in the extreme east (see Maud 2000, Maud & Botha 2000, Compton 2004 for summarising accounts for various stretches of the South African coast).

The present-day estuaries at South African river mouths are still younger geological phenomena, both due to the dynamic character of the sedimentation cycles and the evolutionary changes in the subcontinental drainage network (De Wit 1993, 1999) which often resulted into decay and emergence of new river mouths. The major erogenetic uplift and marginal tilting of the eastern hinterland of the subcontinent in the Late Pliocene caused severe marginal erosion along the southeast coasts, which destroyed all vestiges of truly estuarine deposits older than the Pleistocene (Maud 2000). Global climate change during the next 100 years is expected to cause a considerable rise in sea level (around 0.5 m is predicted) because of polar ice-cap melt. The coupled isostatic settling of the crust due to the added weight of water over the wide (especially Agulhas) continental shelf (Reddering & Rust 1990) may exacerbate the effect of the rising sea levels in estuaries and coastal lakes by a further 25%.

3. Ecology of Coastal Habitats

Since the sea is the major source of habitat variability on the coast, the character and location of coastal habitats is very much dependent on the distance from the seashore (in terrestrial habitats such as coastal dunes) or by the intensity of influence of sea (tidal) waters (in semi-aquatic habitats such as salt marshes). In South Africa, coasts and the sea enjoy the interest of scientists and the public. A number of scientific compendia (Day 1981a: estuaries, McLachlan & Erasmus 1983: beaches), review papers (Brown & Jarman 1978: coastal marine habitats, Boucher & Le Roux 1993, Taylor & Boucher 1993, Weisser & Cooper 1993, Lubke et al. 1997, Lubke 2004: coastal vegetation, Bolton & Anderson 1997: marine vegetation), reports and series (Heydorn & Tinley 1980: estuaries, Tinley 1985: dunes, McGwynne & McLachlan 1992: coastal management), but also popular and semipopular books on coastal and sea biota (Branch & Branch 1981, Lubke et al. 1988, Lubke & De Moor 1998) contain valuable information and sources on ecology and biodiversity of the marine and coastal flora and vegetation. Therefore, we shall concentrate only on selected features of the coastal vegetation, especially those that underlie the current classification and mapping of these ecosystems.

3.1 Aquatic and Semi-aquatic Habitats

3.1.1 Algal Beds

Algal beds are a very special habitat, usually straddling the ecotone between the sea and firm land. Coastal tidal pools, found on rocky platforms in the intertidal zones (Figure 14.4) are a prime habitat for marine algal assemblages. Tidal dynamics create a series of habitats from those permanently under water to those being intermittently exposed during the ebb. Fascinating zonation systems are formed along the tidal gradients (Bolton & Anderson 1997). Kelp beds are formed inshore and although they are exposed to tidal fluctuations, they stay permanently under water. They reach as far as 3 km from the seashore into the open sea, but they prefer sheltered coastal coves.

Further details on ecology, patterns and processes, utilisation and other relevant aspects related to algal beds and marine vegetation in general can be found in in-depth reviews such as those by Branch & Branch (1981) and Bolton & Anderson (1997).

3.1.2 Estuaries

Ecology of Estuaries: Tides and Salinity

Estuaries are places where freshwater of a river meets the salt water of the sea or coastal lagoon and where gradual transitions in physical, chemical and biological characteristics between freshwater and seawater ecosystems can be found (Day 1980, 1981a, Ketchum 1983, Heydorn 1989a). Dynamics of water flows (tides and river input), mixing of fresh and salt waters, erosion and sedimentation processes mould an intricate system of microhabitats making up the phenomenon

called 'estuary' (Figure 14.5). There have been many types of estuaries described based on origin and hydrodynamics (see Day 1981a, Ketchum 1983 for accounts of systems), but for our purpose we shall consider only two major types of estuaries—the open and closed (permanently and temporarily). This simple classification system is supposed to reflect the role and strength of tidal influence in controlling the patterning and dynamics of estuarine habitats.

L. Mucina

Figure 14.4 Salt marshes of the Kromme River Estuary at St Francis Bay, dominated by chenopods such as *Sarcocornia perennis* complex, *Salicornia meyeriana* and *Chenolea diffusa*.

Estuaries are usually composed of sublittoral marine zones (permanently under water), intertidal flats experiencing different periods of flooding (depending on the local tidal conditions and topography), and supratidal terraces. The supratidal zone refers to the area that is situated above the intertidal zone, formerly part of flooded flats and mostly outside the direct tidal influence except for spring tide and other associated high water levels. The floodplain is the area adjacent to the supratidal and is elevated above the rest of the estuary. This area is normally covered with water only during large flood events. In estuaries where the mouth closes the intertidal habitat is reduced or absent. Sometimes freshwater seeps and water springs add a new facet to the estuarine habitat mosaic (see O'Callaghan 1994a, Mucina et al. 2003 for sources on South African salt marshes and related habitats). In places, salt pans are also present, usually indicating the position of tidal creeks a long time ago and currently severed from the contact with the sea.

At the low tidal boundary, some sublittoral tidal flats experience exposure to terrestrial conditions at the lowest tidal conditions (neap tide). Here seagrass 'meadows' are built by rhizomatous graminoids ('rosulate herbs' *sensu* Cook 2004) of the families Zosteraceae (*Zostera capensis*) and Cymodoceaceae (*Halodule*, *Thalassodendron*). Calm brackish pools of deeper creeks within the estuaries often house submerged macrophyte vegetation tolerant of some levels of salinity. Typical aquatic plants of these habitats include salt-tolerant charophytes of the genera *Chara, Lamprothamnium*, *Nitella* and *Tolypella* as well as short-lived angiosperms of the genera *Ruppia*, *Althenia*, *Pseudalthenia* and *Zannichellia*. The life form of all these organisms is classified as 'vittate herb' by Cook (2004). Submerged macrophytes such as pondweed (*Potamogeton pectinatus*) occur only in small freshwater-dominated estuaries.

Intertidal *Spartina maritima* meadows (Pierce 1979, 1982) are a common sight in open estuaries, but they are absent from temporarily closed or closed estuaries, which may be attributed to the plant's requirements for tidal flooding and saturated substrates (Adams & Bate 1995).

A study of four Eastern Cape estuaries (Adams et al. 1992) showed that in the temporarily open/closed Seekoei and Kabeljous Estuaries, diversity and cover of emergent macrophytes was lower than that of the permanently open estuaries (Gamtoos and Kromme). This was attributed to the availability of suitable habitat, fluctuating water levels and periodic hypersaline conditions. Grasses were the dominant plants as species such as *Sporobolus virginicus* grow well under waterlogged conditions and can withstand long periods of submergence (Breen et al. 1977). Closed mouth conditions and an increase in water level result in a rapid die-back of succulent plants. When the mouth opens again and the water levels drop, the resident seed banks play an important role in the re-establishment of salt marshes, e.g. *Triglochin* species in the Great Brak Estuary and *Sarcocornia* species in the Seekoei Estuary. Similarly in the Lake St Lucia system, Ward (1976) found that decreases in water levels in open saline or brackish soils led to colonisation by species of genera such as *Salicornia*, *Sarcocornia* and *Atriplex*. When lake levels rose again, these species were killed off since they are intolerant of prolonged inundation.

L. Mucina

Figure 14.5 Algal beds in tidal potholes on the limestone coast of De Hoop Nature Reserve near Arniston, Western Cape.

There are few obvious links between elevation and tidal regime on one hand and salinity on the other. Adam (1990) reported an inverse linear relationship between salinity and elevation, while

maximum salinity peaked just below maximum high-water spring tide level. Adams et al. (1992) found that sediment salinity of the intertidal macrophyte communities was determined by the salinity of the adjacent water body, since these species are daily inundated by tides. Fluctuations in water column salinity would therefore raise and lower sediment salinities, which would influence macrophyte germination and growth. Salt-marsh plants are dominant at salinities between 10 and 35 ppt. Only a few species germinate in salinities greater than 20 ppt. One of the most critical stages in the life cycle of halophytes is the period of germination and establishment. For the successful establishment of plants in saline environments, seeds must be able to remain viable at high salinities and germinate when the salinity is reduced (Ungar 1978, 1982, 1987). The ambient salinity in a salt-marsh system is not influenced only by the tides. De Leeuw et al. (1991) detected the position along a salt-marsh elevation profile above which substrate salinity was affected by climate variables rather than by tidal regime. According to Adams et al. (1992) supratidal macrophytes are usually associated with low moisture content due to limited tidal flushing in this area, thus rainfall and evaporation are more important in influencing the distribution of these species. Occasional events of flooding can result in increased water levels and in flushing out salts from this habitat.

Recent studies have indicated groundwater salinity and depth to groundwater as important determinants for supratidal and floodplain salt marshes (Bornman et al. 2002, 2004a, b). The Olifants Estuary has the largest area of supratidal (143 ha) and floodplain salt marsh (797 ha) on the dry West Coast (Table 14.1). A single species, *Sarcocornia pillansii*, is dominant in this dry saline habitat. Bornman (2002) showed that the survival of the plants was dependent on the utilisation of saline groundwater particularly during the dry period (eight months) of the year. The cover abundance of *S. pillansii* was visibly reduced where the water table was deeper than 1.5 m and/or where the electrical conductivity of the groundwater had a high ion concentration (>80 $mS.cm^{-1}$). Flooding of the estuary is important in lowering the salinity of the water column, which influences groundwater salinity. Any disturbance to this habitat will result in large areas of bare ground as has happened at the mouth of Orange River (Bornman et al. 2004a).

An investigation by Walker (2004) in the East London estuaries (Tyolomnqa to Kei) showed that reeds, sedges and supratidal salt marsh were found in all estuaries. The supratidal salt-marsh communities are similar to those of permanently open estuaries. Species dominance varied depending on salinity. Compared to permanently open estuaries, temporarily open/closed estuar-

Table 14.1 List of available information on South African estuaries with the largest intertidal and supratidal salt marsh areas and the change in area over time. Past cover (ISM & SSM past, in hectares) was estimated from 1937 or 1961 aerial photographs (Colloty et al. 2001), while the present cover (ISM & SSM pres, in hectares) reflects the situation in 1998. All estuaries with present area >20 ha were included. **Reg**: Bioclimatic region (cT: cool-temperate, wT: warm-temperate, Sub: subtropical). **Class**: Classification system (EB: Estuarine Bay, ELS: Estuarine Lake System, PO: Permanently Open, RM: River Mouth, TO/C: Temporarily Open/Closed). **ISM**: Intertidal Salt Marsh. **SSM**: Supratidal Salt Marsh. **TSM**: Total Current Salt Marsh.

Estuary	Locality	Reg	Class	ISM pres	ISM past	SSM pres	SSM past	TSM
Berg	32°46'S/18°09'E	cT	PO	141.8		1536.1		1677.9
Olifants	31°42'S/18°11'E	cT	PO	91.9		940.1		1032.0
Knysna	34°03'S/23°04'E	wT	EB	634.0	406.0	60.0	389.2	694.0
Langebaan	33°07'S/18°03'E	CT	EB	123.3		250.6		373.9
Keiskamma	33°17'S/27°29'E	wT	PO	210.0		91.3	311.8	301.3
Gamtoos	34°00'S/24°56'E	wT	TO/C	40.0	112.5	163.2	245.1	203.2
Great Fish	33°30'S/27°08'E	wT	PO	46.7	47.3	152.3	154.2	199.0
Orange	28°38'S/16°27'E	cT	RM	84.0	290.0	107.8	136.8	191.8
Swartkops	33°57'S/25°38'E	wT	PO	165.0	215.0	5.0	40.0	170.0
Kromme	34°09'S/24°51'E	wT	PO	18.1	17.6	67.2	74.0	85.3
Mhlathuze	28°49'S/32°05'E	Sub	EB	60.0	50.0			60.0
Mtati	33°25'S/27°16'E	wT	TO/C			54.3	69.3	54.3
Duiwenhoks	33°22'S/21°24'S	wT	PO	50.8				50.8
Breede	34°24'S/20°51'E	wT	PO	20.5	22.5	29.6	32.2	50.1
Cefane	32°49'S/28°08'E	wT	TO/C	28.1		21.4		49.5
Goukou	34°23'S/21°25'E	wT	PO	44.2				44.2
Keurbooms	34°02'S/23°23'E	wT	PO	42.9				42.9
Mlalazi	28°57'S/31°48'E	Sub	PO			39.3	204.5	39.3
Kowie	33°36'S/26°54'E	wT	PO	35.2				35.2
Heuningnes	34°43'S/20°07'E	wT	PO	28.2				28.2
Gourits	34°21'S/21°53'E	wT	PO	21.1				21.1
Mthatha	31°57'S/29°10'E	Sub	PO			21.0	26.9	21.0
Tyolomnqa	33°14'S/27°35'E	wT	TO/C	3.7	10.5	15.7	30.2	19.4

ies did not have intertidal species such as the white mangrove *Avicennia marina* and the grass *Spartina maritima*. These estuaries lack intertidal salt-marsh and mangrove communities.

Plant Adaptations and Life Forms

Plants in salt marshes face challenges such as high and variable salinity, hypoxia and anoxia (albeit only temporary in some habitats), and unusually high concentrations of toxic compounds such as hydrogen sulphide or methane. Disturbance in the form of sudden surges of water rushing down the river beds after particularly heavy rains and associated increased sedimentation rates or man-made water pollution exacerbate the harsh saline environment. The response of the plants to these challenges are manifold and fascinating. Plants react to the lack of oxygen in subtidal and intertidal habitats usually by intricate mechanisms often involving regulation of gas transport, metabolic adaptations and changes in morphology mediated by hormones (e.g. Crawford 1982, 1992, Armstrong et al. 1994a).

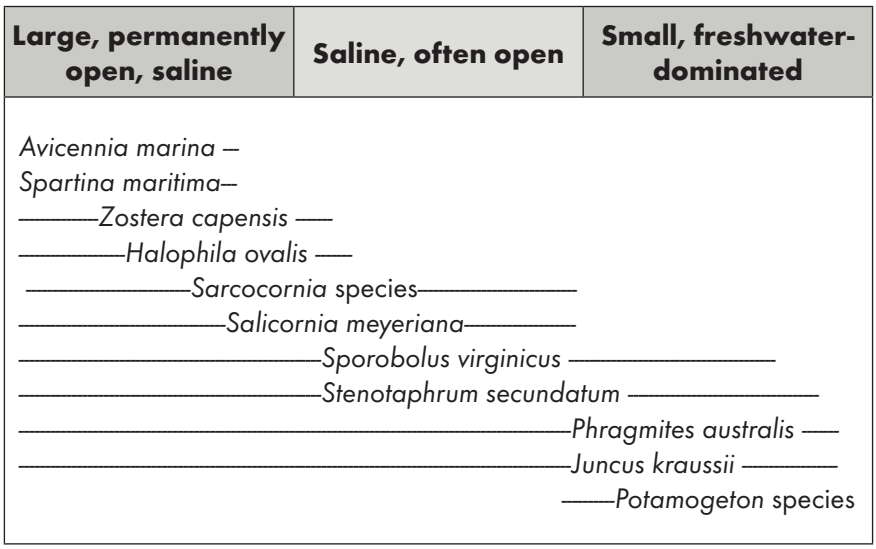

Figure 14.6 Conceptual scheme for the distribution of dominant macrophyte species across different estuary types. The position of the species in the chart indicates the estuarine type in which it is most dominant, while the line indicates the full extent of its range (modified after Walker 2004).

In simple terms, plants tolerating the high concentrations of salt in the environment are usually called 'halophytes' (e.g. Flowers et al. 1977, 1986)—obligate or facultative, the former depending on whether the salt in high concentration is indispensable for optimal functioning of the organism. A high concentration of salt in the environment assists in the development of a plethora of ecomorphological and ecophysiological adaptations (e.g. Flowers et al. 1977, Ungar 1991), which obviously are not of monophyletic origin, yet they do show a certain relation to taxonomic categories. Several major 'physiotypes', based on specific patterns of ion uptake, have been recognised (Albert & Kinzel 1973, Albert 1982, Choo & Albert 1997).

The ecophysiological typological literature on halophytism (Steiner 1934, 1939, see also Albert 1982) recognises several types of strategies how plants cope with a surplus of salt: (1) The 'salt regulators' are able to restrict the dangerous increase of internal salt concentration either by desalination of their tissues through salt glands (*Limonium*) or through increase of succulence (many chenopods including *Sarcocornia, Salicornia, Chenolea, Suaeda* and vygies such as *Disphyma*). (2) The 'salt accumulators' are not able to prevent continuous increase of salt, but develop a series of mechanisms to remove the concentrated salt, for instance by shedding oversaturated tissues (*Plantago*). (3) The category of 'root filtrators' (the 'root excluding types' of Albert 1975) make use of root exclusion capacity of root membranes (Poaceae, e.g. *Puccinellia*). This mechanism, however, seems to be common in both halophytic and nonhalophytic grasses (see Albert 1975 for references).

Succulence (associated with osmotic compensation in old leaves) is a common phenomenon in halophytes and occurs throughout the taxonomic spectrum of plants in estuaries (Aizoaceae, Plantaginaceae, Asteraceae, Caryophyllaceae, Chenopodiaceae). In fact, interesting morphological convergences can be observed with regard to succulence, including a syndrome involving long, slender stems forming a tangle of short half-cylindrical to cylindrical (succulent) leaves. These syndromes include *Chenolea diffusa* and *Suaeda inflata* (both Chenopodiaceae), *Spergularia media* complex (Caryophyllaceae), *Poecilolepis* and *Cotula coronopifolia* (both Asteraceae). Saline environments are considered highly stressed (inductive only to limited growth), hence clonal growth (in the past often referred to as 'vegetative reproduction') should be of great importance to survival here. Indeed many dominant plants in South African estuaries show several modes of clonal growth involving nodal rooting of procumbent stems (*Sarcocornia*), above-ground parts or tillers and stolons (*Paspalum*, *Spartina, Stenotaphrum*), rhizomatous systems (*Halodule, Triglochin, Zostera*), and tillering typical of tussock graminoids such as *Puccinellia angusta* and *Juncus kraussii* (L. Mucina, unpublished data).

Uncertainty and harshness of the salt-marsh habitats are reflected not only in omnipresent clonality, but also by the presence of some annuals such as *Cotula filiformis*, *Salicornia meyeriana* and *S. pachystachys*, as well as by the occurrence of heterocarpy and the accumulation of permanent seed banks. Heterocarpy is known, for example, in *Spergularia* (Salisbury 1958, Telenius & Torstensson 1989) and in *Atriplex* (Khan & Ungar 1984)—both taxa with close relatives in South African salt marshes.

Community Structure and Dynamics

Regularity of the tidal regime, at least in permanently open estuaries, is the underlying factor controlling the formation of distinct vegetation zoning (e.g. Chapman 1974, Long & Mason 1983, Adam 1990) along a tidal elevation gradient including the distinct subtidal, intertidal and supratidal habitats (Figures 14.6 and 14.7). Local changes in microtopography can result in mosaics rather than distinct zonal bands. It has been suggested that several ecological factors, including abiotic environment filters and biotic interactions, control formation of zonation in salt marshes. Most important are tidal inundation frequency and hypoxia related to elevation of microsites (see for instance Olff et al. 1988, De Leeuw et al. 1993, Armstrong et al. 1994a, O'Callaghan 1994a–e, Sanchez et al. 1996, Mucina et al. 2003) together with the influence of biotic interactions such as competition (Pennings & Callaway 1992), grazing (Bakker & Ruyter 1981, Olff et al. 1997) and parasitism (Pennings & Callaway 1996, Callaway & Pennings 1998). In the past, facilitation received very little attention as a factor in structuring salt-marsh plant communities. Callaway (1994) has shown that shrubby *Arthrocnemum subterminale* (Chenopodiaceae) facilitated the

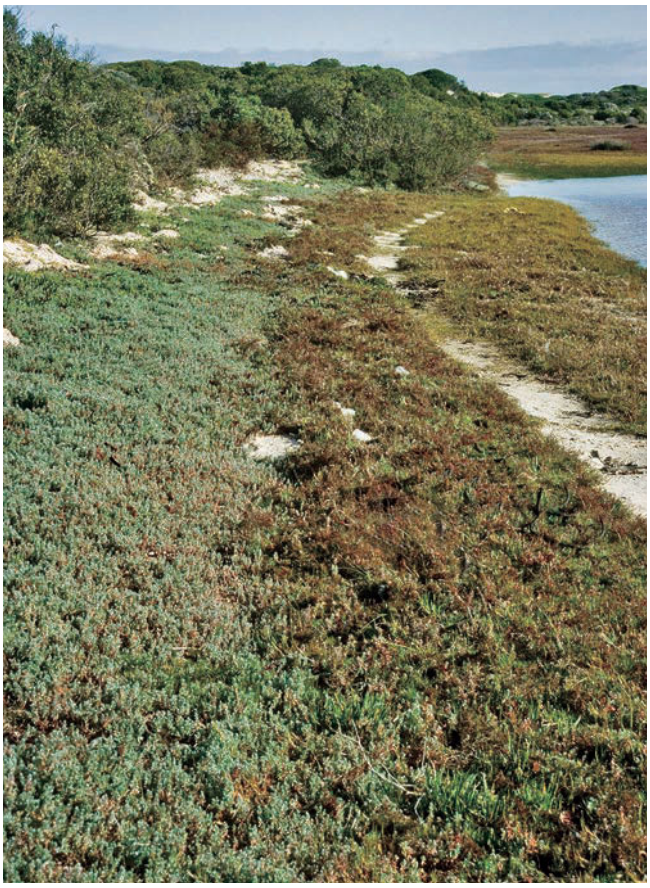

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Figure 14.7 Tidal salt-marsh zonation on the banks of the estuarine Bushmans River at Kenton-on-Sea (Eastern Cape). The lower zone is formed by a mixture of *Sarcocornia perennis* complex and *Salicornia meyeriana*, while the upper zone is dominated by *Chenolea diffusa* (all members of the Chenopodiaceae).

survival of several annuals in a Californian salt marsh, possibly through alteration of soil conditions such as mounding of soil under shrubs and lowering soil salinity under shrubs, hence creating favourable germination conditions. Callaway & Pennings (2000) reported on how several less competitive species can profit from the ability of *A. subterminale* to buffer the strong competitive effect of the perennial grass *Monanthochloe littoralis*. Leaking oxygen transported from leaves to roots through aerenchymous tissues of plants well adapted to hypoxia can enhance aeration of the substrate (soil oxygenation) and oxidation of iron, manganese and sulfide, hence ameliorating conditions for germination and survival rates in other associated plants in marsh communities (see Callaway 1995 for a review).

Generally low numbers of seeds have been found in salt-marsh zones (see for instance Leck 1989 and Ungar & Woodell 1993, Wolters & Bakker 2002 for references). Ungar & Woodell (1993) summarised the reasons for this paucity in terms of five possible factors including rapid germination, wash-out of seeds by tidal action, herbivory, inability of seeds to maintain dormancy, and parasitism. The major feature of the seed bank ecology in tidal salt marshes appears to be the differentiated correspondence between components of the above-ground vegetation and composition of the salt-marsh seed banks. Ungar & Woodell (1993) found a relatively high similarity between standing vegetation and seed banks in annual-dominated communities, while low similarities were found between vegetation dominated by perennials and the seed banks.

Very prohibitive ecological filters such as high salinity and hypoxia impose stress on the growth of plants. Decrease in species richness was observed with an increase of salinity (Garcia et al. 1993 for a salt-marsh profile, and Grillas et al. 1993 for a group of submerged macrophytes). The latter authors also found that higher species richness is associated with moderate values of above-ground biomass. The generally low species richness is exacerbated by the tendency of many salt-marsh dominants to use clonal growth as an effective strategy in the pre-emption of space.

Landscape-shaping Functions

Orson & Howes (1992) showed that salt marshes can remain stable for hundreds, even thousands of years. Temporal changes are most often associated with anthropogenic disturbance.

Salt marshes have a number of important functions that include sediment stabilisation, bank protection and filtering of sediment and pollutants. They are a source of primary production and provide a habitat and food for a variety of marine and estuarine species. They are essential inorganic and organic sources of nutrients for estuaries, although the degree of tidal flushing is important in determining how much of the nutrient is released to the water column (Childers & Day 1990). Salt marshes may make a disproportionately large contribution to the primary production of an estuary. For instance, although they cover only 38% of the area of the Kromme River Estuary, marsh plants contribute over 78% of the total primary productivity. However, less than 10% of this production enters the grazing food chain, the remainder being broken down to sediment detritus (Heymans & Baird 1995).

The conservation value of this vegetation lies in the fact that halophytes are the only plants adapted to grow in these harsh environments and the loss of this vegetation would lead to the formation of bare, dry salt pans that are more easily eroded by wind and water.

3.2 Terrestrial Habitats

Terrestrial coastal habitats are those which are not flooded (by sea or estuarine waters) for most part of the day. (Technically the supratidal terrace of a salt-marsh system is a terrestrial habitat too. However, we prefer it to be handled as a salt-marsh habitat.) Beaches, sand dunes and rocky headlands (coastal cliffs), supporting vegetation which does not show signs of tolerance towards prolonged flooding are the typical coastal terrestrial habitats. Although outside influence of tidal flooding, these habitats remain under direct influence of the sea through the deposition of salt spray and of fine air-borne sediments of sea origin.

According to the type of shoreline, Lubke et al. (1997) estimated that about 50% of the coastline is made of fine-grained sands and about 12% of coarse-grained sands, 19% of exposed rocky headlands, 17% of wave-cut rocky platforms, while pebbles/shingle beaches form less than 1% of the coastline.

3.2.1 Sandy Beaches and Dunes

About 70% of South Africa's 3 000 km long coastline is made up of sandy shores. They are extensive and contain many different types of habitats. Tinley (1985; see also Figure 14.8) has devoted much attention to describing coastal dune habitats and suggested a classification system for both coastal dunes (Tinley 1985, p. 17) and vegetation zones (Tinley 1985, p. 127–149) reflecting the age of the substrate, microtopography, and eventually also the stage of vegetation succession.

Below we shall use four pragmatic habitat zones on the sandy coasts, reflecting the position along landward gradients and age

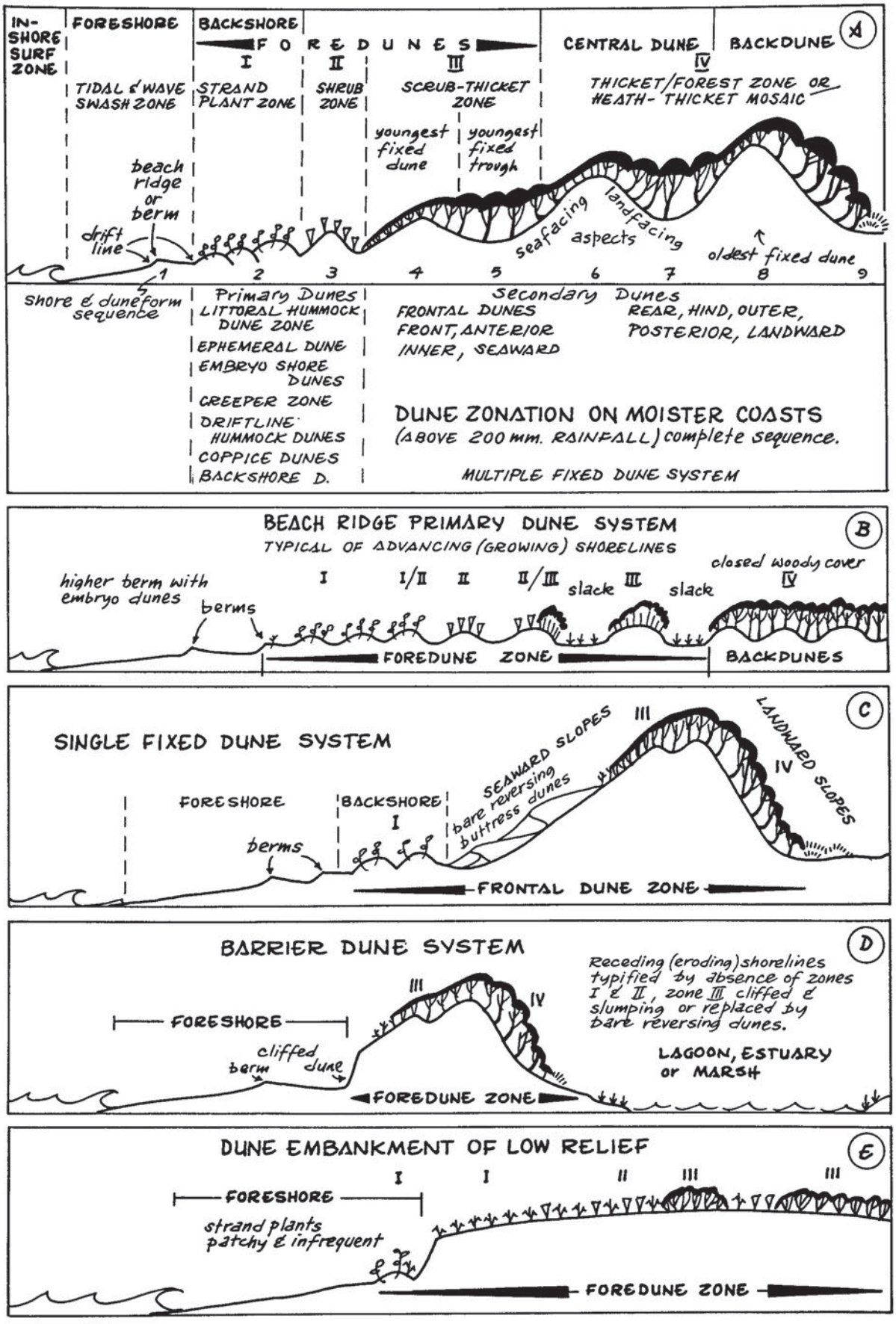

Fig 1 COAST DUNE NOMENCLATURE & VARIATIONS OF ZONATION SEQUENCES.

Figure 14.8 Coastal dune nomenclature and variations of zonation sequences (from Tinley 1985).

of the substrate. Our system includes: (1) sandy beaches (mostly 'vegetation-free'), (2) moving (young) foredunes, (3) stabilised (old) backdunes and (4) dune slacks.

Beaches

Sandy beaches dominate much of the shorelines of the seas of the world (McLachlan & Erasmus 1983, McLachlan 2000). They are unstable sea-borne sediments and debris at the direct sea/land interface—being reworked relentlessly by waves (at lower boundary) and wind (at upper boundary). Tinley (1985; see also Figure 14.8) calls this habitat 'foreshore'. Beaches are a very dynamic environment, constantly adjusting to erosion and accumulation forces in the littoral zone due to changes in wave regime and sidewash currents (Tinley 1985).

Pebble and shingle beaches are a rare phenomenon in South Africa, but shelly beaches, grading into true shell beds are common along the arid West Coast (Figure 14.9).

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Figure 14.9 Strandline formed by coastal shell bed and deposits of fragments of dead thalli of Cape kelp (*Ecklonia maxima*) on the coast at Betty's Bay (Western Cape). The vegetated zones in the foreground are formed by southern African coastal endemics such as *Tetragonia decumbens* (Aizoaceae) in the seaward zone and the grass *Thinopyrum distichum* in the inward zone.

The beach is a hostile environment for plants, hence beaches usually appear barren, without plant life. At the upper beach boundary, berms (beach ridges—unstable embryonic dunes) are formed which may support a few hardy 'pioneer' species such as *Arctotheca populifolia* and *Ehrharta villosa* var. *maxima* that are able to tolerate strong winds, high salt loads and rapid sand movement.

At the upper edge of the swash zone (just where the water surf would retreat back to the sea), much debris can accumulate. In regions where much dead material floats on the sea, this material often accumulates in the form of narrow belts of decaying debris on the beach, forming a special microhabitat called 'strandline' (Figure 14.10). High nutrient input ameliorates the soil conditions in these narrow zones, enabling some nutrient-demanding plant species (e.g. *Atriplex patula* subsp. *austroafricana, Tetragonia decumbens*) to establish. This coastal vegetation type has never been studied in South Africa. Its northern hemisphere analogue is known to syntaxonomy as the Cakiletea maritimae (see Mucina 1997).

Moving and young dunes

Coastal dunes form where sand is deposited onshore by the sea and at river mouths, or exposed by a dropping sea level as during the glacial. Dunes are piles of sand strongly variable in volume, shape (see Tinley 1985, p. 17 for a classification system), mobility (depending on age and vegetation cover and extent of root systems), and sometimes also in physical composition (depending on ratio of sand to other ingredients such as fine loamy particles, shells and other debris). As the accession of sand proceeds, the coastal dunes undergo development—they grow, accumulate humus particles, and finally become overgrown and stabilised by vegetation. Where conditions allow, zoned dune systems of progressing age are formed (see Figure 14.8 for various coastal dune patterns).

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Figure 14.10 Shell beds on the beach are a by-product of nutrient-rich upwelling coastal waters along the West Coast known for their high biomass productivity. Shown here is Mc Dougall's Bay, Port Nolloth (Northern Cape).

Dunes are (or have been) an integral part of an active littoral zone forming a single geomorphic unit, where sand is shifted between four compartments, including (1) beaches, (2) frontal dunes, (3) inshore or surf zone sand bars and banks, and (4) river mouths and estuaries (Tinley 1985). The link between these compartments is vital for the existence of an active dune system. Sandy sediments transported by rivers appear as the most important source of coastal sand as witnessed by increased accumulation of sand on coastal stretches near river mouths, especially those draining water basins with increased erosion activity. Much of the sand pre-destined to form coastal dunes is transported by so-called longshore (littoral) drift propelling the sediments along the southern African coasts northwards along the West Coast

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Figure 14.11 Salt-laden spray hovering over coastal dunes and strandveld thickets (in the background) of the Dune Park near Plettenberg Bay (Western Cape). The dominant creeping, succulent shrub covering the foredunes is *Tetragonia decumbens* (Aizoaceae).

and eastwards along the South and East Coasts. Past a specific point, the longshore transport is of the order 0.5 to 2 million m^3 per year (Heydorn & Tinley 1980, Tinley 1985). It has been estimated that about a third of the sand transported by the longshore drift is returned to land to form dunes (Compton 2004).

Dunes act as a natural sand reservoir for the replenishment of beaches during periods of erosion. They also serve as an important buffer zone between the sea and land, protecting coastal developments from flooding and wave damage. Vegetation is vital to this functioning as it helps to trap mobile sand, stabilising the dunes.

The dunes located closer to the beach or occurring on the upper boundary of the beach are called foredunes and they are 'young' in terms of their phase of development. The classic environmental factors and stresses associated with young dune environments include, salt spray, intense solar radiation (incident and reflected), high substrate mobility, abrasive substrate, low water-retaining capacity of the substrate, high wind speeds, large temperature fluctuations, high air and substrate temperatures, low concentration of macronutrients, and episodic over-wash and immersion (Barbour et al. 1985, Hesp 1991).

Due to the dynamic nature of the moving, hence young dunes, the vegetation occurring in these habitats has only a transient character and can disappear with a single storm event or change in response to changing environmental factors. The plants occurring in such unstable habitats are often called 'pioneers' as they are adapted to grow ahead of the accumulating sand, stabilising it so that other plant species can become established as the dune matures (Tinley 1985, Lubke & De Moor 1998) by building phytogenic hummocks, for which Hesp & McLachlan (2000) featuring aspects of ecology of South African coastal dunes, used the appropriate Arabic term *nabkha*. Near the sea, only a few pioneer plants withstand the salt spray (Figure 14.11), wind and unstable sand.

The microclimate, which is created by proximity to the sea, geomorphology, shading from other plants and the interaction with animals, also influences the vegetation locally. Each species has different adaptations to deal with these environmental stresses. While most species may tolerate sand burial, others may be stimulated by high accretion rates (*Ammophila arenaria*; see Knevel 2001). Salt spray contributes to the physiological desiccation of plants, and can also be responsible for zonation patterns (Donnelly & Pammenter 1983). In addition, dune plants often possess xeromorphic attributes. For example, leaf hairs (*Arctotheca populifolia*; Ripley et al. 1999), leaf succulence, waxy cuticles (*Scaevola plumieri*; Pammenter 1983), leaf rolling and sunken stomata (*Ammophila arenaria*; Peter 2000) are all traditionally associated with plants of dry environments. Yet there is little consensus as to whether it is a xeric environment, as there is still little information on the extent to which dune plants experience water stress (Peter 2000). Many species have extensive root systems and probably utilise the dune aquifer water (Peter & Ripley 2000), while others may utilise water in the superficial layers of sand resulting from precipitation, dew or fog (Barbour et al. 1985, Köpke 1988).

Old stabilised dunes

As the stabilisation of dunes progresses, primitive dune soils enriched by humus are formed, allowing establishment of shrubby vegetation which protects the dune (soil) surface from moving, desiccation, and removal of litter by wind, thus further enriching the soils.

On the established foredunes a little further inland, the pioneer species give way to coastal dune shrubland. Due to their generally dense cover, these shrublands have been termed 'thicket'. Where exposed to wind (and associated sand blasting during

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Figure 14.12 Alexandria Dune Field: One of the largest coastal seas of sand in the southern hemisphere (a view from Diaz Cross near Boknes westwards).

Figure 14.13 A: Miocene aeolinite coastal cliffs on Swartklip in the Wolvengat Nature Reserve near Khayelitsha (Cape Town). B: Coastal rocks built of Table Mountain Group sediments at Cape Point (Cape Peninsula), with typical TM sandstone in the upper layers and dark slates of the Graafwater Formation at the base. C: Cape granite coastal rocks with dolerite intrusions (dark rock) that penetrated the granite plutons at the time of the break-up of Gondwana. D: Large boulders of Cape shale on the stony beach of Kogelbaai near Rooiels in False Bay (Western Cape). Photographer: L. Mucina.

stormy weather) and frequent salt spray 'showers', the windward stands of the coastal thicket are low and 'wind-sheared' in places. Species such as *Morella cordifolia, Passerina rigida, Rhus crenata, Robsonodendron maritimum* and *Maytenus procumbens* as well as climbers such as *Cynanchum natalitium* and *Rhoicissus digitata* are typical of such habitats. On leeward slopes of the older dunes, tall thickets can develop; these are also found on the oldest and best stabilised dunes, sometimes deep inland. This vegetation consists of a dense community of dwarf(ed) trees and shrubs with a compact canopy flattened by wind pruning. Instead of a dense understorey, there is a thick layer of plant litter covering the sandy floor.

In areas of high rainfall and well-developed soils, dune thicket communities can develop on the oldest dunes (backdunes) furthest from the sea. In sheltered dune depressions in the south (Eastern Cape) and on the leeward slopes in general in a broad band in the north (KwaZulu-Natal), dune forests replace the dune thickets (see Von Maltitz et al. 2003 for detailed descriptions of these dune forests; see also Chapter 12 in this book).

In the low-rainfall areas—from De Hoop as far as Kenton-on-Sea—several dunefields are found (i.e. Alexandria Dunefield; Figure 14.12). They are built of relatively old dunes, but the foredunes remain largely unvegetated. Few plants are adapted to withstand these conditions of low rainfall, strong winds and mobile sand. However, deep within the dunefield isolated patches of (usually shrubby) vegetation called 'bushpockets' can be found (Talbot & Bate 1991). Bushpockets migrate with the dunes—the plants constantly extend their eastern borders while sand inundates their western borders. In this way they migrate with the dunes at a rate of around 2–3 m per year in an easterly direction (McGwynne & McLachlan 1992, Lubke & De Moor 1998).

Dune slacks

The complex dune systems (especially extensive dunefields) usually contain damp interdune depressions known as dune slacks. As the dune migrates, it exposes virgin sand that is colonised by salt-tolerant pioneer species. Here the groundwater, which is rich in nutrients, lies close to the surface as it flows towards the sea. Since root systems can reach down to the water table, plants in the slack are not limited by availability of water, as they are in other parts of the dune field. In turn they are limited by salt deposition (salt spray) and burial and abrasion by sand. Especially within large mobile dune systems on the south and east coast, dune slack communities are frequently found. However, on the KwaZulu-Natal coast, slack communities are often less frequent since more permanent plant communities rapidly establish in the dune hollows. Plants of dune slacks often share many characteristics with dune pioneer communities, for instance occurrence of species such as *Sporobolus virginicus* (south and east coasts) and *Cladoraphis cyperoides* (west coast). The role of dune slacks in vegetation succession within dune systems of the Eastern Cape is given in Lubke & Avis (1982a, b 1988, 2000) and McLachlan et al. (1987).

3.2.2 Rocky Shores: Coastal Cliffs and Headlands

Rocky substrates range from headlands with vertical cliffs to wide, wave-cut platforms or jumbles of boulders polished by the motion of the ocean. They differ from dune coasts in having stable substrates and shallow soils and variable geology. In False Bay alone, the coastal cliffs can be built of Proterozoic Malmesbury shales and Cape granite, Devonian Table Mountain sandstones, Jurassic dolerites, and finally Plio-Pleistocene calcium-rich aeolinites (Figure 14.13). High salt deposition (exposure to salt spray and seawater splash), extremely high insolation and high levels of UV radiation, nutrient input by birds, constant deposition and erosion of fine soil by relentless winds are ecologically critical. Along rocky headlands with exposed cliff faces salt spray is often a limiting factor to plant growth. Stormy weather in winter may reach higher elevated cliffs, forming temporary salty pools which desiccate and leave pockets of salt bloom (Figure 14.14). In the pockets of dune rocks the soil accumulated is nutrient-poor and often saturated with salt.

Rocky coasts are home to interesting stress-tolerant flora and vegetation. Consequently the vegetation is as species-poor as in much of the remainder of the coastal vegetation composed of plants able to tolerate extreme environmental stress. The combination of broadly distributed (salt-tolerant) generalists such as *Chenolea diffusa, Disphyma crassifolium* and *Tetragonia decumbens* and local endemics such as several taxa of *Limonium* (Plumbaginaceae), *Drosanthemum, Prenia* and *Ruschia* (Aizoaceae) and *Sarcocornia littorea* (Chenopodiaceae) adds to the uniqueness of the coastal rocky habitats. Where sand accumulates in pockets on the rocks, herbaceous communities similar to those of the young dunes can occur (Lubke & Van Wijk 1988, Taylor & Boucher 1993). Low coastal thickets often cover coastal cliffs, with a typically wind-sheared appearance (Figure 14.15) in windward positions. They often support shrubby succulents such as species of *Carpobrotus*, *Drosanthemum*, *Euphorbia* and *Tetragonia* (Avis 1992, Weisser & Cooper 1993, Lubke et al. 1997).

Firm ground of remote coastal cliffs and boulder beaches (usually on islands and exposed promontories) offer perfect resting and roosting habitats for colonies of marine birds, including southern African endemic Jackass penguins (*Sphaeniscus demersus*; Figure 14.16), cormorants (*Phalacrocorax* species), Cape gannets (*Sula capensis*), but also marine mammals such as fur seals (*Arctocephalus pusillus pusillus*) and rarely also Cape clawless otters (*Aonyx capensis*). The bird and seal colonies are responsible for large deposits of nutrients onto otherwise nutrient-poor rocky shores. They rework the sparse soil and create

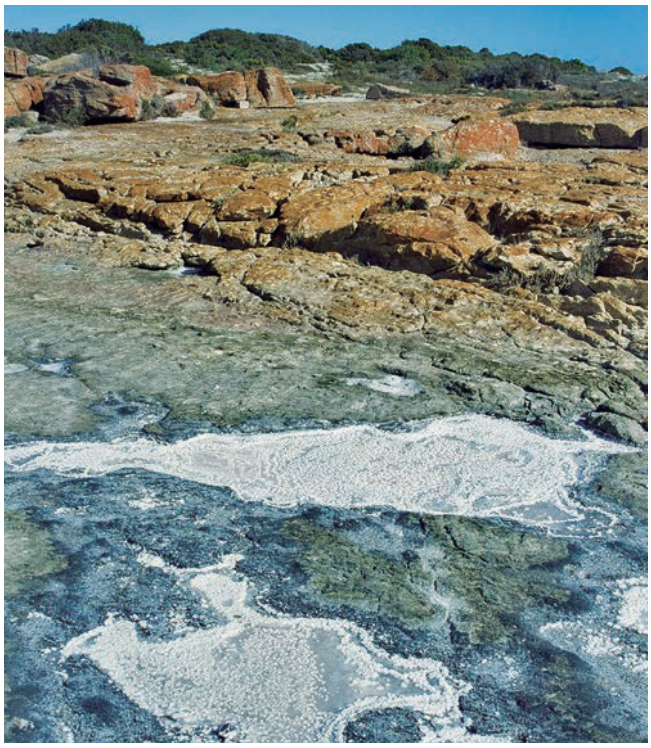

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Figure 14.14 The semi-arid West Coast (here near Elands Bay) is a stressed environment—salt bloom precipitated by repeated evaporation of sea surf in rock pools on coastal sandstone cliffs.

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Figure 14.15 Coastal granite cliffs and steep slopes near Herold's Bay near George (southern Cape) covered by wind-sheared coastal thicket.

new microhabitats. Marine animals are a vital part of the coastal ecosystem cycles and enjoy protection.

Vegetation of coastal rocky headlands is a neglected topic of vegetation ecology in southern Africa. Only a few accounts address this unique type of vegetation specifically (Ward 1980, pp. 25–28, 45, 46, Lubke 1983, Hoare et al. 2000).

West Coast would fall under the Benguela Province, with Cape Point as the southernmost border. The narrow coastal stretch between Cape Point and Cape Agulhas is called the Western Overlap, linking the (cold) temperate Benguela Province with the (warm) temperate Agulhas Province. The latter province then spans from Cape Agulhas as far as East London, where it gives way to the Eastern Overlap, which according to Bolton & Anderson (1997) reaches as far as Durban. However, as shown by Bolton et al. (2004), based on re-analysis of seaweed distribution data, this overlap should be extended as far north as the St Lucia estuary. The other tropical province, the Indo-Pacific Province, includes the marine waters offshore of Maputaland, along the South African Indian Ocean seaboard north of St Lucia. A different classification of the marine environments was suggested by Seagrief (1988), encompassing three zones (East Coast, South Coast and West Coast) and two overlaps, conceptually roughly corresponding to the scheme described above, but spatially different.

The recent classification of marine biozones (Lombard et al. 2004, Driver et al. 2005) recognises five 'intertidal biozones', addressing the estuaries in the first place. The system includes: (1) Namaqua Intertidal Biozone (mouth of Orange River to St Helena Bay), (2) Southwestern Cape Intertidal Biozone (St Helena Bay to Cape Point), (3) Agulhas Intertidal Biozone (Cape Point to Kei Mouth), (4) Natal Intertidal Biozone (Kei Mouth to St Lucia), and (5) Delagoa Intertidal Biozone (St Lucia to the Mozambique border). The above-mentioned sources also define biozones in purely marine environments, including shallow photic, deep photic, subphotic zones, upper and lower slope of continental shelf, and abyss.

On *terra firma* Tinley (1985) adopted a combination of rainfall regime, wind directions, coastal geomorphology and habitat complexity to coin his system of six coastal regions including the West Coast (Kunene River to Olifants River), South West Coast (Olifants River to Cape Agulhas), South Coast (Cape Agulhas to Cape St Francis), South East Coast (Cape St Francis to Kei River), Transkei Coast (Kei River to Mtamvuna River), and KwaZulu-Natal Coast (from the mouth of Mtamvuna northwards). The team of the National Biodiversity Assessment 2004 adopted the Tinley's classification in their marine biozone delimitation (Lombard et al. 2004, Driver et al. 2005) while each of the coastal regions became a 'Supratidal Biozone'. In this chapter

4. Biogeographical Patterns

4.1 Major Biogeographical Divisions

The current biogeographical classification of marine inshore environments of southern Africa recognises two tropical and two temperate marine provinces as well as a further two regions of overlap. The origins of this classification recognise the influence of sea currents (hence sea temperatures) on the distribution of marine fauna and flora (Stephenson 1939, 1944, 1948, Brown & Jarman 1978, Bolton et al. 2004). The Tropical West Africa Marine Province does not reach our region since its southernmost limit lies around the Kunene River mouth at the Namibian/Angolan border. The rest of the Namibian and South African

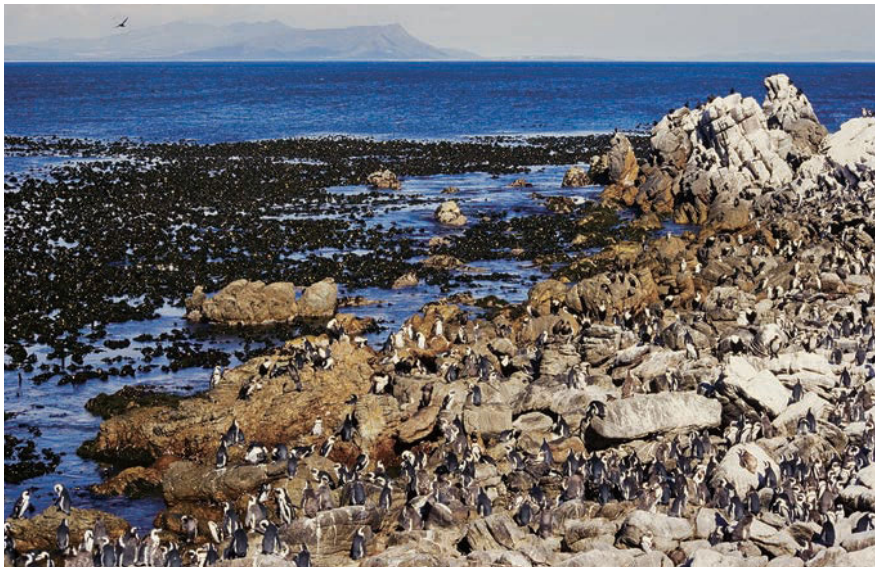

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Figure 14.16 Mixed colony of jackass penguins (*Spheniscus demersus*) and Cape cormorants (*Phalacrocorax capensis*) on coastal sandstone cliffs overlooking a cove filled with Cape kelp (*Ecklonia maxima*) at Stony Point, Betty's Bay (Western Cape).

Table 14.2 Coastal regions of South Africa (modified after Tinley 1985 and Lubke et al. 1997).

Coastal region	Coastal stretch	Main habitat types		Rainfall patterns	Wind directions
West Coast	Alexander Bay to Olifants River	fine-grained sandy beaches and shell beds	rarely rocky coast	erratic, but mostly in winter; coastal fog	S, SW
South West Coast	Olifants River to Cape Agulhas	fine-grained sandy beaches	exposed rocky headlands/ wavecut platforms	low, winter	SW, S/NW
South Coast	Cape Agulhas to Cape St Francis	wavecut rocky platforms	fine-grained sandy beaches	all seasons (more in winter in the western part)	SW, W, E
South East Coast	Cape St Francis to Kei River	fine-grained sandy beaches	wavecut rocky platforms	all seasons (mostly spring and autumn in the west and summer in the east)	SW, SE, E, NE
Wild Coast	Kei River to Mtamvuna River	wavecut rocky platforms	rarely coarse-grained sandy beaches	summer	SW, NE
KwaZulu-Natal Coast	Mtamvuna River to Mtunzini	coarse-grained sandy beaches	rarely exposed rocky headlands	summer	S, SE, NE
Maputaland Coast	Mtunzini to Mozambique	coarse-grained sandy beaches	rarely exposed rocky headlands	high, summer	S, SE, NE

we also follow the Tinley's (1985) classification except that we renamed the 'Transkei Coast' 'Wild Coast' and separated the tropical Maputaland Coast from the original 'KwaZulu-Natal Coast' of Tinley (1985) (Table 14.2).

4.2 Algal Beds

South Africa has 878 species of seaweeds described in the literature (J.J. Bolton, unpublished data), which is around 10% of the global total. The marine habitats are very varied, with three of the four major seaweed floras of Sub-Saharan Africa occurring in South Africa. The West Coast shares a flora of cool-temperate species with Namibia (Benguela Marine Province), which is rapidly replaced in southern Angola by tropical West African species. Between the Cape Peninsula and Cape Agulhas is a true overlap flora, with relatively equal numbers of West Coast and South Coast species. The South Coast (Agulhas Marine Province) has a distinct warm-temperate flora. From around Port Elizabeth eastwards, including most of KwaZulu-Natal, there is a gradual overlap of warm-temperate South Coast species being replaced by tropical species, which generally have wide distributions in the tropical Indo-West Pacific. In the extreme north of KwaZulu-Natal, in the region of St Lucia/Cape Vidal, there is a more rapid turnover of species. More than 70% of species in the extreme north (Maputaland) have tropical affinities. The major points of species changeover along the coastline are thus around the Cape Peninsula, around Cape Agulhas, and to a somewhat lesser extent St Lucia/Cape Vidal.

Almost 40% of South African species are endemic to temperate southern Africa. South African endemism is highest on the south coast, with most West Coast species also occurring in Namibia (Bolton 1999, Bolton & Stegenga 2002). South Coast endemism declines gradually from Port Alfred eastwards. The seaweeds of the East Coast are best described as an overlap flora, with very few species endemic to KwaZulu-Natal. The West Coast flora is relatively species-poor, with around 140–150 species recorded in each 50 km coastal section. At any one point, the South and East Coast floras are around twice as diverse, with around 270–330 species recorded in each coastal section. Throughout the region, around 60–70% of the species present at any one point are red algae (Rhodophyta). The West and South Coast floras have fairly equal numbers (15%) of each of the brown algae (Phaeophyceae) and green algae (Chlorophyta). Moving eastwards in KwaZulu-Natal, there is a slight increase in brown algae (to 17–18%), and a larger increase (to 25%) in green algae, as the flora becomes tropical.

The overwhelming factor determining large-scale, biogeographical ranges of seaweed species is seawater temperature regime. The cool-temperate flora of the West Coast is determined by major upwelling from the Benguela Current, with the range of monthly mean temperatures around 11–14°C. The northernmost section of the East Coast (Maputaland) is affected by the inshore flow of the tropical Agulhas Current, with monthly means of 23–29°C. In between, the South Coast has a generally wider range of monthly means at any one point (12–22°C), where eddies from the Agulhas Current and sporadic upwelling periodically affect conditions.

The upwelling of cool, nutrient-rich water on the West Coast supports large subtidal beds of kelps (*Ecklonia maxima* and *Laminaria pallida*: large brown algae of the Laminariales). There is very little grazing pressure in kelp beds on the West Coast proper, resulting in an abundant understorey of predominantly foliose red algae. East of Cape Point, sea urchin grazing results in extensive cover of coralline red crusts. Grazing by herbivorous fish gains in importance as an ecological factor moving eastwards. Biomass of fleshy and foliose intertidal species is also highest on the west coast, possibly due to a combination of higher nutrients and coastal fog which reduces desiccation during low tides. On the West Coast, much seaweed biomass is composed of Gigartinaceae (*Gigartina*, *Sarcothalia*, *Mazzaella*), while on the South and East coasts species of *Hypnea* are particularly abundant. On the South and East Coasts the subtidal zone is generally dominated by articulated coralline red algae (*Amphiroa*, *Arthrocardia*, *Cheilosporum* etc.), with large populations of siphonous green algae particularly in sandy gullies (especially species of *Caulerpa*, *Codium* and *Halimeda*). In Maputaland, communities assume a more tropical aspect, with many subdominant species, and many hard substrates covered with extremely diverse communities of small filamentous and foliose species, forming a low 'turf' due to grazing, particularly by herbivorous fish. The tropical seagrass *Thallasodendron cili-*

atum is also common in the Maputaland intertidal zone.

4.3 Estuaries

According to O'Callaghan (1994a) and Adams et al. (1999), all salt marshes (including intertidal and supratidal) in South Africa cover approximately 17 000 ha with 75% confined to the top five largest estuarine systems namely St Lucia, Berg, Olifants, Knysna and Langebaan (Table 14.1). Lake St Lucia (68 000 ha) is the largest estuary in South Africa, making up just over half of the country's estuarine area. The narrows of St Lucia estuary are tidal when the mouth is open. Salt-marsh plants are found on fringes of the mangroves. Stands of *Juncus kraussii* occur in sites less frequently flooded. The dominant plants are the grasses *Sporobolus virginicus* and *Paspalum vaginatum* as well as the succulents *Sarcocornia natalensis* complex and *Salicornia meyeriana*. These plants also occur on the western shoreline of the estuary and along the False Bay shoreline where there is no significant inflow of groundwater. Salt marshes also occur on the floodplains of the rivers entering False Bay as well as on the islands, the peninsulas and along those parts of the eastern shoreline where the estuary edge topography acts as a barrier preventing inflow of surface water (Taylor et al. 2006). Although tidal influence does not occur in these areas, the wet/dry cycles and wind cause large fluctuations in salinity and water level.

The data in Table 14.1 indicate that the estuary with the second largest salt-marsh area in the country is that of the Berg River. The value for the supratidal salt marsh is possibly an over-estimation as it probably includes the large floodplain wetlands that are brackish and mostly characterised by reeds and sedges. A recent mapping exercise for the Olifants estuary indicated the extensive supratidal and floodplain areas where a single species, *Sarcocornia pillansii*, is dominant (Adams et al. 2005). According to Maree (2000) the intertidal wetlands of Knysna cover an area of 1 000 ha. This includes 355 ha of the submerged aquatic *Zostera capensis*. The intertidal salt marsh around George Rex Drive and Thesen Island covers 170 ha and around Brenton-on-Lake 314 ha. The supratidal salt marsh is not as extensive and covers approximately 60 ha. The marshes in the upper reaches of the estuary cover 150 ha and consist mostly of *Juncus kraussii*.

Due to the high rainfall and brackish nature of the temporarily open/closed estuaries in KwaZulu-Natal, salt marsh

	M	K	T	E	S	C	W	Distribution Limit	
ZONE I									
Cyperus crassipes	■							Cape St Lucia	S
Scaevola sericea	■							Kosi Bay	S
Canavalia rosea	■	■	■	■				Kei Mouth	W
Launaea sarmentosa	■	■	■	■				Coega (PE)	W
Phylohydrax carnosa	■	■	■	■	■			Plettenberg Bay	W
Ipomoea pes-caprae	■	■	■	■	■			Knysna	W
Gazania rigens var. uniflora	■	■	■	■	■			Mossel Bay	W
Scaevola plumieri	■	■	■	■	■	■		Arniston	W
Arctotheca populifolia	■	■	■	■	■	■	■		
Dasispermum suffruticosum		■	■	■	■	■		Durban	E
Ehrharta villosa var. maxima			■	■	■	■		Port Edward	E
Tetragonia decumbens			■	■	■	■	■	Port St Johns	E
Hebenstretia cordata**				■	■	■	■	Kei Mouth	E
Senecio litorosus				■	■			Great Fish River	E
Gazania rigens var. leucolaena				■	■	■		Coega (PE)	E
Thinopyrum distichum				■	■	■		Kei Mouth	E
Senecio elegans				■	■	■		Tolora Mouth	E
Silene crassifolia				■	■	■		Port Alfred	E
Carpobrotus acinaciformis				■	■	■		Port Elizabeth	E
Eragrostis sabulosa					■	■		Still Bay	E
Senecio maritimus					■	■		Still Bay	E
Oncosiphon sabulosum					■	■	■	De Hoop	E
Trachyandra divaricatum					■	■	■	Plettenberg Bay	E
Didelta carnosa var. tomentosa**					■	■	■	De Mond	E
Cladoraphis cyperoides**						■	■	Macassar	E
Manulea tomentosa						■	■	Pearly Beach	E
ZONE II									
Guettarda speciosa	■							Black Rock	S
Sophora inhambanensis	■							Sodwana Bay	S
Tephrosia purpurea subsp. canescens	■	■						Hibberdene	S
Stipagrostis zeyheri subsp. barbata	■	■		■	■			Plettenberg Bay	W
Carpobrotus dimidiatus	■	■	■	■	■			Boknes	W
Passerina rigida	■	■	■	■	■	■		Rooiels	W
Chrysanthemoides monilifera*	■	■	■	■	■	■	■	Brandsebaai	N
Metalasia muricata			■	■	■	■		Nxaxo Mouth	E
Morella cordifolia				■	■	■		Kei Mouth	E
Psoralea repens				■	■	■		Kenton-on-Sea	E
Passerina paleacea					■	■		Still Bay	E
Passerina corymbosa				■	■	■		East London	E
Phylica littoralis					■	■		East London	E

Figure 14.17 Geographical distribution of two groups of coastal plant taxa typical of Zone I and Zone II (according to Tinley 1985). For the delimitation and characteristics of the Coastal Regions see Table 14.4. M: Maputaland Coast, K: KwaZulu-Natal Coast, T: Wild Coast, E: South East Coast, S: South Coast, C: South West Coast, W: West Coast. The shaded area indicates the occurrence of a taxon in a given Coastal Region. Sources of the distribution of the taxa: Tinley (1985), Pooley (1998), Goldblatt & Manning (2000), PRECIS database, L. Mucina (unpublished data). Two subspecies of *Chrysanthemoides monilifera** appear to prefer coastal habitats: C. *monilifera* subsp. *rotundata* is characteristic for the eastern coasts (M, K), while C. *monilifera* subsp. *pisiformis* typically occurs along the western and southwestern coasts (W, C, S). The meeting zone of these two subspecies is possibly Coastal Region E, but due to taxonomic (identification) problems this remains open to further investigation. **Of the West Coast species, the ones indicated by double asterisk reach as far north as AZd 1 Namib Seashore Vegetation unit.

is mostly absent (despite the largest area of salt marsh in the country being in St Lucia estuary). Hygrophilous grasses (e.g. *Sporobolus virginicus, Paspalum notatum* and *Cynodon dactylon*) are, however, common.

South African estuaries occur within three biogeographical zones, the cool-temperate zone on the West Coast, the warm-temperate zone that extends from about Cape Point to the Mbashe estuary in the Eastern Cape and the subtropical zone on the East Coast (Table 14.2). In the subtropical zone, mangroves tend to replace intertidal salt marsh. Colloty et al. (2002) found that in permanently open estuaries, mangroves occurred north of the Great Kei estuary and swamp forest north of the Mngazana estuary. In temporarily open/closed estuaries swamp forest, reed and sedge beds occurred north of the Mngazana estuary where they replaced the salt marsh. However, in some estuaries all three habitat complexes were present and thus the East Coast transitional area has a high biodiversity. Species distribution was associated with the increase in rainfall northwards.

Reeds and sedges are the dominant macrophytes in temporarily open/closed estuaries throughout the country. In the subtropical KwaZulu-Natal Province, rooted submerged macrophytes are rare in these estuaries. This has been attributed to an increase in catchment and bank erosion, sediment deposits and a lack of available light. Steeper gradients and greater water velocities during rainfall events also disturb sediments and remove these macrophytes (Perissinotto et al. 2004). Many of the Eastern Cape estuaries (e.g. Seekoei and Kabeljous) have extensive submerged macrophyte beds consisting of both *Ruppia cirrhosa* and *Zostera capensis*. During the closed phase, extensive blooms of filamentous green macroalgae can occur.

4.4 Dunes

The South Africa coastline is diverse, with a wide variety of habitats stretching over an area which is transitional between winter- and summer-rainfall climates (Avis 1992), corresponding to the distribution of one or more biomes in the hinterland and to one or more patterns of the sea currents (Table 14.3). The distribution of particular species (for a selection see Figure 14.17) shows clear patterns of diminishing importance of the coastal tropical element in a westward direction and increased endemism towards the Cape coasts. Several important regional discontinuities in species distributions have been identified (e.g. East London–Kei Mouth interval) and incorporated into the definition of our vegetation units (for more details see below), while some of the other discontinuities (such as co-occurrence of western limits of distribution in some species around Still Bay and Plettenberg Bay) are still awaiting explanation. One of the approaches to the question of distribution of plants along the coast was to seek ecophysiological explanations, such as demonstrated for *Scaevola plumieri* by Peter & Ripley (Peter 2000, Peter & Ripley 2000, Ripley 2001, Peter et al. 2003).

The West Coast of southern Africa, north of Cape Columbine, has a mixture of dry-coast elements and taxa recruited from the generic pools of the neighbouring semidesert biomes (Aizoaceae) and Cape elements (Tinley 1985, Lubke & Van Wijk 1988, Lubke et al. 1997). The vegetation of the southern coasts is dominated by elements of the Cape flora and it has a considerable coastal endemism. All the floras listed above interact in a complex manner along the southeast coasts of the Eastern Cape (Lubke & Van Wijk 1988). The East Coast is strongly influenced by (sub)tropical elements and some links to afrotemperate woody flora (Lubke & Van Wijk 1988) as well as to distant Madagascar (Tinley 1985, Venter & Scott 1999, Venter 2000). Several coastal species have subcosmopolitan or wide (sub)tropical distribution (*Canavalia rosea, Ipomoea pes-caprae*, *Sporobolus virginicus*), pointing to the many common features of sand-coast ecology and the ability for long-distance dispersal of coastal flora.

5. Principles of Delimitation of Vegetation Units

The classification system of vegetation units as presented in this chapter is a synthetic product of habitat and biogeographical subdivisions of the coast (and adjacent sea waters) of South Africa.

Four groups of the coastal vegetation have been recognised (see Figure 14.18 for schematic distribution of the mapped patches):

(a) Coastal macroalgal beds.

(b) Estuarine salt marshes (Figure 14.14).

(c) Seashore (or strand) vegetation (including vegetation of habitats under immediate and current influence of the sea—beaches, coastal cliffs, coastal dunes).

(d) Azonal/intrazonal strandvelds.

5.1 Algal Beds

Within this category we include only two alga-dominated vegetation units of notable spatial extent—the Cape Kelp Beds (unit AZm 1) described in this chapter (see below), and AZm 2 Subantarctic Kelp Beds from the islands of Marion and Prince Edward, described in Chapter 15. Both units occur in the form of relatively small patches not shown on our Map. However, the inventory of extant patches of the Cape Kelp Beds is in progress (R.J. Anderson, personal communication) and mapping of the Subantarctic Kelp Beds remains a challenge for the future. Satellite imagery combined with 'sea-truthing' should generate the desired data for possible future editions of our Map.

5.2 Estuarine Vegetation

Three units were recognised and mapped within this group. AZe 1 Arid Estuarine Salt Marshes are ecologically and floristically very different from the other two units: in fact, the 'arid-climate' estuaries are more reminiscent of the concept of *sabkha* known to the Arabic-speaking world. In South Africa, these habitats are in many respects more saltwater-soaked flats on head-bays in poorly drained coastal lagoons straddling 'desert' and the sea, than true tidal salt marshes. The freshwater component is either negligible (due to the often intermittent nature of the rivers) or missing altogether. The salt-marsh/*sabkha* complex in the mouth of the Orange (Gariep) River is the most typical example in South Africa, while the salt flats on bays around Lüderitz (Namibia) are probably the best example of such an arid 'estuarine' (or rather *sabkha*) habitat on the southwestern desert coasts of Africa. The estuaries of AZe 1 are embedded within the Desert and Succulent Karoo Biomes.

The Cape estuaries (AZe 2) are typical of the warm-temperate climate region of the Cape Floristic Region (cold-temperate and warm-temperate marine temperatures). These estuaries range from brackish to hypersaline environments. Due to the small-scale nature of the estuarine habitat mosaic we have not mapped (at our working scales) the sublittoral, littoral and supralittoral habitats as separate units, although we appreciate the considerable ecological differences between these. Naturally, these habitats and constituent communities are mappable at larger scales as shown by a series of detailed maps of the Cape

estuaries in the CSIR inventory reports (see References). The separation of the subtropical AZe 3 unit was motivated by the general impoverished character of the salt-marsh flora and vegetation complexes, recognising that salt marshes are a phenomenon typical of extratropical regions. The zonal hinterland of the subtropical estuaries in South Africa is formed by the Indian Ocean Coastal Belt. Mangroves are an important element of the (sub)tropical estuaries. The mangroves are treated as a separate vegetation unit (FOa 3) in Chapter 12. Capturing the subtropical estuarine salt marshes has been a problem due to a lack of proper coverage. Therefore the largest patch of the AZe 3 unit (St Lucia) has not been distinguished from the lagoon proper at this stage.

Admittedly not all known estuaries (see Whitfield 1995, 2000 and Colloty et al. 2001 for exhaustive lists of the South African estuaries) are contained in our Map, both due to lack of mapping coverage of acceptable quality as well as the small scale of many of the salt-marsh patches. Larger estuaries open to the sea have not been distinguished from the sea on the Map.

5.3 *Dry Seashore Vegetation*

The delimitation of the seashore units follows the same principle as that of the estuarine (or 'wet seashore') units, except that the arid seashore is subdivided into AZd 1 Namib Seashore Vegetation and AZd 2 Namaqualand Seashore Vegetation. The former unit follows the part of the coast of one of the oldest and most arid deserts of the world—the Namib Desert. This hyperarid coastal vegetation extends to South Africa only marginally, and reaches its southernmost distribution limit on the Holgat River—the limit of a group of species identified as 'Namib intrusion' by Boucher & Le Roux (1993). The AZd 3 Cape Seashore Vegetation and AZd 4 Subtropical Seashore Vegetation represent warm-temperate versus subtropical coastal vegetation units. The major vegetation turnover appears roughly within the coastal interval spanning the mouth of the Buffalo River (East London) and Kei Mouth—in the region where Albany Thicket gives way to Indian Ocean Coastal Belt in the oceanic hinterland.

The dry seashore vegetation fringes the coast of South Africa in the form of an almost continuous belt, being interrupted only by the estuaries. Still it was technically infeasible to depict this belt on our Map in its entirety due to scale problems. In places it therefore happens that the strandveld units, both the intrazonal strandvelds classified within the Succulent Karoo and Fynbos Biomes (the latter summarised as Western Strandveld) as well as the azonal Eastern Strandveld (see below), become the coast-fringing vegetation on our Map.

The principles of the spatial and conceptual distinction between the coastal (seashore) vegetation and the hinterland strandveld units are discussed in Chapter 4 (Fynbos Biome) in this book.

5.4 *Eastern Strandveld*

The Eastern Strandveld units cover a large, about 1 000 km long, stretch of the East Coast, following the seaboards of the Indian Ocean. The vegetation units are well differentiated in climatic

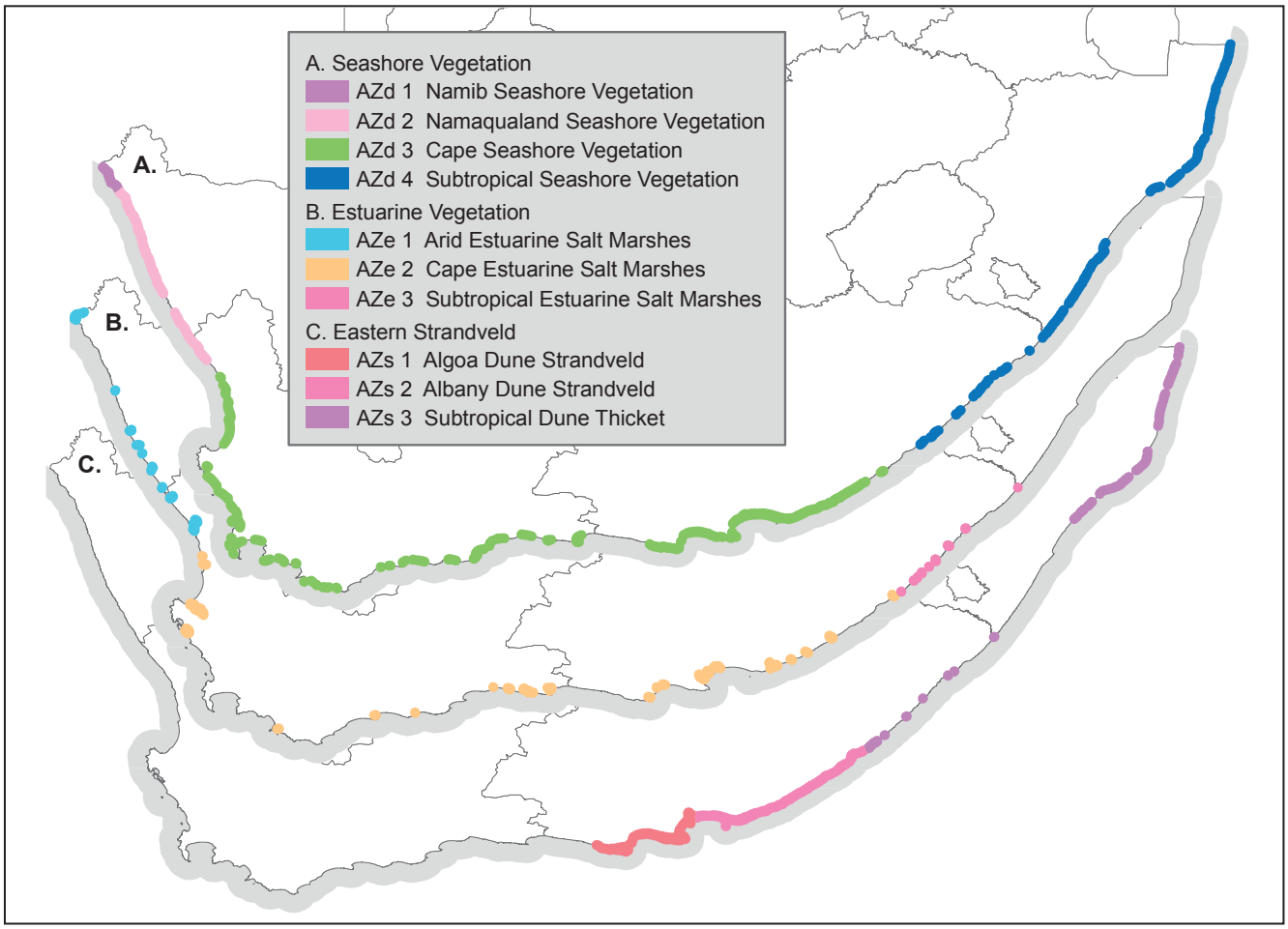

Figure 14.18 Distribution of coastal vegetation units along the South African seaboards. A: Seashore Vegetation, B: Estuarine Vegetation, C: Eastern Strandveld.

Table 14.3 Correspondence between biomes (as defined in this book), marine provinces and overlap (according to Bolton & Anderson 1997, modified by Bolton et al. 2004), and vegetation units of coastal affiliation, such as intrazonal and azonal strandveld units, seashore vegetation and estuarine salt-marsh units.

Biomes	Strandveld units	Seashore vegetation	Estuarine salt-marshes	Marine province or overlap
Desert	Dn 1	AZd 1	AZe 1	Benguela Province
Succulent Karoo	SKs 1, SKs 7, SKs 8	AZd 1, AZd 2	Aze 1	Benguela Province
Fynbos	FS 1–9, AZs 1	AZd 3	AZe 2	Benguela Province Western Overlap Agulhas Province
Afrotemperate Forest	FS 9	AZd 3		Agulhas Province
Albany Thicket	AZs 1, AZs 2	AZd 3	AZe 2	Agulhas Province Eastern Overlap
Indian Ocean Coastal Belt	AZs 3	AZd 4	AZe 3	Eastern Overlap Indo-West Pacific Province

terms, spanning a gradient of increasing precipitation (from 680 mm in Algoa Strandveld to over 1 000 mm in Subtropical Thicket) and temperature (MAT: 17.2°C, 18.0°C and 20.0°C). The delimitation between two units occurring in Albany Thicket (Algoa and Albany Strandvelds) follows Vlok et al. (2003). Much of the Subtropical Thicket has not been mapped due to scale problems—the patches of this vegetation occur as very narrow bands (often only several tens of metres) in KwaZulu-Natal, while in the Eastern Cape (along the Wild Coast) this type is rare due to specific coastal geomorphology (steep coastal cliffs), and it is limited to only small pockets on dunes in river mouths.

6. Conservation Challenges: Status, Threats and Actions

6.1 Algal Beds

South Africa has a seaweed industry that is based on the commercial collection of kelps and the red seaweeds *Gelidium* and *Gracilaria*, as well as the cultivation of *Gracilaria* and the green seaweed *Ulva* for abalone feed. Although the industry is relatively small compared to major producers such as Chile, it is worth about R25 million annually, provides hundreds of jobs and is viable and sustainable.

The mainstay of the local industry is the extensive beds of kelp (*Ecklonia maxima* and *Laminaria pallida*) that grow in the cool-temperate waters from Cape Agulhas up the West Coast and into Namibia. Beach-cast kelp has been collected, dried, milled and exported for almost 50 years for the production of alginate, a colloid with many industrial uses such as in dyes and paints. An extract from *E. maxima*, marketed as Kelpak®, is used locally and exported to over 30 countries where it is highly effective as a plant-growth stimulant in agriculture and horticulture. In the last decade, the huge increase in the farming of abalone in tanks has created a local industry based on harvesting and supplying fresh *E. maxima* fronds as feed for these valuable molluscs. More than 5 000 tons of fresh kelp fronds are currently cut for abalone feed per annum.

The red alga *Gracilaria gracilis* is collected from periodic wash-ups at Saldanha Bay on the west coast. The material is dried, sorted and exported for the extraction of agar, a colloid with wide uses in food and pharmaceutical products. Good-quality agars are obtained from the three *Gelidium* species that are harvested from shores in the warm-temperate waters of the Eastern Cape. *Gelidium pristoides*, a strictly intertidal species, is the most valuable on account of the high gel strength of its agar. *G. abbottiorum* and *G. pteridifolium* are found lower on the shore and in pools and gulleys, and fetch a slightly lower price. Teams of pickers cut the tops off the *Gelidium* plants, leaving the basal fronds to regenerate. Research has shown that the plants re-grow rapidly, and that harvesting has minimal ecological effects on the environment.

Seaweed harvesting is managed by the national Department of Environmental Affairs and Tourism on the basis of scientific research that is largely funded by the cost of commercial and recreational permits. The coastline is divided into 23 Concession Areas, and the rights to harvest a particular species in each area can be applied for periodically.

Several abalone farms cultivate quantities of seaweed (*Ulva* and *Gracilaria*) as abalone feed, particularly in the Eastern Cape, where there are no large supplies of feed in the form of kelp beds. One farm currently grows 3 tons of *Ulva* per working day in a series of 30 m long shallow ponds, with water movement provided by large paddle wheels. Even in the Western Cape, some farms are now growing their own *Ulva* and *Gracilaria* as a supplement to kelp, and ongoing research assists them to improve their cultivation methods. Ultimately, the goal is to integrate the farming of seaweed and abalone, so that feed is produced while the seaweeds remove inorganic nutrients from the abalone effluent, thus cleaning it for re-circulation within the farm.

6.2 Estuaries

Salt marshes have experienced a long history of destruction and alteration by human activities. Filling, dredging, ditching, impounding and draining as well as pollution have greatly reduced the total area throughout the world.

Reduction in freshwater input due to freshwater withdrawal from the estuary catchment results in an increase in salinity and loss of the species preferring brackish habitats (e.g. *Juncus kraussii*, *Cotula coronopifolia*). Freshwater reduction can also reduce the frequency and duration of open mouth conditions in temporarily open/closed estuaries. This can lead to the loss of intertidal species such as *Sarcocornia perennis* complex and

Spartina maritima. Prolonged closed mouth conditions and an increase in water level can lead to the loss of those species sensitive to submerged conditions. Too much freshwater may eliminate the salt-marsh community. O'Callaghan (1990b) has shown how poorly developed the halophytic vegetation in the False Bay estuaries is because of human impact and reduced saline input. He identified restriction in tidal input as a serious threat to Western Cape salt marshes.

Threats to seagrass, *Zostera capensis*, include bait digging and boating activities. Catchment degradation, erosion and an increase in sediment load results in smothering and a decrease in light available to these plants. *Z. capensis* has been lost from the Mthatha estuary and some KwaZulu-Natal estuaries due to an increase in sediment load.

The most common impact in supratidal salt marshes is encroachment by invasive plants followed by trampling and formation of footpaths constituting probably the most common impact affecting intertidal salt marshes (Coetzee et al. 1997). Water-saturated low marsh sediments and associated plants are highly susceptible to trampling and recover slowly. In the Knysna estuary, Maree (2000) found that the construction of roads, bridges and commercial developments often results in an increase in elevation, with the resultant establishment of terrestrial or alien species. Threats in the more rural areas of the former Ciskei and Transkei include agriculture and grazing. In estuaries closer to city centres or holiday resorts, encroachment by developments is the major threat. In the Swartkops estuary, 35 ha of supratidal salt marsh has been lost due to bridges, roads and other developments and 50 ha of intertidal marsh has been lost due to the development of Swartkops and Redhouse villages, salt works and roads (Colloty et al. 2000).

Intertidal salt marshes occur in the large permanently open estuaries. Only 18% of South African estuaries are permanently open and their status is threatened due to reduced freshwater input. An assessment of the habitat integrity of South African estuaries (Colloty 2000) showed that 'pristine' estuaries were mostly found in the former Ciskei and Transkei regions. Decreases in plant cover in the Transkei estuaries were mostly due to removal for agriculture or utilisation of wood in the case of mangroves. In the Ciskei, the estuaries that had the lowest habitat integrity scores, were those where plant cover was lost due to road construction at or near the mouth, e.g. Bira, Mpkeweni. In Cape and KwaZulu-Natal estuaries, residential and industrial developments have removed areas of estuarine habitat.

The National Spatial Biodiversity Assessment (Turpie 2004a, b, Driver et al. 2005) has identified estuaries that are critically endangered, vulnerable and least threatened. Permanently open estuaries in the cool-temperate and warm-temperate regions, which generally have the largest salt-marsh areas, were identified as endangered. The few large estuaries on the West Coast (Orange, Olifants, Berg) are under great pressure as they are each linked to a major river system and a large catchment that is heavily utilised, particularly for abstraction of freshwater.

Whitfield (2000) reported that 62% of South Africa's estuaries were in good or excellent condition, but the healthy estuaries were not evenly distributed among 13 different groups as defined by Turpie (2004b, see also Driver et al. 2005), based on climate zone and five basic types (including estuarine bays, permanently open estuaries, river mouths, estuarine lakes and temporary closed estuaries). There are 259 estuaries in South Africa (Turpie 2004b, Driver et al. 2005), but only a small fraction enjoys formal protection—14 enjoy high levels of protection and a further 27 have medium and low levels of protection. Estuaries that currently enjoy some protection status and have salt marsh present and are listed as Ramsar sites include the Orange River mouth, Heuningnes, Swartvlei as well as the World Heritage Site of the Greater St Lucia Wetland Park which includes two further Ramsar sites—St Lucia Estuary and Kosi Bay. Knysna is a partially protected estuary under jurisdiction of South African National Parks. A large portion of salt marsh is protected in the Langebaan Lagoon, part of the West Coast National Park.

A recent paper by Turpie et al. (2002) indicates the 32 estuaries in South Africa that should be included in a protected area network to ensure biodiversity conservation of all biota. The six estuaries with the largest intertidal salt-marsh areas in the country are included in this list. Intertidal salt marsh can be considered rare in South Africa because very few estuaries remain permanently open to the sea. The government must recognise salt marshes as a valuable national asset. There should be no further loss of marsh due to development or human interference. This can be easily monitored from aerial photographs.

Three major priorities for action have been identified by the National Spatial Biodiversity Assessment, namely (1) determine, implement and monitor the freshwater reserve for priority estuaries, (2) expand the number of protected estuaries, and (3) integrate resource management and land use planning in estuarine systems (Turpie 2004b, Driver et al. 2005). Guidelines for a strategy for the protection of estuarine biodiversity have been proposed by Turpie (2004a).

6.3 Beaches, Dunes and Strandveld

Coastal conservation areas play an important role in protecting the biodiversity of the coastal habitats and maintaining a coastal corridor for the movement of coastal fauna.

It is apparent that the coastal dune systems are diverse, vulnerable and variable environments. They are often multifunctional systems of great importance to society, and people are attracted to the coast for a number of reasons—aesthetic appreciation, recreation, harvesting of marine life, transport, a place to live, work or play, or for tourism. Hence, the coast has become a centre for economic activity and the increased pressure has many kinds of consequences on the (local) beach and dune environment.

On the West/Southwest coasts the main pressure comes from the human population (i.e. through fisheries, harbours, tourism/recreation) and the mining of heavy metals and diamonds (Boucher & Le Roux 1993). Along the South/Southeast coasts, mining activities are few, but coastal resorts are plentiful and subjected to intensive development (see for instance Taylor & Boucher 1993). Nearly 90% of the 6 million people of the Western Cape Province live in this area. The (smaller) coastal towns and resorts experience a seasonal influx of holiday makers, resulting in seasonal exacerbation of the impact of recreational development on the natural coastal ecology. Intensive tourism—an economic boost to most of the coastal regions—also has some negative facets such as direct damage to sensitive dune vegetation, especially during the holiday season (trampling), the spread of alien vegetation, sand starvation of certain beaches (i.e. Cape St Francis), pollution associated with urban development, building of excessive road networks and the like.

Further east, along the Transkei/KwaZulu-Natal coast (East Coast), human settlements can be found that date back centuries (Weisser & Cooper 1993). In this area the dune ecosystems have been more affected compared to rock or cliff ecosystems. The main forces are agriculture (sugarcane plantations, overgrazing, forest clearing, veld burning), mining of heavy metals,

tourism, and industrialisation. The developments of cities and coastal resorts have, together with modern agriculture, left their mark on the coastal area by destroying the original vegetation (Weisser & Cooper 1993). Besides direct human impact through development, many coastal areas suffer from heavy infestation by alien plants—species of *Acacia* along the South/Southeast coasts, and *Chromolaena odorata, Lantana camara* and species of *Pereskia* along the East Coast.

Some of these threats to the sandy beaches and dunes were already recognised decades ago and stated as a potential problem (i.e. Avis 1986, 1992). As is obvious from the above-mentioned threats, they remain a problem. Fortunately some action has been taken. For instance, the aliens are currently being removed by the local Working for Water (DWAF 2005) campaign (Figure 14.19), and many of the coastal areas are protected and preserved in conservation areas and this should be an ongoing process!

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Figure 14.19 Alien Australian shrubby *Acacia cyclops* (rooikrans) is a prime target of the Working for Water alien plant eradication programme. Freshly cut rooikrans is left on the steep dune slopes to curb erosion and facilitate the establishment of native dune shrubs (Diaz Cross site near Boknes, Eastern Cape coast).

Priorities to any further development should be in terms of requirements of conservation and responsible tourism, rather than in terms of industrial endeavours that could equally well be situated inland, as stated by Heydorn & Tinley (1980). A more effective system of land use management and planning is required, one that would more effectively discourage coastal sprawl and encourage more compact, nodal developments.

The current state of biodiversity protection of South African sandy coast is reasonable. Not all vegetation units have the status of 'vulnerable'. Most are considered to be 'least threatened', even though the sandy beaches and dunes of the South African coast are known as sensitive systems that can easily be damaged or disrupted (Tinley 1985, Lubke et al. 1997, Turpie 2004b; see also Conservation sections in the descriptions of the vegetation units below).

7. Future Research

The coast is a place subject to direct and indirect influences—especially the human impact on the coastal system is enormous (i.e. building of roads, houses and resorts, mining of dunes, building of harbours and breakwaters, pollution). Therefore this distinctive and complex system requires a dedicated management effort.

The *ad hoc*, sectoral management approach that was common along the coast the last years ignored the wider consequences of local activities, and failed to realise the full spectrum of benefits provided by the coastal system. Management should focus on the coastal system as a whole and force decision-makers and developers to recognise that individual actions might have system-wide consequences.

However, before a proper management plan can be set in motion, it is of great importance to understand the interrelationships between the natural and human components of the coastal system, to improve sustainable development and to resolve conflicting coastal issues, to name a few. Knowledge and understanding of the (local) coastal ecosystem is thus significant. This information is needed, for instance, to restore or rehabilitate damaged or destructed coastal areas, or to predict what (long-term) effects certain activities will have on the coastal system. To be able to make these predictions, long-term monitoring programmes will be needed to follow the changes in the dune ecosystem (i.e. removal of alien plants, any coastal development), but also to alert (local) management authorities of potential problems so that appropriate actions might be taken before irreversible damage is done.

Besides the need for monitoring, there is unfortunately still a lack of knowledge on the (local) ecological processes that are a fundamental part of the sandy shore. This type of research will be needed to be able to answer questions such as:

- Which indigenous species are suitable for rehabilitation/restoration projects? What are their growth/reproductive requirements (water, light, temperature)?
- What is the current status of endangered and alien species? Which species might be endangered in the future?
- What will happen when the climate changes? Will alien noninvading species become invasive?
- What is the status of protected areas? Which coastal environments/areas/features need protection?
- What is the impact of current and future recreational activities and developments?

Answers to these questions are needed to be able to consider the long-term and cumulative impacts on the coastal area and its reaction to these impacts.

Past coastal management approaches have been fragmented and poorly co-ordinated between the different spheres of government, largely due to a lack of capacity to perform coastal management functions. Due to a lack of clarity on the roles and responsibilities between various departments, certain areas of the coastal zone have been poorly managed. As a result, a people-centred approach to coastal management was adopted in the recent Policy Document: The White Paper for Sustainable Coastal Development (DEAT 2000). This national policy provides the guiding principles for coastal management in South Africa and led to the development of Provincial Coastal Management Programmes (DEAT 2000).

Besides the obvious enormous importance for the South African economy (especially tourism and fisheries) and associated applied research, the needs for fundamental research into origins of the coastal habitats, evolution of its biota, biodiversity patterns, and processes generating those patterns, are far from being met. Although South African coasts rank undoubtedly among the best researched ecosystems in the region (Lubke et al. 1997, Whitfield 2000, and this chapter), it would be wrong to assume we know enough to conserve and exploit these fragile systems wisely. Turpie (2004b) named a few gaps that estuarine research should address, namely a review of the estuary classification system to (1) devise a more robust system useful in applied conservation research, (2) develop methods for quantitative assessment of estuary health, and (3) quantify interactions between estuarine and marine systems. We believe that at least with regard to point (1), our Map and this chapter with a new classification of coastal vegetation units is a step in the right direction. We wish to add that some aspects of biodiversity research are still needed. More vegetation-oriented research looking into local variability of habitat-level community types is needed. New species of plants are awaiting formal description. Coasts are a fascinating biogeographical subject, offering excellent models for study of evolutionary processes shaping biodiversity on many levels of complexity (from local populations to large-scale vegetation complexes).

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Figure 14.20 AZm 1 Cape Kelp Beds: *Ecklonia maxima* kelp bed near Betty's Bay (Western Cape).

8. Descriptions of Vegetation Units

Algal Beds

AZm 1 Cape Kelp Beds

Distribution Western and Northern Cape Provinces: Along the West Coast of South Africa, from a few km west of Cape Agulhas as far north as Rocky Point in northern Namibia. Smaller kelps (*Ecklonia radiata*) occur eastwards as far as KwaZulu-Natal, but do not form kelp beds.

Vegetation & Seascape Features In the south (coastline of the Western Cape Province), inshore beds are dominated by the sea bamboo *Ecklonia maxima*, with plants up to 15 m long. In this region, *Ecklonia* forms a dense canopy from the subtidal fringe to ca. 10 m deep. In sheltered coves and in deeper water (down to ca. 14 m) solid-stiped plants of *Laminaria pallida* are dominant (Bolton & Anderson 1994, 1997, Stegenga et al. 1997). *Laminaria* is rare east of Cape Point, but further north (coastline of the Northern Cape Province) plants have a hollow stipe and tend to be dominant inshore, with *Ecklonia maxima* being rarer. These hollow-stiped *Laminaria* plants formerly known as *Laminaria schinzii*, were considered a variety of *L. pallida* by Stegenga et al. (1997). West of Cape Point, there is a dense understorey of foliose seaweeds, dominated by red algae such as *Botryocarpa prolifera*, *Hymenena venosa*, *Neuroglossum binderianum* and *Epymenia obtusa*. Between Cape Point and Cape Agulhas, there are large numbers of grazers present (sea urchins, abalone etc.), and much of the bottom is covered with grazer-resistant crustose coralline red algae (Anderson et al. 1997, Leliaert et al. 2000). The only other kelp present (*Macrocystis angustifolia*) is rare, occurring only in relatively small populations inshore of *Ecklonia maxima* beds, at a few sites from the Cape Peninsula to Paternoster.

Hydrology & Substrate Kelp beds occur on the West Coast wherever there is rocky substrate in shallow water. The marine environment is dominated by the Benguela Upwelling System, which is driven by the longshore Southeaster (wind), mainly occurring in summer. The West Coast marine flora is generally considered cool-temperate (Bolton & Anderson 1997), with absolute minimum temperatures around 8°C, but monthly means not dropping below 11°C or rising above 15°C (Bolton 1986) on most of the west coast. In False Bay, *Ecklonia* beds thrive in warmer temperatures (monthly mean of almost 20°C in summer), whereas *Laminaria* is uncommon east of the Cape Peninsula.

Important Taxa Kelp: *Ecklonia maxima* (d), *Laminaria pallida* (d), *Macrocystis angustifolia* (d). Foliose Algae: *Botryocarpa prolifera* (d), *Hymenena venosa* (d), *Neuroglossum binderianum* (d), *Epymenia obtusa* (d). Epiphytic Algae (both on *Ecklonia maxima*): *Suhria vittata, Carradoria virgata.* Parasitic Algae: *Carpoblepharis flaccida* (on *Ecklonia maxima*), *C. minima* (on *Laminaria pallida*).

Conservation West Coast kelps have been utilised commercially for many decades, dried and shipped overseas for alginate production (Anderson et al. 2003). In addition, for many years small amounts (ca. 50 tons fresh weight per year) have been cut near Kommetjie for the production of the fertiliser supplement Kelpak®. In the last few years, kelp has been harvested in ever-increasing amounts (reaching 6 000 tons wet weight per year currently) for use as feedstock in the rapidly growing onshore abalone aquaculture industry. The available kelp in some areas is reaching sustainable limits. The kelp beds are protected, for example around the Cape Peninsula in the Marine Protected Areas within the Restricted Zones of Karbonkelberg, Kalk Bay, Boulders, Castle Rock, Paulsberg and Cape of Good Hope (coastal waters of the Table Mountain National Park).

Remark 1 The West Coast *Ecklonia* beds have been calculated to produce between 4.1 and 7.8 kg dry mass m^{-2} y^{-1} (Newell et al. 1980), and *Laminaria* stands have been shown to turn over

twice per year, with a production of 27.9 kg wet mass m^{-2} y^{-1} (Dieckmann 1980).

Remark 2 Annual production of *Ecklonia maxima* has been calculated to lose 10% as a result of storms (Simons & Jarman 1981). The large quantities of drift kelp which consequently wash up on West Coast beaches support a characteristic fauna of small crustaceans, which in turn provide food for birds and larger crustaceans (Griffiths et al. 1983).

Remark 3 The extent of the Cape Kelp Beds has not been captured in the current version of the Map.

References Dieckmann (1980), Newell et al. (1980), Simons & Jarman (1981), Griffiths et al. (1983), Bolton (1986), Bolton & Anderson (1994, 1997), Stegenga et al. (1997), Leliaert et al. (2000), Anderson et al. (2003).

Estuarine Vegetation

AZe 1 Arid Estuarine Salt Marshes

Distribution Northern Cape and Western Cape Provinces: At mouths of the Namaqualand rivers such as the Orange (Gariep), Buffels, Swartlintjies, Spoeg, Bitter, Groen, Sout and Olifants Rivers. Further north this salt-marsh unit is found at river mouths along the Namib Desert coast of Namibia as far as southern Angola.

Vegetation & Landscape Features Estuarine salt marshes in the river mouths with patches of supratidal salt marshes on elevated terraces. Vegetation is formed mainly of low succulent dwarf shrubland patches, forming a mosaic with creeping grassy mats and patches of reed beds.

Geology, Soils & Hydrology Recent riverine (and partly also marine) sediments, with Table Mountain Group quartzitic sandstones and Gariep Supergroup metasediments (underlying the estuaries) are exposed in places (i.e. Olifants and Orange Rivers). The intertidal and supratidal salt marshes experience regular tidal action (diurnal and spring tidal, respectively) that is responsible for sediment deposition and erosion. The floodplains were formed through ancient alluvial sedimentary processes (palaeo-floodplains) and do not experience flooding under present river flows. The floodplain salt marsh uses the groundwater where the groundwater depth is less than 1.5 m and the salinity is less than 70 ppm.

Climate Arid, characterised by cool-temperate regime (MAT close to 18°C) with a very low, erratic MAP, ranging from less than 150 mm at Lutzville (Olifants estuary) to 45 mm at Alexander Bay (Orange estuary). Rain generally falls in wind-driven showers spread over the season from May to August, but it can (in some years) fall with a single heavy shower. The air passing from the cold Benguela Upwelling System onto the land surface gives rise to the frequent occurrence of fog. On average fog occurs for 89 and 48 days at the Orange and Olifants estuaries, respectively. The greatest occurrence of fog is from March to September. The importance of fog for the salt-marsh plants in semi-arid environments has not yet been quantified, but it is expected to be significant. The region is generally frost-free. See also climate diagram for AZe 1 Arid Estuarine Salt Marshes (Figure 14.3).

Important Taxa Estuarine water bodies: Aquatic Herb: *Potamogeton pectinatus*. **Tidal salt marshes**: Succulent Shrub: *Chenolea diffusa*. Herb: *Cotula coronopifolia*. Geophytic Herb: *Triglochin striata*. Succulent Herb: *Salicornia meyeriana* (d). Graminoids: *Juncus kraussii* subsp. *kraussii* (d), *Sporobolus virginicus* (d), *Ficinia nodosa, Juncus acutus* subsp. *leipoldtii, J. rigidus*. **Supratidal terraces**: Succulent Shrubs: *Salsola zeyheri*, *Suaeda fruticosa*. Succulent Herb: *Psilocaulon dinteri*. Graminoids: *Odyssea paucinervis* (d), *Phragmites australis* (d).

Biogeographically Important Taxa Supratidal terraces: Succulent Shrubs: *Lycium decumbens* (Gariep endemic), *Sarcocornia natalensis* var. *affinis* (West Coast endemic).

Conservation Least threatened. Target 24%. None conserved in statutory conservation areas. Some 15% transformed for cultivation or by mining (diamond prospecting) activities.

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Figure 14.21 AZe 1 Arid Estuarine Salt Marshes: Decaying lagoon of the Jakkals River at Lambert's Bay (Western Cape) after being artificially cut off from the tidal influence of the sea. The centre of the lagoon is dry at present and covered with a papery layer of dead algal bloom and a species of *Ruppia*, while the banks support typical supratidal halophilous vegetation with chenopods *Sarcocornia natalensis* var. *affinis* (pink patches), *Salicornia meyeriana* (deep red patches) and *Atriplex prostrata* subsp. *austroafricana* (in the foreground).

Remarks Estuaries in Namaqualand (south of Kleinzee) are relatively undisturbed, except for salt works in the Olifants and Sout Rivers. Increased freshwater abstraction in the Olifants estuary is a major threat, which would cause salinity intrusion into the middle reaches of the estuary in summer and loss of brackish habitats (*Cotula coronopifolia*, *Juncus kraussii*). An increase in groundwater salinity would result in die-back of the large supratidal and floodplain areas. The Orange estuary has also been impacted by freshwater alteration and die-back of a large floodplain salt-marsh area. Although barren areas are a natural feature of salt marshes on the West Coast of southern Africa, more than 70 ha have been lost at the mouth of the Orange River through bad management practices. Large-scale die-back of reed beds (mostly *Schoenoplectus scirpoideus* and *Phragmites australis*) occurs in the lower reaches of the Orange estuary as, in response to the low flows, saline water is pushed higher up the river.

References Day (1981b), Parsons & Le Roux

(1981a–f), Morant & O'Callaghan (1990), Boucher & Le Roux (1993, 1994), Lubke et al. (1997), Bornman (2002), Boucher (2003), Bornman et al. (2004a, b).

AZe 2 Cape Estuarine Salt Marshes

Distribution Western Cape and Eastern Cape Provinces: Estuaries and coastal salt-marsh plains of temperate coasts of the Atlantic Ocean from Lambert's Bay on the West Coast as far as the mouth of the Great Kei River (Eastern Cape) on the Indian Ocean coast. The most important estuarine systems of this type include salt marshes located at the Berg, Uilkraalsmond, Breede, Goukou, Groot and Klein Brak, Keurbooms/Bitou, Kromme, Seekoei, Kabeljous, Gamtoos, Swartkops, Kowie, Bushmans (penetrating inland as deep as Ghio Marsh), Kariega, Great Fish, Buffels, Keiskamma and Great Kei Rivers as well as estuarine lakes such as Kleinmond, De Mond (near Struisbaai), Swartvlei and estuarine bays such as Knysna Lagoon.

Vegetation & Landscape Features Estuarine flats and systems of low riverine terraces supporting complexes of low herblands and shrublands dominated by succulent chenopods and other flood-tolerant halophytes (especially on supratidal terraces and in middle and lower tidal zones), salt-marsh meadows dominated by rushes and sedges (often indicating freshwater seeps), *Spartina* swards and (temporary) submerged *Zostera* sea meadows at the lower boundary of the tidal zone.

Geology, Soils & Hydrology Most Cape estuaries drain Table Mountain Sandstone vegetated with Fynbos that gives the riverine water a characteristic black colour (high tannin load and low pH), with low amounts of sediment (medium-grained sand). The estuarine sediment has an increasingly higher clay fraction as one moves east due to the Karoo sediments through which these rivers drain, e.g. the Kromme, Gamtoos, Sundays Rivers, etc. Recent sandy sediments of layered mixed riverine and marine origin are submitted to a diurnal tidal flooding regime. The highest terraces are flooded only at the highest tides. Floodplains are flooded only during river floods. Floodplain salt marshes in estuaries with floodplains, e.g. the Berg, Breede, Gourits, Kromme and Gamtoos Rivers, are still dependent on groundwater as their major source of water, but the higher rainfall creates a higher cover of *Sarcocornia pillansii* and an increase in brackish species. The tidal range varies greatly; for instance in False Bay it is 0.5–2 m.

Climate Warm-temperate winter-rainfall (Atlantic coast and False Bay) and transitional winter-summer-rainfall (eastwards of the Cape Hangklip) regions. MAP between 175 mm (Lambert's Bay) and 850 mm (Garden Route). MAT from 16.0°C (Overberg) to 17.8°C (Albany region). The coastal waters and coastal climate of the region is under the decisive influence of the coastal cold-water upwellings of the Benguela Current (along the west coast) and of the cold Agulhas Counter-Current. Easterly winds in summer create localised coastal upwelling events along the South Coast that may decrease the estuarine water temperature by as much as 10°C (Schumann 2000). See also climate diagram for AZe 2 Cape Estuarine Salt Marshes (Figure 14.3).

Important Taxa **Estuarine water bodies**: Graminoids: *Ruppia cirrhosa* (d), *R. maritima* (d), *Zostera capensis* (d). **Tidal salt marshes**: Succulent Shrubs: *Chenolea diffusa* (d), *Sarcocornia perennis* complex (d). Low Shrubs: *Samolus porosus* (d). Herbs: *Cotula filifolia*, *Seidelia pumila*. Geophytic Herbs: *Triglochin bulbosa* complex (d), *Romulea tabularis, Triglochin striata*. Succulent Herbs: *Spergularia media* complex (d), *Plantago crassifolia* complex (d), *Salicornia meyeriana* (d), *Cotula coronopifolia*, *Suaeda inflata*. Graminoids: *Juncus kraussii* subsp. *kraussii* (d), *Spartina maritima* (d), *Sporobolus virginicus* (d), *Puccinellia angusta*, *Schoenoplectus triqueter*, *Stenotaphrum secundatum.* **Supratidal terraces**: Succulent Shrubs: *Disphyma crassifolium* (d), *Sarcocornia capensis* (d), *S. pillansii* (d). Graminoid: *Stenotaphrum secundatum* (d).

Biogeographically Important Taxa (both West Coast endemics) **Supratidal terraces**: Succulent Shrub: *Sarcocornia natalensis* var. *affinis* (d). Herb: *Limonium decumbens* (d).

Endemic Taxa **Tidal salt marshes**: Succulent Herbs: *Poecilolepis ficoidea*, *P. maritima*.

Conservation Least threatened. Target 24%. Already 21% statutorily conserved in the West Coast (including much of the Langebaan Lagoon) and Garden Route National Parks (including Knysna Lagoon), Rietvlei, Kleinmond, Walker Bay, De Mond, Swartkops Valley, Seekoei, Kabeljous River, Kap River, Great Fish River Wetland as well as in the private Emlanjeni Game Reserve (near Kenton-on-Sea). Langebaan Lagoon and the De Mond estuary are Ramsar sites. Some 14% transformed for cultivation, by urban sprawl, mining or road building.

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Figure 14.22 AZe 2 Cape Estuarine Salt Marshes: Tidal salt marsh in the head of the Langebaan Lagoon (West Coast National Park), with clones of *Sarcocornia perennis* complex (Chenopodiaceae), *Sporobolus virginicus* (Poaceae) and *Limonium decumbens* (Plumbaginaceae) forming a mosaic with algal slick patches.

References Dyer (1937), Boucher & Jarman (1977), Howard-Williams & Liptrot (1980), Day (1981b), Heinecken (1981, 1982a, b, 1985), Bickerton (1982, 1984), Cliff & Grindley (1982), Grindley (1982, 1985), Heinecken & Grindley (1982), Heinecken et al. (1982), Heydorn & Bickerton (1982), Koop (1982), Morant & Grindley (1982), Boucher (1983, 1987, 1998c–e), Carter (1983), Heinecken & Damstra (1983), Lubke (1983), Morant (1983, 1984), Morant & Bickerton (1983), Whitfield et al. (1983), Wiseman et al. (1983), Duvenhage & Morant (1984), Baird et al. (1986), Sinclair et al. (1986), Bickerton & Pierce (1988), Burns et al. (1988), Grindley (1988), Grindley & Dudley (1988), Boucher & Le Roux (1989), Clarke (1989), De Decker (1989), Heydorn (1989b), Bloemhoff & Craven (1990), Carter & Brownlie (1990), O'Callaghan (1990a, b, 1994a–e), Adams (1991), Morant (1991), Lubke et al. (1997), Adams et al. (1999), Allanson & Baird (1999), Boucher & Rode (1999), Colloty et al. (2000, 2001, 2002), Schumann (2000), Withers et al. (2002), Mucina et al. (2003).

AZe 3 Subtropical Estuarine Salt Marshes

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Figure 14.23 AZe 3 Subtropical Estuarine Salt Marshes: Grasses *Sporobolus virginicus* and *Paspalum distichum* are dominant in salt marsh grassland on the edge of a brackish coastal lagoon isolated from the sea by a sand bar (in the background)—Thompson's Lagoon at the Wild Coast Sun complex on the Eastern Cape/KwaZulu-Natal border.

Distribution Eastern Cape and KwaZulu-Natal Provinces: The subtropical coasts of Indian Ocean from north of Kei Mouth eastwards as far as the border between KwaZulu-Natal and Mozambique. The occurrence of the Subtropical Estuarine Salt Marshes roughly parallels the extent of the Mangrove Forest in South Africa.

Vegetation & Landscape Features Estuaries and coastal salt-marsh plains supporting complexes of low herblands dominated by succulent chenopods and other flood-tolerant halophytes. Also containing salt-marsh meadows dominated by rushes and sedges, *Spartina*-flooded swards and submerged *Zostera* sea meadows.

Geology, Soils & Hydrology Recent sandy sediments of mixed marine and riverine origin submitted to a diurnal tidal flooding regime. A high average salinity of water (18–23 g of soluble salt per litre) was recorded in the southernmost permanently open estuaries of this unit (Group B in Colloty et al. 2002). The estuaries on the KwaZulu-Natal coast usually have a lower salinity, often containing brackish mud flats fringing mangroves.

Climate Subtropical, year-round precipitation patterns with higher precipitation in summer (especially along the KwaZulu-Natal coast). MAP 932 mm (Maputaland) to 1 014 mm (Transkei). MAT 18.4°C (Transkei) to 21.1°C (Maputaland). The coastal waters as well as the climate of the coasts hosting this type of estuarine vegetation are under the influence of the warm Agulhas Current. No frost has been recorded. See also climate diagram for AZe 3 Subtropical Estuarine Salt Marshes (Figure 14.3).

Important Taxa **Estuarine water bodies**: Graminoids: *Spartina maritima* (d), *Zostera capensis* (d), *Halodule uninervis*, *Halophila ovalis*, *Thalassodendron ciliatum*. **Tidal salt marshes**: Succulent Shrub: *Chenolea diffusa* (d). Low Shrub: *Samolus porosus*. Geophytic Herbs: *Triglochin striata* (d), *T. bulbosa* complex. Succulent Herbs: *Sarcocornia natalensis* complex (d), *Salicornia pachystachya*. Graminoids: *Cyperus laevigatus* (d), *Juncus kraussii* subsp. *kraussii* (d), *Schoenoplectus litoralis* (d), *Sporobolus virginicus* (d). **Supratidal terraces**: Succulent Shrubs: *Disphyma crassifolium* (d), *Sarcocornia pillansii* (d). Herbs: *Atriplex patula* subsp. *verreauxii*, *Ethulia conyzoides* subsp. *kraussii*, *Nidorella linifolia*. Graminoids: *Paspalum vaginatum* (d), *Pycreus polystachyos*, *Stenotaphrum secundatum*.

Conservation Least threatened. Target 24%. Unknown percentage statutorily conserved in the Dwesa-Cwebe Wildlife Reserve & Marine Sanctuary, Mpenjati, Beechwood, Umgeni Lagoon, Amathikulu, Umlalazi and Richards Bay Nature Reserves as well as in the Greater St Lucia Wetland Park. Threats: dune mining, development (especially in KwaZulu-Natal), increased freshwater runoff and nutrient input from sugar cane fields (agriculture) and increased sedimentation and turbidity from soil erosion in catchment exacerbated by poor agricultural practices.

Remark 1 Low species diversity and limited extent of the Subtropical Estuarine Salt Marshes as compared to the AZe 2 Cape Estuarine Salt Marshes in South Africa support the general notion of the estuarine salt marshes being a temperate vegetation system.

Remark 2 A further four species (*Halodule wrightii, Cymodocea rotundata, C. serrulata* and *Syringodium isoetifolium*) of rhizomatous dioecious seagrasses of the family Cymodoceaceae found in sublittoral (and partly intertidal) 'sea meadows' have been reported form Maputo (Delagoa) Bay in Mozambique (Cook 2004).

References Day et al. (1953), Broekhuysen & Taylor (1959), Edwards (1967), Venter (1972), Campbell (1976), Begg (1978), Ward (1980), Day (1981b), Lubke et al. (1997), Adams et al. (1999), Allanson & Baird (1999), Colloty et al. (2000, 2001, 2002), Taylor et al. (2006).

Seashore Vegetation

AZd 1 Namib Seashore Vegetation

Distribution Northern Cape Province: Richtersveld coast, between the Holgat River and Orange River mouth. Larger portion of this unit extends further north along the Sperrgebiet coast into Namibia.

Vegetation & Landscape Features Slightly sloping beach and adjacent moving and fixed sand dunes with vegetation dominated by dwarf shrubs up to 1 m tall and spiny grasses on the windblown dunes. Small succulent dwarf shrubs are dominant on exposed rocky cliffs on the seafront.

Geology, Soils & Hydrology Recent marine sandy sediments forming beaches and coastal dunes (Strandveld Formation) and overlying Gariep Supergroup metasediments and metavolcanics. Not subjected to submersion, but under constant maritime influence (sea spray).

Climate Hostile, arid coast with the lowest precipitation in South Africa (45 mm at Alexander Bay). Fog is almost always present in winter at night and in the early morning. Because of the exceptionally low rainfall, the vegetation depends largely on sea fog as a source of moisture. MAT 17.2°C at Alexander Bay (see also climate diagram in Figure 6.2). Temperature does not vary greatly between winter and summer.

L. Mucina

Figure 14.24 AZd 1 Namib Seashore Vegetation: Coastal dunes of blown sand and shell debris at Diaz Point near Lüderitz (Namibia). The tall whitish shrub on the dune is *Salsola* cf. *nollothensis* (Chenopodiaceae), with the low cushion-forming *Zygophyllum clavatum* (Zygophyllaceae).

Important Taxa Succulent Shrubs: *Lycium tetrandrum* (d), *Tetragonia fruticosa* (d), *Didelta carnosa* var. *tomentosa*, *Zygophyllum clavatum*. Succulent Herb: *Psilocaulon dinteri*. Low Shrubs: *Atriplex vestita* (d), *Asparagus capensis* var. *littoralis, Hebenstretia cordata*. Herb: *Polygonum maritimum*. Graminoid: *Cladoraphis cyperoides* (d).

Biogeographically Important Taxa ([W]West Coast endemic, [G]Gariep endemic) Succulent Shrubs: *Salsola nollothensis*[W] (d), *Amphibolia rupis-arcuatae*[W], *Arctotis scullyi*[W], *Brownanthus marlothii*[G], *Drosanthemum luederitzii*[W], *Hypertelis angraepequenae*[W], *Lycium decumbens*[G]. Succulent Herb: *Fenestraria rhopalophylla* subsp. *aurantiaca*[W]. Herb: *Limonium* sp. nov.[W] (*Mucina 7238/8* STEU).

Conservation Vulnerable. Target 26%. None conserved in statutory conservation areas, but some off limits to the public due to coastal diamond mining, which is responsible for transformation of 14% of the area of the unit. Heavy minerals are also found here, but they have not yet been subject to exploitation.

References Boucher & Le Roux (1981, 1993), Williamson (1997).

AZd 2 Namaqualand Seashore Vegetation

Distribution Northern Cape Province: Namaqualand, very narrow strip above the high tide zone along the sea from the Holgat River to just south of the Olifants River.

Vegetation & Landscape Features Slightly sloping beach, coastal rocky formations supporting sparse vegetation composed of (partly) succulent hummock-forming and spreading dwarf shrubs and herbs on the beach, in shell beds and on low dunes. Leaf succulent chenopod shrubs are dominant on coastal cliffs and shell beds.

Geology, Soils & Hydrology Recent sandy marine sediments forming beaches and coastal dunes and extensive deep shell beds. The coastal cliffs consist of either Gariep Supergroup quartzitic sandstones or Mokolian granites and gneisses. Outside the direct influence of the sea (submersion), but under constant maritime influence (salt spray).

Climate Hostile, arid coast characterised by erratic rainfall, high solar irradiation and frequent desiccating winds. MAP 105 mm, increasing from around 60 mm (Port Nolloth) in the north to 150 mm (Strandfontein) in the south. Fog present in winter at night and in the early morning. MAT 17.6°C and seasonal temperature has a slightly higher variation than that of AZd 1 Namib Seashore Vegetation. Incidence of frost negligible. See also climate diagram for AZd 2 Namaqualand Seashore Vegetation (Figure 14.3).

Important Taxa **Shell beds**: Succulent Shrub: *Zygophyllum cordifolium* (d). Succulent Herbs: *Psilocaulon dinteri* (d), *Arctotheca populifolia*, *Mesembryanthemum guerichianum*. Low Shrub: *Frankenia repens*. **Dunes & beaches**: Succulent Shrubs: *Sarcocornia littorea* (d), *Crassula plegmatoides*, *C. tomentosa*, *Didelta carnosa* var. *tomentosa*, *Lycium tetrandrum*, *Othonna floribunda*, *Stoeberia utilis*, *Tetragonia decumbens, T. fruticosa*, *Zygophyllum morgsana*. Low Shrubs: *Atriplex vestita* (d), *Lebeckia cinerea* (d), *Asparagus capensis* var. *litoralis*, *Hebenstretia cordata*. Herbs: *Dasispermum suffruticosum*, *Polygonum maritimum*. Geophytic Herb: *Trachyandra divaricata*. Graminoids: *Cladoraphis cyperoides* (d), *Sporobolus virginicus*.

Biogeographically Important Taxa (all West Coast endemics) **Shell beds**: Succulent Shrubs: *Drosanthemum luederitzii*

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Figure 14.25 AZd 2 Namaqualand Seashore Vegetation: Upper-beach habitat with *Sarcocornia terminalis* (Chenopodiaceae), *Psilocaulon dinteri* and the alien *Salsola kali* north of Strandfontein near the mouth of the Olifants River (Western Cape).

L. Mucina

Figure 14.26 AZd 2 Namaqualand Seashore Vegetation: Shell beds on the beach at Mc Dougall's Bay (Port Nolloth, Northern Cape), with shrubby chenopods *Salsola nollothensis* and the leaf-succulent *Zygophyllum rotundifolium* (Zygophyllaceae).

(d), *Hypertelis angrae-pequenae*. Herb: *Limonium* sp. nov. (*Mucina 7238/8* STEU). **Dunes & beaches**: Succulent Shrubs: *Amphibolia rupis-arcuatae* (d), *Salsola nollothensis* (d), *Arctotis scullyi*, *Vanzijlia annulata*. Succulent Herb: *Fenestraria rhopalophylla* subsp. *aurantiaca*. **Cliffs**: Herb: *Limonium decumbens*.

Endemic Taxa Dunes & beaches: Herbs: *Gazania* sp. nov. (*Mucina 050905/02* STEU), *Limonium* sp. nov. ('*diamanticolum*') (*Mucina 050905/13* STEU).

Conservation Target 26%. None conserved in statutory conservation areas. Diamond mining in this area is a great threat to the strand vegetation whether it is land surface or marine mining (about 5% of the area of this unit has already been transformed). Heavy minerals are intensively mined near Brand-se-Baai and although the present mining is not yet on the strand, it will extend to the beaches. The guided Diamond Coast 4x4 trail runs through a restricted-access part of this unit between Noup and Kleinzee, providing some measure of protection. Establishment of a national park (including the coast between the Spoeg and Groen River mouth) is currently being negotiated.

Remark *Amphibolia rupis-arcuatae* and *Fenestraria rhopalophylla* subsp. *aurantiaca* are found only from the vicinity of Kleinzee northwards to the Orange River mouth, indicating a floristic relationship between the Namib and Namaqualand Seashore units.

References Boucher & Le Roux (1981, 1989, 1993), L. Mucina (unpublished data).

AZd 3 Cape Seashore Vegetation

Including *Didelta–Psoralea* Littoral-dune Open Grassland (Boucher & Jarman 1977). *Ehrharta–Ficinia* Strand Pioneers (Boucher 1978). *Tetragonia decumbens–Agropyron distichum* Fore-dune Community (O'Callaghan 1990a).

Distribution Western Cape and Eastern Cape Provinces: Temperate coasts of the Atlantic Ocean (Olifants River mouth to Cape Agulhas) and Indian Ocean (Cape Agulhas to East London). According to Tinley (1985; see also Lubke et al. 1997), this stretch of coast comprises the South West and South Coasts.

Vegetation & Landscape Features Beaches, coastal dunes, dune slacks and coastal cliffs of open grassy, herbaceous and to some extent also dwarf-shrubby (sometimes succulent) vegetation, often dominated by a single pioneer species. Various plant communities reflect the age of the substrate and natural disturbance regime (moving dunes), distance from the upper tidal mark and the exposure of dune slopes (leeward versus seaward).

Geology, Soils & Hydrology Young coastal sandy sediments forming beaches and dunes (Strandveld Formation), exposed to reworking by relentless winds and frequent sea storms. Some stretches of the West Coast are covered by extensive shell beds.

Climate The climate diagram for this unit (Figure 14.3) shows a largely uniform, all-year precipitation pattern, but this pattern must be interpreted with care since the unit encompasses regions of very diverse precipitation regimes. The West Coast (under influence of the Benguela Current) and the portion of the South Coast bordering on the Atlantic Ocean are characterised by cold seawater and frequent upwelling events. The local precipitation is low (as low as 100 mm in places) and typically seasonal (winter-rainfall peak). From Cape Agulhas westwards the coast is influenced by occasional eddies of the Agulhas Current, but the water stays generally cold. The precipitation becomes transitional, with a considerable increase of summer rainfall eastwards. MAP in Lambert's Bay, Cape Town, Plettenberg Bay and Port Elizabeth is 128 mm, 517 mm, 661 mm and 604 mm, respectively. The temperature varies less than precipitation (17–18°C for both Lambert's Bay and Port Elizabeth). See also climate diagram for this unit (Figure 14.3).

Important Taxa Dunes & beaches: Succulent Shrubs: *Drosanthemum candens* (d), *Pelargonium capitatum* (d), *Tetragonia decumbens* (d), *Didelta carnosa* var. *tomentosa*, *Exomis microphylla* var. *axyrioides*, *Lycium tetrandrum*, *Scaevola plumieri*. Low Shrubs: *Hebenstretia cordata* (d), *Frankenia repens*, *Oncosiphon sabulosum*. Semiparasitic Shrub: *Thesidium fragile*. Herbaceous Climbers: *Cynanchum ellipticum*, *C. obtusifolium*. Herbs: *Gazania rigens* (d), *Senecio littoreus* (d), *Amellus asteroides*, *Dasispermum suffruticosum*, *Manulea tomentosa*, *Polygonum maritimum*, *Senecio elegans*. Geophytic Herb: *Trachyandra divaricata*. Succulent Herbs: *Arctotheca populifolia* (d), *Carpobrotus acinaciformis*, *C. edulis*. Graminoids: *Cladoraphis cyperoides* (d), *Ehrharta villosa* var. *maxima* (d), *Sporobolus virginicus* (d), *Stipagrostis zeyheri* subsp. *barbata*. **Cliffs**: Succulent Shrubs: *Disphyma crassifolium* (d), *Sarcocornia littorea* (d). Herb: *Gazania rigens* (d).

Endemic Taxa Dunes & beaches: Low Shrub: *Psoralea repens* (d). Succulent Shrub: *Amphibolia laevis* (d). Herbs: *Amellus capensis*, *Gazania maritima*, *G. rigens* var. *leucolaena*, *Silene crassifolia*. Succulent Herbs: *Senecio litorosus*, *S. maritimus*. Graminoids: *Thinopyrum distichum* (d), *Eragrostis sabulosa*. **Dune slacks**: Herb: *Vellereophyton vellereum*. **Cliffs**: Succulent Shrubs: *Drosanthemum marinum* (d), *D. stokoei*, *Erepsia steytlerae*, *Prenia vanrensburgii*. Low Shrub: *Syncarpha sordescens*. Herbs: *Limonium* sp. nov. (*Mucina 6942/1* STEU), *Lobelia boivinii*.

Conservation Least threatened. Target 20%. Almost half of the area statutorily conserved in the West Coast, Cape Peninsula,

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Figure 14.27 AZd 3 Cape Seashore Vegetation: Dune cordons in De Mond Nature Reserve near Arniston (Western Cape), close to Cape Agulhas (the southernmost point of the African continent). The dominant grasses are *Thinopyrum distichum* and *Ehrharta villosa* var. *maxima* and the yellow-flowered daisy is *Didelta carnosa* var. *tomentosa*.

Agulhas, proposed Garden Route and Greater Addo Elephant National Parks as well as the Rocher Pan, Cape Columbine, Dassen Island, Wolvengat, Kleinmond, Walker Bay, De Mond (Ramsar site), De Hoop, Kleinjongensfontein, Geelkrans, Robberg, (all Western Cape), and Cape St Francis, Cape Recife, Joan Muir, Gxulu, Cape Henderson, Kwelera and Bosbokstrand Nature Reserves (all Eastern Cape). A number of private conservation areas such as Donkin Bay, Robben Island, Rein's Coastal Reserve and Tharfield Nature Reserve protect other considerable portions of the Cape Seashore Vegetation. Only about 1.7% has been transformed, mainly by urban development.

Remark Extensive dunefields are found at De Hoop, Cape St Francis, Gamtoos, Alexandria and Boknes along this coastal stretch (Tinley 1985, Young 1987, Talbot & Bate 1991).

References Muir (1929), Dyer (1937), Martin & Noel (1960), Comins (1962), Boucher (1972, 1977, 1978, 1986, 1987, 1989, 1992, 1993, 1994, 1995, 1997, 1998a, b, c, e, 1999a–e), Heydorn (1975), Boucher & Jarman (1977), Boucher & Le Roux (1981), Taylor & Morris (1981), Van Rooyen (1981), Lubke & Avis (1982a, b, 1988, 2000), Lubke (1983), Boucher et al. (1986), La Cock (1986), McLachlan et al. (1987), Young (1987), Avis (1989, 1992, 1995), Lubke & De Villiers (1991), Parker-Nance et al. (1991), Talbot & Bate (1991), Bate & Dobkins (1992), Turner (1992), Boucher & Le Roux (1993), Taylor & Boucher (1993), Boucher & Rode (1995a, b, 1999), Britton & Jackelman (1995), Lubke et al. (1995, 1997), Gray (1997), Hertling (1997), Hertling & Lubke (1999a, b), Hesp & McLachlan (2000), Hoare et al. (2000), Ripley (2001), Barker et al. (2002).

AZd 4 Subtropical Seashore Vegetation

Dune Pioneers (Weisser 1978). A34 Strandveld p.p. (Acocks 1988). VT 4 Dune Thicket p.p. (Low & Rebelo 1996).

Distribution Eastern Cape and KwaZulu-Natal Provinces: Beaches, coastal dunes, dune slacks and coastal cliffs of the subtropical coasts of the Indian Ocean (from northeast of Kei Mouth in the Eastern Cape to the Mozambique border), the region includes South East, Transkei and KwaZulu-Natal coasts (*sensu* Tinley 1985, Lubke et al. 1997).

Vegetation & Landscape Features Open, grassy, herbaceous and to some extent also dwarf-shrubby, often dominated by a single species of pioneer character. Various plant communities reflect the age of the substrate and the natural disturbance regime (moving dunes), distance from the upper tidal mark and the exposure of dune slopes (leeward versus seaward).

Geology, Soils & Hydrology Recent coastal sandy sediments forming beaches and dunes, exposed to reworking by relentless wind and sea storms.

Climate Rainfall can occur any time during the year but with more in summer in the western part of the area (Kei Mouth region), with a pronounced summer precipitation peak along most of the northern coastal stretch. Overall MAP more than 1 000 mm. MAT of 20.3°C is indicative of a subtropical thermal regime. No frost occurs in the region. Very intensive solar irradiation enhanced by reflected albedo from the white dunes and the sea.

Important Taxa **Dunes & beaches**: Succulent Shrubs: *Phylohydrax carnosa* (d), *Scaevola plumieri* (d), *S. sericea*. Herbaceous Climbers: *Ipomoea pes-caprae* (d), *I. wightii*. Herbs: *Canavalia rosea* (d), *Gazania rigens* (d), *Chironia decumbens*, *Dasispermum suffruticosum*, *Gladiolus gueinzii*, *Helichrysum praecinctum*, *Launaea sarmentosa*, *Phyllopodium cuneifolium*, *Silene primuliflora*, *Tephrosia purpurea* subsp. *canescens*,

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Figure 14.28 AZd 4 Subtropical Seashore Vegetation: *Scaevola plumieri* (Goodeniaceae) is a typical subtropical dune element forming dense populations from Maputaland (this view) as far west as Arniston (Western Cape).

Zaluzianskya maritima. Geophytic Herb: *Trachyandra divaricata*. Succulent Herb: *Arctotheca populifolia* (d). Graminoids: *Ficinia nodosa* (d), *Juncus kraussii* subsp. *kraussii* (d), *Sporobolus virginicus* (d), *Cyperus crassifolius*, *Imperata cylindrica*, *Stipagrostis zeyheri* subsp. *barbata*. **Cliffs**: Succulent Shrub: *Chenolea diffusa* (d). Herbs: *Chironia decumbens*, *Gazania rigens*. Succulent Herb: *Carpobrotus dimidiatus*. Graminoid: *Ficinia lateralis*.

Conservation Least threatened. Target 20%. Some 30% statutorily conserved in the Greater St Lucia Wetland Park as well as in the Richards Bay, Umlalazi, Amathikulu and Beachwood Mangroves Nature Reserves (all KwaZulu-Natal) and in the Mkambati Nature Reserve and Dwesa-Cwebe Wildlife Reserve & Marine Sanctuary (both Eastern Cape). Almost 10% already transformed by urban (largely tourism) development.

Ş.M. Proches

Figure 14.29 AZs 1 Algoa Dune Strandveld: Low strandveld thicket dominated by *Tetragonia decumbens* (Aizoaceae) and *Dimorphotheca fruticosa* (Asteraceae) on Bird Island in Algoa Bay near Port Elizabeth (Eastern Cape), supporting a large colony of jackass penguins (*Spheniscus demersus*).

Remarks The tropical coastal elements increase along the south-north gradient. The subtropical beaches and young dune systems of KwaZulu-Natal stand out through the occurrence of tropical floristic elements (*Canavalia, Phylohydrax, Ipomoea, Scaevola*).

References Edwards (1967), Moll & Pierce (1975), Campbell (1976), Weisser & Marques (1979), Donnelly & Pammenter (1983), Weisser & Müller (1983), Lubke et al. (1995, 1997), Hertling & Lubke (1999a, b), Smith (2001), Barker et al. (2002), L. Mucina (unpublished data).

Eastern Strandveld

AZs 1 Algoa Dune Strandveld

VT 34a Dense Strandveld Scrub p.p. (Acocks 1953). *Pterocelastrus tricuspidatus* Bushclumps, Dune Woodland (Taylor & Morris 1981). Subtropical Transitional Thicket p.p., *Cassine aethiopica-Cussonia thyrsiflora* South-East Dune Thicket (Cowling 1984). Dune Scrub and Thicket p.p. (Lubke & Van Wijk 1988). LR 4 Dune Thicket p.p. (Low & Rebelo 1996). STEP Algoa Dune Thicket, STEP Colcester Strandveld (Vlok & Euston-Brown 2002, Vlok et al. 2003).

Distribution Eastern Cape Province: Narrow coastal strip along the Indian Ocean seaboard from the mouth of the Tsitsikamma River to the Sundays River mouth.

Vegetation & Landscape Features Tall (up to 5 m) dense thickets on dunes mainly outside the influence of salt spray, dominated by stunted trees, shrubs (often armed with spines and thorns), abundant lianas and sparse herbaceous and grassy undergrowth.

Geology, Soils & Hydrology Aeolian dune sands of the Schelm Hoek Formation of the Algoa Group.

Climate Nonseasonal precipitation regime, with MAP approximately 680 mm, of which about 300 mm falls in summer (October–March) and 350 mm in winter (April–September). The mean daily maximum and minimum temperatures are 25.1°Cand 8.3°C for February and July, respectively. See also climate diagram for AZs 1 Algoa Dune Strandveld (Figure 14.3).

Important Taxa ([S]Stunted shrubby forms of trees) Succulent Tree: *Aloe africana* (d). Succulent Shrubs: *Cotyledon velutina*, *Lycium cinereum*, *Zygophyllum morgsana*. Tall Shrubs: *Azima tetracantha* (d), *Brachylaena discolor*[S] (d), *Chrysanthemoides monilifera* (d), *Cussonia thyrsiflora*[S] (d), *Euclea racemosa* subsp. *racemosa*[S] (d), *Maytenus procumbens* (d), *Mystroxylon aethiopicum*[S] (d), *Pterocelastrus tricuspidatus*[S] (d), *Rhus crenata* (d), *Schotia afra* var. *afra*[S] (d), *Scutia myrtina*[S] (d), *Sideroxylon inerme*[S] (d), *Tarchonanthus littoralis*[S] (d), *Canthium spinosum*[S], *Cassine peragua*[S], *Dovyalis rotundifolia*[S], *Euclea natalensis*[S], *E. racemosa* subsp. *macrophylla*, *Grewia occidentalis*, *Gymnosporia buxifolia*, *G. capitata*, *Nylandtia spinosa*, *Olea exasperata*, *Putterlickia pyracantha*, *Rhus glauca*, *R. pterota*, *Zanthoxylum capense*[S]. Low Shrubs: *Carissa bispinosa* (d), *Dimorphotheca fruticosa, Pelargonium suburbanum* subsp. *suburbanum*, *Robsonodendron maritimum*. Succulent Woody Climber: *Sarcostemma viminale*. Woody Climbers: *Rhoicissus digitata* (d), *Asparagus retrofractus*, *Solanum africanum*. Herbaceous Climbers: *Cynanchum natalitium* (d), *C. ellipticum*, *C. obtusifolium*, *Secamone alpini*. Succulent Herb: *Sansevieria hyacinthoides*. Graminoids: *Brachiaria chusqueoides* (d), *Panicum deustum*.

Endemic Taxa Succulent Shrub: *Cotyledon adscendens*. Tall Shrubs: *Gymnosporia elliptica*, *Rapanea gilliana*. Herb: *Lobelia zwartkopensis*. Geophytic Herb: *Brunsvigia litoralis*.

Conservation Least threatened. Target 20%. About 4% statutorily conserved in the Greater Addo Elephant National Park, Cape Recife, Sardinia Bay, The Island, Kromme River Mouth, Gamtoos River Mouth, Huisklip, Cape St Francis and Seal Point Nature Reserves as well as in the private Upe and Rebelsrus Nature Reserves, Thyspunt Natural Heritage Site and in the Seaview Game Park. More than 10% already transformed for cultivation, urban development and road building. Some of the dune systems suffer heavy infestation by *Acacia cyclops* and *A. saligna*, which are now being removed by the local Working for Water activities. Erosion very low (63%) and moderate (10%).

Remarks The structure and dynamics of this vegetation unit are similar to those of the thickets of FS 9 Groot Brak Dune Strandveld (see chapter on Fynbos in this book). However, the present unit differs from the latter in having a richer assemblage of woody species. It is somewhat surprising that forest vegetation is not dominant in this seemingly suitable climatic regime. This is probably because the substrate consists of aeo-

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Figure 14.30 AZs 1 Algoa Dune Strandveld: Typical coastal dune thickets on the coast of Algoa Bay east of Port Elizabeth (Eastern Cape).

Important Taxa ([S]Stunted shrubby forms of trees) Succulent Tree: *Aloe africana*. Succulent Shrubs: *Cotyledon orbiculata*, *Crassula nudicaulis*, *Delosperma ecklonis*, *D. litorale*. Tall Shrubs: *Brachylaena discolor*[S] (d), *Chrysanthemoides monilifera* (d), *Euclea undulata* (d), *Metalasia muricata* (d), *Pterocelastrus tricuspidatus* (d), *Sideroxylon inerme*[S] (d), *Azima tetracantha*, *Cassine peragua*[S], *Clausena anisata*[S], *Cordia caffra*, *Cussonia thyrsiflora*[S], *Diospyros dichrophylla*, *Euclea natalensis*[S], *E. racemosa* subsp. *macrophylla*, *Eugenia capensis*[S], *Grewia occidentalis*, *Gymnosporia buxifolia*, *Hippobromus pauciflorus*, *Maytenus procumbens*, *Mystroxylon aethiopicum*[S], *Plumbago auriculata*, *Putterlickia pyracantha*, *Rhus crenata*, *R. glauca*, *R. longispina*, *R. lucida*, *R. pterota*, *Robsonodendron eucleiforme*, *Schotia afra* var. *afra*[S], *Scutia myrtina*[S], *Tarchonanthus littoralis*[S], *Zanthoxylum capense*[S]. Low Shrubs: *Passerina rigida* (d), *Anthospermum littoreum*[S], *Asparagus capensis* var. *litoralis, Carissa bispinosa* subsp. *bispinosa*, *Helichrysum tereti-*

lian quaternary sands, salt-laden winds are prevalent in this region and because fires may periodically occur here (Vlok & Euston-Brown 2002).

References Taylor & Morris (1981), Olivier (1983), Cowling (1984), Cowling & Pierce (1985), Taylor & Boucher (1993), Vlok & Euston-Brown (2002), Vlok et al. (2003).

AZs 2 Albany Dune Strandveld

Psammophilous Macchia and Littoral Scrub (Dyer 1937). VT2 Alexandria Forest p.p., VT1 Coastal Forest and Thornveld p.p. (Acocks 1953). *Cassine aethiopica–Schotia afra* Alexandria Dune Thicket (Cowling 1984). Dune scrub and thicket p.p. (Lubke & Van Wijk 1988). LR 4 Dune Thicket p.p. (Low & Rebelo 1996). STEP Albany Dune Thicket (Vlok et al. 2002). For further synonyms see Avis & Lubke (1996, p. 242).

Distribution Eastern Cape Province: A narrow coastal strip of the Indian Ocean extending from the Sundays River to south of Kei Mouth.

Vegetation & Landscape Features Very dense shrubby thicket composed of 2–4 m high, mostly sclerophyllous shrubs accompanied by several woody and herbaceous vines, and with a sparse grassy understorey. This unit also includes low (wind-sheared and salt-sprayed), dense thickets found on seaward slopes of the coastal dune cordons and rocky headlands (coastal cliffs). The occurrence of bulbous geophytes and succulent herbs is an important feature of this vegetation unit.

Geology, Soils & Hydrology Dune systems of the Schelm Hoek Formation, which also consists of dune sands in which shell material and calcrete lenses occasionally occur, as well as older Algoa Group calcareous sandstones and shallow marine deposits.

Climate Rainfall can occur any time of the year (but with most in summer), but the probability of rain is the highest in March and October (slight bimodality). MAP slightly higher than 700 mm. The temperature regime is ameliorated, with the mean daily maximum and minimum temperatures being 26.4°C and 8.8°C for February and July, respectively. The unit lies in a broad transition including warm-temperate and subtropical regions. Local salt-laden sea winds constitute a serious stress factor. See also climate diagram for AZs 2 Albany Dune Strandveld (Figure 14.3).

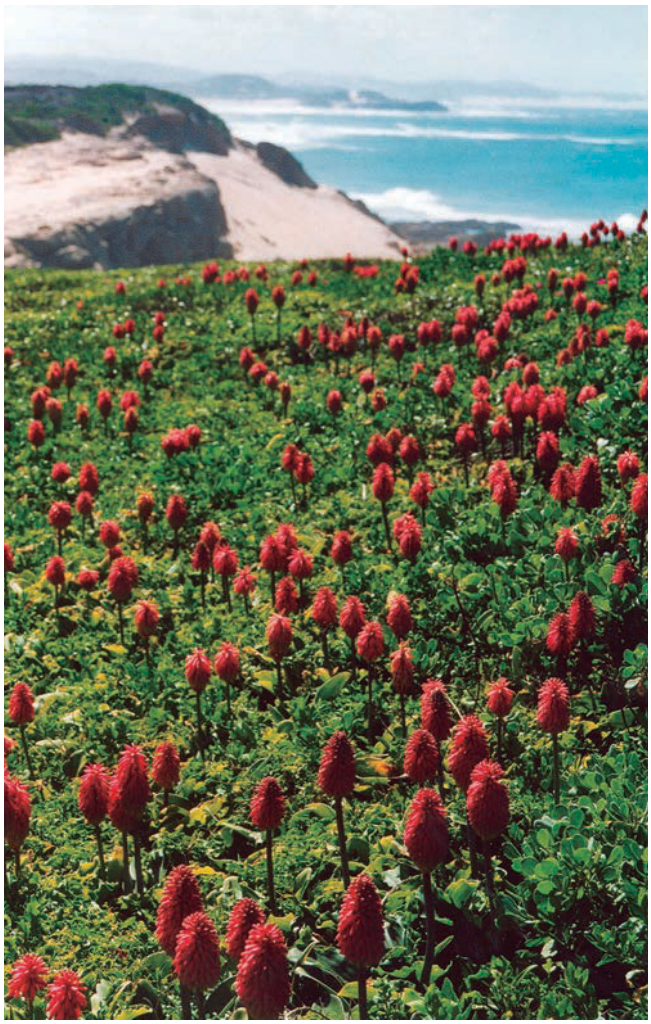

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Figure 14.31 AZs 2 Albany Dune Strandveld: Spring display of bulbous *Veltheimia bracteata* (Hyacinthaceae) in a wind-sheared *Pterocelastrus tricuspidatus* and *Robsonodendron maritimum* (both Celastraceae) coastal thicket on an aeolinite headland at the Diaz Cross site between Boknes and Kenton-on-Sea (Eastern Cape).

folium, *Lauridia tetragona*, *Pavetta revoluta*, *Psoralea repens*, *Rhoiacarpos capensis*, *Robsonodendron maritimum*, *Salvia africana-lutea*, *Senecio burchellii*. Semiparasitic Shrub: *Osyris compressa*. Succulent Woody Climber: *Sarcostemma viminale*. Woody Climbers: *Asparagus asparagoides*, *A. racemosus*, *Capparis sepiaria*, *Rhoicissus digitata*. Herbaceous Succulent Climber: *Senecio angulatus*. Herbaceous Climbers: *Astephanus marginatus*, *Cynanchum ellipticum*, *C. natalitium*, *C. obtusifolium*, *Kedrostis nana*, *Senecio deltoideus*. Herbaceous Parasitic Climber: *Cassytha filiformis*. Herb: *Felicia erigeroides*. Geophytic Herbs: *Haemanthus albiflos* (d), *Veltheimia bracteata* (d), *Androcymbium longipes*, *Bonatea speciosa*, *Bulbine frutescens*, *Chasmanthe aethiopica*, *Dietes iridioides*, *Gladiolus floribundus*, *Massonia echinata*, *Sansevieria hyacinthoides*, *Trachyandra revoluta*. Succulent Herbs: *Carpobrotus deliciosus*, *C. edulis*, *Crassula cotyledonis*, *Gasteria acinacifolia*, *G. croucheri*. Graminoids: *Stenotaphrum secundatum* (d), *Brachiaria chusqueoides*, *Panicum deustum*.

Conservation Least threatened. Target 20%. Some 25% statutorily conserved in the Greater Addo Elephant National Park, Gulu, Christmas Vale, Cape Morgan, Cintsa, Cove Rock, Bluebend and Sunshine Coast Nature Reserves as well as in private conservation areas such as the Glendour and Kasouga Farm Natural Heritage Sites and Waterloo Bay Forest Reserve. Alien Australian acacias (*Acacia cyclops, A. saligna, A. longifolia*) have invaded large stretches of the coastal thicket and are dominant in places. *Lagurus ovatus* and species of *Lolium* occur in disturbed patches of this coastal thicket. At present these plants are targeted for eradication by the Working for Water Programme of DWAF. Some 8% transformed for urban development and cultivation. Erosion very low (26%), moderate (22%), high (14%) and low (11%).

Remarks Most of the woody species present in the Algoa Dune Strandveld vegetation also occur in AZs 2 Albany Dune Strandveld, but here the species richness is enhanced by several subtropical elements such as *Pavetta revoluta* and *Phoenix reclinata*—taxa that reach their southernmost distribution here. The presence of species such as *Euphorbia triangularis, Plumbago auriculata* and *Scutia myrtina* in this unit indicates a direct relationship with the neighbouring Albany Thicket. This relationship may well indicate that the thickets of the Albany Dune Strandveld have long been a precursor of climax forest vegetation, probably not dissimilar to those of the present Alexandria Forest.

References Dyer (1937), Martin & Noel (1960), Comins (1962), Lubke (1983), Burns (1986), La Cock (1986), Young (1987), Lubke & De Villiers (1991), Talbot & Bate (1991), Weisser & Cooper (1993), Avis & Lubke (1996), Vlok & Euston-Brown (2002), Vlok et al. (2003).

AZs 3 Subtropical Dune Thicket

Passerina rigida Low Scrub, Seeward, Coastal Thicket and Low Forest (Weisser 1978). Closed Dune Scrub, Open Dune Scrub (Ward 1980). Dune Thicket (Weisser et al. 1992a). STEP Transfish Dune Thicket (Vlok & Euston-Brown 2002, Vlok et al. 2003).

Distribution Eastern Cape and KwaZulu-Natal Provinces (further north also in Mozambique): Coastal dune cordons along the subtropical coasts of the Indian Ocean between Kei Mouth and the KwaZulu-Natal/Mozambique international border.

Vegetation & Landscape Features Very dense shrubby thickets of spiny shrubs (up to 4 m), large-leaved megaherbs (*Strelitzia nicolai*), dwarfed trees (species of *Allophylus, Apodytes, Mimusops*), abundant vines, and with poorly developed undergrowth due to the shading effect of the closed canopy. Dwarf coastal dune shrublands on exposed, wind-blasted and salt-sprayed dune slopes bordering on tall thickets are also included here.

Geology, Soils & Hydrology Recent dunes overlying calcretes as well as Maputaland Group calcareous sandstones and shallow marine deposits.

Climate Characterised by relatively high MAP (1 028 mm) and a high probability of rain any time of the year (with pronounced higher rainfall in all seasons, except for the winter months of June and July. Subtropical thermal regime with MAT 19.0°C and no incidence of frost. See also climate diagram for AZs 3 Subtropical Dune Thicket (Figure 14.3).

Important Taxa ([S]Stunted shrubby forms of trees) Succulent Tree: *Euphorbia triangularis*. Small Trees: *Encephalartos altensteinii*, *Phoenix reclinata*. Tall Shrubs: *Brachylaena discolor*[S] (d), *Chrysanthemoides monilifera* (d), *Acokanthera oblongifolia*[S], *Allophylus natalensis*[S], *Apodytes dimidiata* subsp. *dimidiata*[S], *Azima tetracantha*, *Canthium inerme*[S], *C. spinosum*[S], *Cordia caffra*, *Deinbollia oblongifolia*[S], *Diospyros rotundifolia*[S], *Dodonaea viscosa*, *Euclea natalensis* subsp. *rotundifolia*[S], *E. racemosa* subsp. *macrophylla*, *Eugenia capensis*[S], *Grewia occidentalis*, *Gymnosporia buxifolia*, *G. nemorosa*, *Harpephyllum caffrum*[S], *Hyperacanthus amoenus*, *Maytenus procumbens*, *Mimusops caffra*[S], *Monanthotaxis caffra*[S], *Mystroxylon aethiopicum*[S], *Psychotria capensis*, *Psydrax obovata* subsp. *obovata*[S], *Putterlickia pyracantha*, *P. verrucosa*, *Rhus glauca*, *R. lucida*, *R. nebulosa*, *Rothmannia globosa*[S], *Scutia myrtina*[S], *Sideroxylon inerme*[S], *Tarchonanthus littoralis*[S], *Tricalysia sonderana*[S], *Zanthoxylum capense*[S]. Low Shrubs: *Carissa bispinosa* subsp. *bispinosa*, *C. macrocarpa*, *Helichrysum kraussii*, *Passerina rigida*, *Pavetta revoluta*, *Robsonodendron marit-*

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Figure 14.32 AZs 2 Albany Dune Strandveld: Wind-sheared coastal thickets on a dune at Kenton-on-Sea (Eastern Cape), with *Pterocelastrus tricuspidatus* and *Robsonodendron maritimum* (both Celastraceae) dominant.

imum. Soft Shrub: *Isoglossa woodii*. Succulent Woody Climber: *Cyphostemma flaviflorum*. Woody Climbers: *Adenopodia spicata*, *Coptosperma littorale*, *Rhoicissus digitata*, *R. rhomboidea*, *Tragia glabrata* var. *glabrata*. Herbaceous Climbers: *Cynanchum natalitium*, *C. obtusifolium*, *Gloriosa superba*, *Ipomoea ficifolia*, *I. wightii*. Herbs: *Asystasia gangetica*, *Lobelia pinifolia*, *Rubia cordifolia*. Megaherb: *Strelitzia nicolai* (d). Geophytic Herbs: *Crocosmia aurea*, *Microsorum scolopendria*, *Scadoxus puniceus*. Parasitic Herb: *Hyobanche fulleri*. Graminoids: *Stenotaphrum secundatum* (d), *Panicum deustum*.

Biogeographically Important Taxon (shared with Mascarene Islands and Madagascar) Succulent Shrub: *Lycium mascarenense*.

Endemic Taxa Succulent Shrub: *Aloe thraskii* (d). Low Shrub: *Sophora inhambanensis*.

Conservation Least threatened. Target 20%. About 27% statutorily conserved in the Greater St Lucia Wetland Park as well as in the Richards Bay, Umlalazi, Amathikulu (all KwaZulu-Natal), Bosbokstrand, Kwelera, Cape Henderson and Cape Morgan Nature Reserves. Unknown percentage transformed by urban sprawl and especially by coastal heavy-mineral mining. Aliens such as *Chromolaena odorata, Lantana camara* and a species of *Pereskia* occur as serious infestations in places. Erosion very low (12%), other erosion categories only at low values.

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Figure 14.33 AZs 3 Subtropical Dune Thicket: *Aloe thraskii* (Asphodelaceae), a tall succulent that can tolerate high levels of salt in the soil and a typical element of subtropical dune thickets (Amanzimtoti south of Durban, KwaZulu-Natal).

Remarks There is a clear floristic link between this vegetation unit and the Eastern Cape Dune Forest in the southern parts of the distribution area and KwaZulu-Natal Dune Forest (for concept and terminology see Von Maltitz et al. 2003 and Geldenhuys & Mucina 2005) in the northern parts of the area. Besides floristic differences, the most striking difference lies in the vegetation structure and age of dunes populated by the respective types.

References Edwards (1967), Moll & Pierce (1975), Weisser (1978), Ward (1980), Weisser et al. (1982, 1992a), Donnelly & Pammenter (1983), MacDevette (1989a, b), Weisser & Cooper (1993), Lubbe (1997), Boucher (1998b), Smith (2001), Vlok & Euston-Brown (2002), Vlok et al. (2003).

9. Credits

The concept of the coastal vegetation units were coined by L. Mucina and M.C. Rutherford with the assistance of the authors of the particular descriptions (see below). L.W. Powrie contributed considerably to the precise delimitation of the vegetation units by using satellite imagery of the coastal regions. The introductory text is a team effort by L. Mucina (all sections), I. Knevel (sections on sand dunes), J.B. Adams and T.G. Bornman (sections on estuaries), J.J. Bolton and R.J. Anderson (sections on algal beds) and J.H.J. van der Merwe (section on origins of the coastal features). The descriptions of all units (except for AZm 1) were written by L. Mucina. He was assisted by A. le Roux (units AZe 2, AZd 1 and 2), J.A.M. Janssen (AZe 2), J.B. Adams (AZd 1 and 2) and T.G. Bornman (AZd 2). The data on conservation (status and targets) were provided by the team spearheading the National Spatial Biodiversity Assessment at SANBI (in particular by M. Rouget, P.G. Desmet and others—see also Chapters 16 and 17 in this book). The other relevant sections (alien infestation, erosion, conservation areas) were prepared by L.W. Powrie using various GIS sources (see Chapter 2 for further details). Figure 14.2 was reproduced with courtesy of American Meteorological Society, Figure 14.8 from Tinley (1985) with kind permission of the CSIR. Figure 14.6 was prepared by J.B. Adams and Figure 14.17 by L. Mucina. Table 14.1 was compiled by I. Knevel and L. Mucina, Table 14.2 and 14.4 by J.B. Adams and Table 14.3 by L. Mucina. The maps of distribution of the vegetation units (Figure 14.18) were prepared by L. Mucina and L.W. Powrie. M.C. Rutherford and L.W. Powrie provided all climate data and the climate diagrams (Figure 14.12). M. Rouget and others within the SANBI Directorate of Biodiversity Programmes, Policy and Planning provided the quantitative information on conservation status, targets and areas transformed through road construction for each vegetation unit. R.A. Ward kindly checked and corrected the sections on geology. All photographs were taken by L. Mucina, except for two which were kindly supplied by W.S. Matthews (the opening photograph) and Ş.M. Procheş. The list of references was compiled and collated by L. Mucina using own as well as co-authors' sources.

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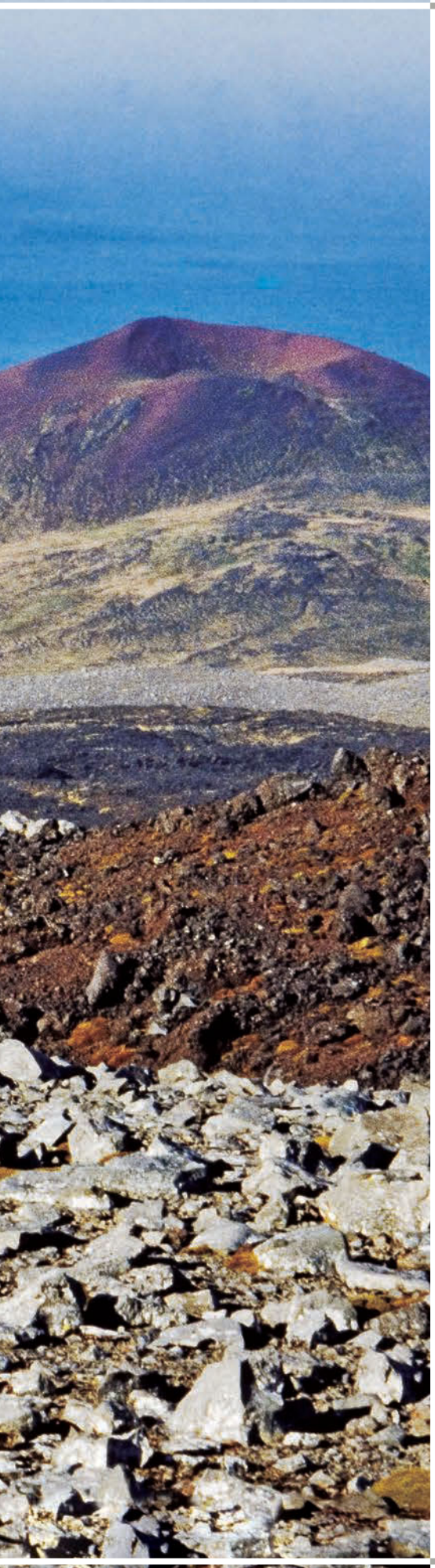
'Marion was a lovely picture. She rose, a jade jewel, out of the sea. Her lush green coat was fringed with the black lace of the cliffs and her heights draped in scintillating snow.'

from J. H. Marsh, 1948. *No pathway here*. Howard B. Timmins, Cape Town. p. 71



V.R. Smith

Vegetation of Subantarctic Marion and Prince Edward Islands

15

Valdon R. Smith and Ladislav Mucina

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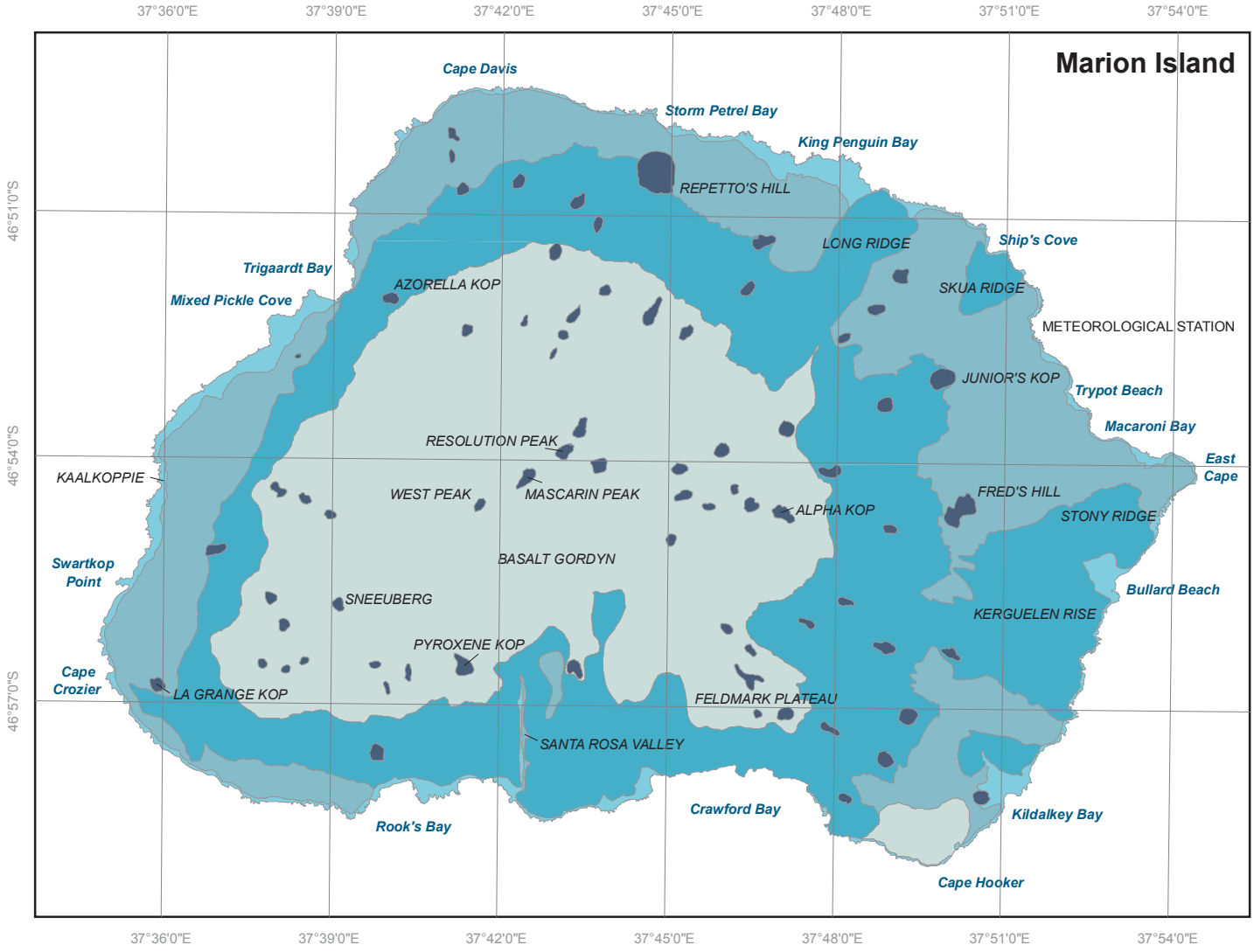
List of Vegetation Units

Figure 15.1 Fellfield vegetation with *Azorella selago* on Marion Island. In the foreground a narrow tongue of Holocene black lava extends over a Pleistocene grey lava flow. In the background, 4 km away, is the meteorological station surrounded by a mosaic of mire, slope and fellfield. The cinder cone on the right is Junior's Kop.

Prince Edward Islands



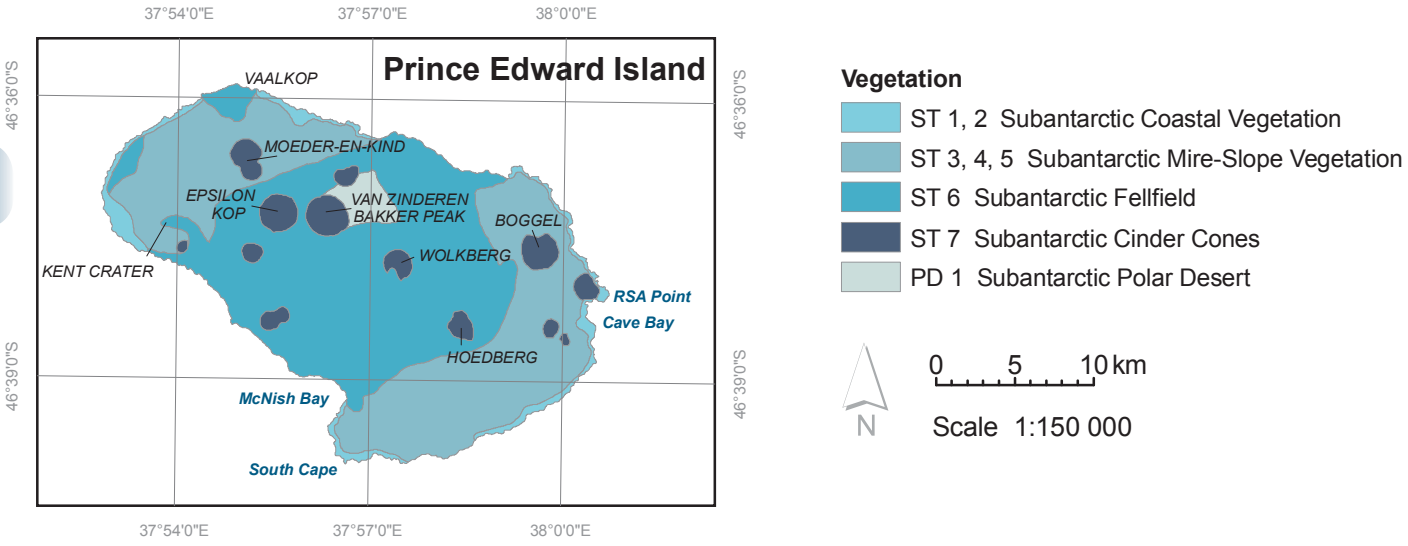


Figure 15.2 Vegetation maps of the Prince Edward Islands.

1. Introduction

South Africa possesses two subantarctic islands—Marion Island (46° 54′ S, 37° 45′ E) and Prince Edward Island (46° 38′ S, 37° 57′ E) (Figure 15.3). Together they are known as The Prince Edward Islands. Marion Island was annexed by South Africa on 29 December 1947 and Prince Edward Island on 4 January 1948. The annexations became effective with the passing by Parliament of the Prince Edward Islands Act (43) of October 1948. Marion Island has been occupied permanently by South African research and logistic personnel since February 1948. There is no permanent occupation of Prince Edward Island.

2. The Subantarctic Region and Tundra

The term subantarctic refers to various regions of the Southern Ocean, depending upon whether it is used in an oceanographic, limnological or biological context. Even within these disciplines, workers have considered different numbers of islands and island groups as subantarctic. Oceanographers generally define the subantarctic region as the zone of waters between the Antarctic and Subtropical Convergences (Deacon 1960). The latitudinal distributions of those organisms dependent entirely upon the sea for their existence seem to follow these boundaries quite well but the limits of the main types of terrestrial vegetation (Wace 1965), insect fauna (Gressitt 1970) and avifauna (Barrat & Mougin 1974) do not coincide with them so closely.

Botanists have generally preferred to define the subantarctic region on plant physiognomic, vegetation structure or climatic criteria. For instance, Wace (1960, 1965) proposed delimiting the subantarctic region as the area south of the southern limit of tree or shrub growth (distinguishing it from the cool temperate zone) and north of the southern limit of closed phanerogamic vegetation (delimiting it from the maritime or low-ant-

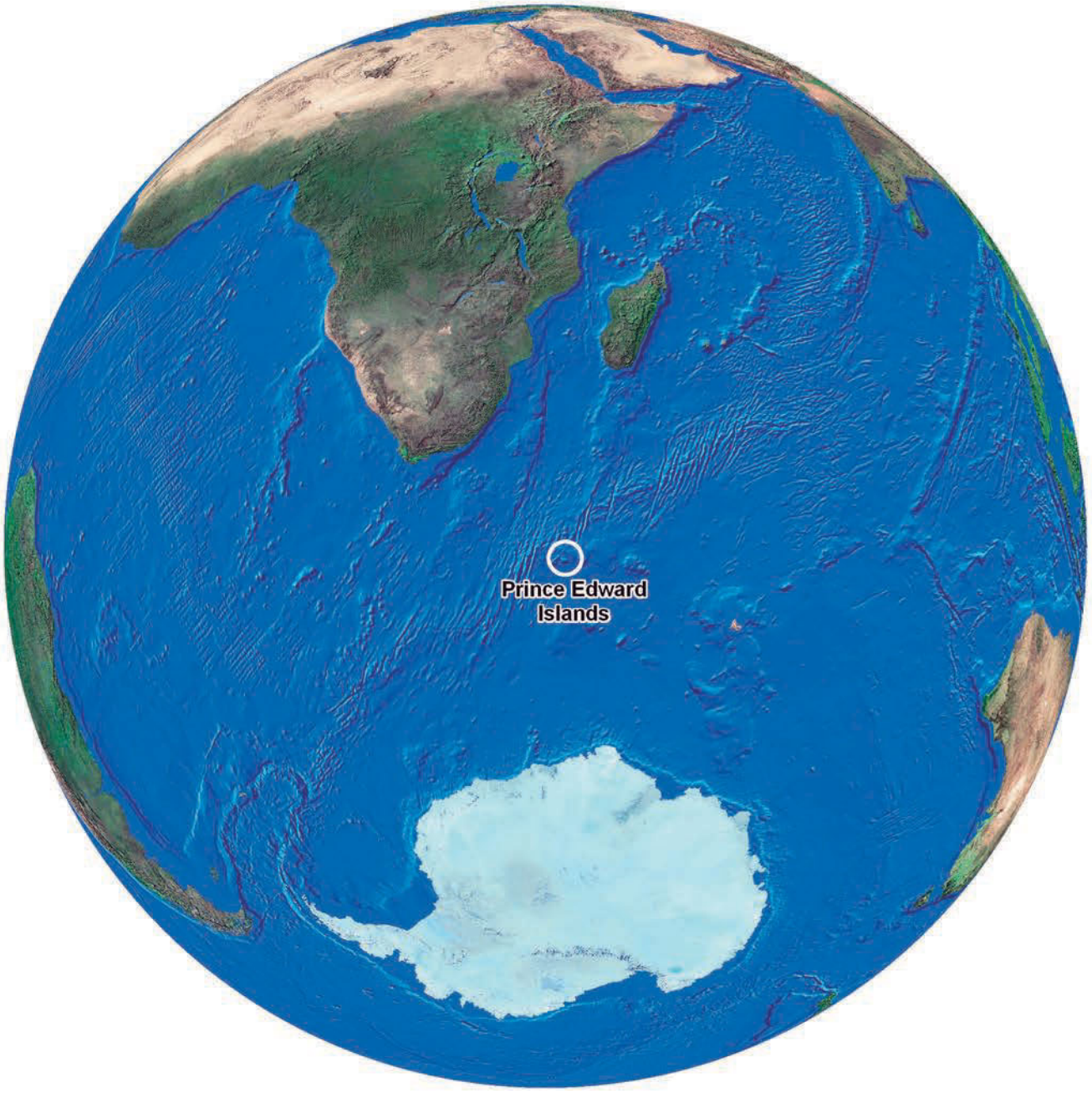


Figure 15.3 Position of the Prince Edward Islands in Southern Ocean, between Antarctica and Africa (courtesy of I. Meiklejohn).

arctic to the south). In Wace's scheme the following terrestrial plant communities were considered to characterise the subantarctic vegetation zone:

- Closed herbfield communities in which large-leaved perennial herbs are conspicuous.
- Communities of pedestal-forming tussock grasses, especially on the coast.
- Soligenous mires in which the peat-forming plants are bryophytes and sedges (not sphagna or cushion-forming vascular plants).
- Fellfield or wind-desert communities composed of flowering plants with very compact mat or cushion growth forms.

Although Wace (1965) considered this classification to be independent of climatic, geological or other environmental data, the delimitation boundaries correspond closely to those of the climatological classification of Holdgate (1964) based on the range of mean monthly temperatures. In that classification the subantarctic zone is characterised by the absence of temperatures warmer than 8.5°C, considered to preclude the occurrence of trees (Pearsall 1950, Holdgate 1964).

Holdgate (1970, 1977) proposed a more definitive classification of the southern subpolar zone that, with some modification, has been widely accepted (Block 1984, Pickard & Seppelt 1984, Clark & Dingwall 1985, Bonner & Lewis Smith 1985, Smith & Lewis Smith 1987). The geographic, climatic and biotic characteristics of the various subdivisions (regions and provinces) of the zone are outlined by Lewis Smith (1984). The subantarctic region comprises six islands or island groups (South Georgia, Macquarie, Heard and McDonald, Kerguélen, the Crozets, Marion and Prince Edward), all situated within a few degrees latitude of the Antarctic Convergence. Because of the cold Bouvet Current that originates in the Weddell Sea, the Convergence extends farther north in the Indian Ocean so that relatively low-latitude islands such as Marion, Prince Edward and Îles Crozet are included as subantarctic, even though they are farther north than the islands of the New Zealand continental shelf (Campbell, Antipodes, Auckland, Snares). These latter, because they possess a well-developed shrub and/or low tree vegetation, are considered to belong to the cool temperate zone, together with the Tristan da Cunha-Gough Island group, Île Amsterdam, Île Saint-Paul, Falkland Islands and southern Tierra de Fuego. At the other extreme, Bouvetoya and the South Sandwich Islands are sometimes included in the subantarctic region (Walton 1985), although they are more typically maritime antarctic, like the South Orkney Islands and South Shetland Islands (Lewis Smith 1984). Alternative classifications of mid- to high-latitude regions of the southern hemisphere are discussed by Smith & Lewis Smith (1987).

Tundra is usually defined as areas where the average annual temperature is below 0°C and permafrost occurs. It has also been used when referring to areas where the temperature is too low, and precipitation and wind too great, for a natural forest vegetation to develop. For example, oceanic moorland, some mountainous regions and two subantarctic islands, all of which have somewhat higher annual mean temperatures than tundra *sensu stricto*, were included in the Tundra Biome Study of the International Biological Programme (Rosswall & Heal 1975, Bliss et al. 1981). In fact, subantarctic vegetation has traditionally been decribed as tundra. Very few taxonomic affinities exist between the biotas of subantarctic islands and the Arctic or Subarctic, but there are several physiognomic similarities in their vegetations. In order to highlight the unique nature of subantarctic ecosystems, it is useful to compare terrestrial areas of the Subantarctic briefly with those of the Antarctic and also with those of the Subarctic.

Owing to the overwhelming influence of the ocean, the subantarctic region exhibits a very limited annual temperature range, so that winters are warmer and summers cooler than continental subpolar sites of the northern hemisphere (e.g. see Figure 2 in French & Smith 1985). Thus, while the subarctic environment may be considered to be a less severe version of that of the Arctic, the difference between subantarctic and antarctic conditions was described by Rudmose-Brown (1928) as follows:

'The term subantarctic is justified rather by proximity to the Antarctic than by any real approximation to Antarctic conditions. The truly Antarctic climate is typically continental, in contrast to the climate of the subantarctic islands, which is essentially oceanic, and in most respects cool-temperate, rather than polar.'

This important difference between subantarctic and subarctic regions is due to the unequal proportion of land and sea in the two zones (Di Castri et al. 1970). While large continental masses of North America, Asia and Europe belong to the subarctic region, subantarctic terrestrial areas are very discontinuous. This has a series of climatic, biogeographical and ecological consequences, some of which have been demonstrated by French (1974, 1981) and French & Smith (1985) in multivariate comparisons of subantarctic and maritime antarctic terrestrial ecosystems with northern hemisphere tundra and tundra-like ecosystems (ranging from high arctic to cool-temperate and temperate alpine). The comparisons, based on climate, soil chemical composition and vegetation, emphasise the effects of the extreme oceanity and the influence of sea spray and animal manuring on the ecosystems of the southern hemisphere subpolar sites. They clearly show that subarctic ecosystems are generally less severe forms of arctic ones, and decreasing latitude leads to increasingly milder environments with no great changes overall in continentality. In contrast, the Subantarctic combines elements from the extremes of the range of northern hemisphere tundra (i.e. high-arctic and cool-temperate oceanic) with its own peculiar features, e.g. geographical isolation, wind exposure, high rainfall, small seasonal temperature range and the strong influence of the marine ecosystem (especially of seals, seabirds and salt spray) to produce ecosystems that are qualitatively different from both subarctic systems and the continental antarctic regions to which they are geographically closest.

The isolation of terrestrial subantarctic ecosystems and, in most cases, their relatively recent origin causes their floras to be species-poor, in contrast to most subarctic and low arctic areas of the northern hemisphere. Despite this, the multivariate analyses done by French & Smith (1985) show that the southern hemisphere sites exhibit almost the full range of vegetation types found in the northern hemisphere. Cluster analyses of climates and soils link the Southern Ocean islands with northern hemisphere sites at higher latitudes, indicating the effect of the Antarctic continent on the climate of the southern islands. Climatic wetness, together with strong winds, applies a significant chill factor so that the vegetation of the southern islands resembles that of much higher latitudes in the northern hemisphere. The latitudinal difference between northern and southern sites with equivalent vegetation types is as much as 20 or even 30 degrees. The range of soil nutrient levels at the southern hemisphere subpolar sites is approximately equal to that at the northern hemisphere subpolar sites; however, in the southern sites soil nutrient levels are inversely related to climatic severity, while in the north the reverse is true. The two most

important causes of these opposed trends are the relative geological and pedological ages of the sites (younger sites tend to be at higher latitudes in the north but at lower latitudes in the south) and the much greater effects of sea-based vertebrates on the southern islands.

Subantarctic islands are geologically comparatively young compared with land masses of the northern hemisphere subpolar region. The islands are also extremely remote, mostly more than 1 500 km from the nearest continent. Their indigenous biota has been established by the slow process of immigration and colonisation over large expanses of ocean, so that the floras and faunas of the islands exhibit low diversity. For instance, Lewis Smith (1984) listed 72 vascular plant species indigenous to the Subantarctic, whereas the Canadian Arctic Archipelago, a climatically far more extreme region and ca. 25° of latitude nearer the Pole than the Subantarctic, has more than 340 indigenous vascular plant species (Porsild 1964). Several vascular plant species are endemic to the Subantarctic, but occur on more than one island or island group (Walton 1985). Only four species are endemic to one island or island group (Lewis Smith 1984). The low degree of endemism in the vascular floras of the subantarctic islands, compared with those of the older cool-temperate islands to the north—for instance 31% of the 200 vascular species on the New Zealand shelf islands are endemic (Devine 1984)—probably results from the relatively short time available for the evolution of new species since the last glaciations. However, despite their floristic poverty, subantarctic islands exhibit almost the full range of vegetation types found in tundra (*sensu* I.B.P.) of the northern hemisphere (French & Smith 1985). Perhaps the most notable exception is that lichen-dominated communities similar to those found in tundra of the northern hemisphere do not occur.

3. Geography of Marion and Prince Edward Islands

3.1 Climate

The Prince Edward Islands are amongst the warmest of the subantarctic islands; only the Crozet Archipelago is as warm. Mean monthly and mean annual temperature, precipitation and sunshine at Marion Island are shown in Table 1. Other climatic data are depicted in Figure 15.4. The surrounding Southern Ocean causes the islands' climate to be thermally stable. The difference between mean temperature of the coldest and warmest months is only 4.1°C and the mean diurnal temperature variation is only 1.9°C. Precipitation is high, more or less equally distributed throughout the year and, although snow and ice rain do occur, is mostly in the form of rain at the coast. The high precipitation is associated with a high incidence of cloudiness and infrequent direct sunshine.

Despite the thermal stability of the islands, annual mean temperature has increased steadily in the past three decades and six of the last seven years (1996 to 2002) were the warmest on record. Since 1969 air temperature has increased, on average, by 0.04°C per year (Smith 2002) and warming has occurred in all months except June. The highest rate of warming has been from late austral winter to midsummer (September to January), and the lowest in late summer, autumn and winter (February to August), with the notable exception of April which showed the greatest warming of all the months. Recently, Mélice et al. (2003) showed that annual mean sea temperature around Marion Island has risen, on average, by 0.04°C per year since the 1970s, the same as the mean increase in air temperature. Similar air temperature increases have been reported for three other subantarctic islands (for Macquarie Island by Adamson et al. 1988, Kerguélen Island by Frenot et al. 1997 and Heard Island by Budd 2000).

Annual precipitation has decreased since the mid-1960s, so that the 1990s was the driest of the five decades that precipitation has been measured on the island. All months except October have become drier. Interannual variability in annual total sunshine hours is irregular, but a significant proportion of it can be ascribed to an average increase of 3.3 hours per year between 1951 and 2002. Hours of sunshine increased for all months in that period.

The radiation, air and sea temperature increases, and the precipitation decrease, on Marion Island might be associated with changing atmospheric circulation patterns (perhaps also changing oceanic circulation). Smith & Steenkamp (1990) pro-

Table 15.1 Average monthly and annual air temperature, precipitation and sunshine for Marion Island. Values are derived from data supplied by the South African Weather Bureau and were obtained from measurements made between 1949 and 2002 at the Meteorological Station which is about 25 metres above sea level.

	Temperature (°C)			Precipitation (mm)			Sunshine (hours day^{-1})		
	Ave. mean	Min. mean	Max. mean	Ave. total	Min. total	Max. total	Ave. mean	Min. mean	Max. mean
Jan	7.3	5.8	9.1	209	90	350	5.1	3.4	6.4
Feb	7.8	6.2	9.3	188	73	333	4.8	3.8	6.3
Mar	7.5	6.5	8.9	199	52	397	3.8	2.8	5.6
Apr	6.4	4.5	8.2	210	125	363	3.1	1.7	4.3
May	5.3	3.7	7.1	222	100	428	2.5	1.4	3.3
Jun	4.6	2.8	6.0	203	91	461	1.9	0.9	2.8
Jul	4.1	2.6	5.9	196	98	319	2.1	1.3	2.9
Aug	3.7	2.1	4.7	180	98	250	2.8	1.5	4.3
Sep	3.8	2.3	5.3	183	101	360	3.4	2.4	4.6
Oct	4.6	3.4	6.2	171	75	288	4.5	2.8	7.2
Nov	5.5	4.1	7.7	172	48	316	5.3	3.2	6.9
Dec	6.4	4.7	8.2	200	73	302	5.2	3.8	6.7
Year	5.6	4.8	6.6	2327	1861	2992	3.7	3.2	4.1

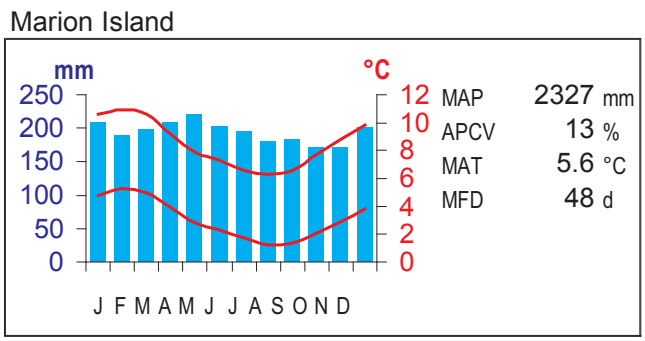


Figure 15.4 Climate diagram of the weather station Marion. The graph shows mean monthly precipitation (blue bars), and mean of daily minimum and maximum temperatures for each month (red lines). MAP: Mean Annual Precipitation. APCV: Annual Precipitation Coefficient of Variation. MAT: Mean Annual Temperature. MFD: Mean Frost Days per year.

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Figure 15.5 Landscapes of Marion Island: A view from the Meteorological Station across straw-coloured mires (dry *Agrostis magellanica*), dark green belt of fernbrakes towards the snow-clad slopes of the central mountains carrying Polar Desert on the summits.

posed a model whereby interannual differences in radiation, temperature and precipitation can be explained by the positions of cyclone tracks relative to the island. Approximately 100 cyclones pass the island in a year. In warmer years the cyclonic centres pass, on average, further to the south of the island so that it spends a longer period subjected to the rain-bearing northwesterly winds of the warmer sector of the cyclones, and less time to the icy southwesterly winds of the post-cold front sector. Validation of this model awaits a detailed analysis of sea level atmospheric pressure records for the South Indian Ocean sector of the Southern Ocean. Such an analysis for the Pacific region of the Southern Ocean showed that the direction of atmospheric pressure gradients governs whether warm north-easterly or cold southerly air flows over Macquarie Island and hence determines air temperature there (Adamson et al. 1988).

3.2 Topography

Marion Island is 290 km^2 in area and the highest peak is 1 230 m above sea level. Prince Edward is 45 km^2 in area and the highest peak is 672 m above sea level. Marion Island consists of a central highland area sloping down to a coastal plain which on the northern and eastern sides forms a 4 to 5 km wide area rising gently from sea level to the foot of the mountainous interior at about 300 m altitude (Figure 15.5). The western and southern coastal areas consist of a narrow discontinuous plain of less than 100 m altitude, having been eroded by wave action caused by the strong westerly winds. Much of the low-altitude area supports closed vegetation. The southeastern part of the Prince Edward Island slopes up gently from the coast to the top of a central plateau, a distance of about 7 km. The plateau is separated from the northwestern coastal lowlands by a precipitous escarpment.

3.3 Geology

The islands are located near the centre of the West Indian Ocean Ridge and are the surface expressions of a mantle plume marking the present position of a long-lived hotspot. They were considered to be extinct volcanoes but in September 1980 there was a small eruption on the west coast that resulted in a lava flow covering about 9 ha (Verwoerd et al. 1981) and some soil profiles contain buried A-horizons under volcanic ash deposits near the surface, attesting to sporadic volcanic activity in the recent past.

The lavas are typical oceanic island basalts. McDougall et al. (2001) recognised eight periods of volcanic activity, from 450 ka up to the Holocene one that started about 10 ka and extends up to the present. Two 'types' of lava flow can clearly be distinguished in the field (Verwoerd 1971, McDougall et al. 2001; Figure 15.6):

(1) Older grey lavas that have been glaciated (smooth striated outcrops, roches moutonées, moraines) and can be regarded as Pleistocene. They build much of the higher ground, as a radially arranged series of horsts, or wide ridges that are separated by depressions, or grabens, filled by younger flows. Glaciations have stripped the surface of the older lavas of all volcanic surface features. This horst and graben topography of alternating high and low segments has been ascribed to radial faulting (Verwoerd 1971). Although evidence of radial fracturing does exist, slope failure and land-sliding under the influence of gravity probably played a more important role in shaping the larger valleys (Chevallier 1986, McDougall et al. 2001).

(2) Younger black lavas that are all of Holocene age, because none of them show any glacial erosion effects and some

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Figure 15.6 Marion Island (below First Red Hill cinder cone): Three different geologies represented by young black lava (on the left), old grey lava (on the right) and cinder-cone scoria (in the foreground) converging and accommodating a small lava lake (tarn). The cushions on the scoria are *Azorella selago*.

encroach upon moraines. They comprise aa and (less commonly) pahoehoe flows and are associated with cinder cones (approximately 130 on Marion Island and 14 on Prince Edward). In addition, phreatomagmatic activity along coastal plains resulted in surtseyan tuff cones and hyaloclastite deposits (Verwoerd & Chevallier 1987).

3.4 Soils

Low temperatures and waterlogging result in low rates of chemical decomposition and clay mineral synthesis, but are optimal for accumulation of organic matter. The soils thus do not have well-differentiated profiles and those under vegetation at lower altitudes are highly organic. On the younger black lava flows the peat is shallow, generally less than 1 m deep but profiles up to 2 m have been found. On the older grey lava flows the peat can be deeper, 3 m being the deepest found (Schalke & Van Zinderen Bakker 1971).

Azorella selago cushions are the cardinal agent of soil formation on the island; decomposition of old leaves in the cushion interior results in an organic matrix mixed with volcanic ash. The cushions tend to grow toward the wind, the leeward margin dying off and exposing the organic/ash substrate which is then colonised by other plants (in fact, several vascular and bryophyte species establish directly on the cushions, rooting themselves in the decomposing matrix of the cushion interior). On flat areas the build-up of the organic matrix leads to impeded drainage and a higher water table, encouraging bryophytes which become the main agent of peat formation so that mire or bog vegetation develops. Typically, the water table in mire vegetation is near or at the surface and the peat is light brown and amorphous throughout the whole depth. Where drainage is better and the water table fluctuates, there is some horizon differentiation (Figure 15.7a); generally a light brown surface horizon up to 20 cm deep overlies a yellow-orange to light brown layer that extends to bedrock and which Smith (1978a) termed 'organic clay'. Indurated iron pans and/or organic pans sometimes occur in this clay layer, in which case gleying takes place and the clay is a yellow-grey colour beneath the induration.

Soils under slope plant communities possess better-developed profiles, especially where they are deep and where there is free drainage. Shallower soils (10–30 cm deep) consist of an organic horizon directly overlying mineral material which is generally scoria (volcanic ash). Deeper slope soils, especially those under fernbrake (Figure 15.7b), consist of a dark coloured A-horizon containing much litter and up to 30 cm deep. Below this a well-developed B-horizon of a 'yellow-brown loamy clay' (Smith 1976a) occurs, usually stained in the upper regions by the organic A-horizon. Red indurated plinthic layers sometimes occur in this B-horizon. In poorly drained soils on less steep slopes a gleyed horizon occurs beneath the plinthic layer and extends to bedrock.

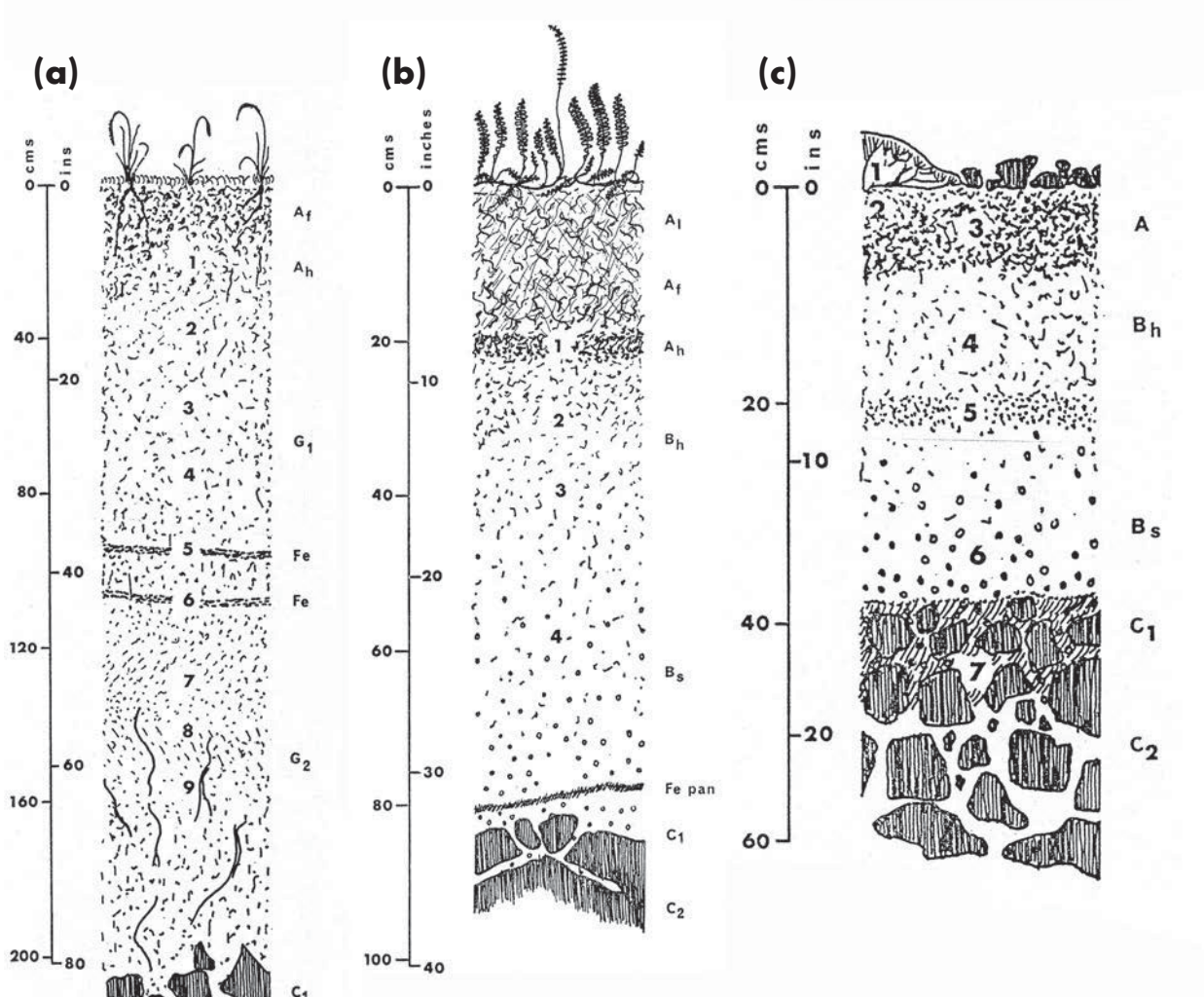

Figure 15.7 Profiles of soil under (a) mire, (b) fernbrake slope and (c) fellfield vegetations. Subhorizons are indicated thus: l = litter, f = fermentation, h = humus-enriched, s = sesquioxide-enriched, Fe pan = iron pan, G = gley horizon (from Huntley 1971; courtesy of A.A. Balkema, Cape Town).

Fellfield soils (Figure 15.7c) consist of skeletal, shallow gravelly 'loams' (Smith 1976a, 1978a). An A-horizon occurs beneath *Azorella* cushions but, where no plants are growing, the soil surface is either bare or covered by a layer of small pebble-sized scoria. Beneath the surface is a brown gravelly loam that becomes orange-brown with depth and contains much scoria. Bedrock is mostly within 10–15 cm of the surface, but some fellfield soils are deeper.

The polar deserts of the islands do not have soils, merely coarse scoria where any trapped moisture undergoes frequent freeze-thaw cycles. Vegetation (mosses, also with *Azorella selago* at lower altitudes) occurs mainly where seepage allows some moisture accumulation or where rock surfaces are exposed to moisture-laden winds.

True ornithogenic soils (soils essentially devoid of organic matter other than guano which overlies, but does not mix with, weathered rock) as described from Antarctica (Syroechkovsky 1959, Ugolini 1972) do not occur on the islands. Even in penguin rookeries the high rainfall prevents the build-up of guano deposits. However, many soils in the coastal zone are heavily influenced by birds and their profiles often contain evidence that birds were present at the site during their development (squid beaks, feathers; Smith 1977a). Following Tatur (1989), these may also be considered as ornithogenic soils. Rates of peat accumulation, especially around penguin rookeries, are strongly stimulated (Lindeboom 1979) and the soils are much darker (dark brown to black, compared with the light brown peat in areas not influenced by birds; Smith 1978b).

Since the soils of the islands developed from weathering of volcanic ash under cool humid conditions, they are suspected of containing allophanes as the dominant clay mineral, and the horizons of lowland soil profiles have been described as clays, organic clays or loamy clays (Huntley 1971, Smith 1976a, 1978a). However, the few mineralogical analyses carried out so far have not revealed crystalline or amorphous clay minerals (Gribnitz et al. 1986). There is a large concentration of glass fragments in the volcanic ash component of the soils. In many cases hydrolysis of the glass has lead to a yellow, brown or orange palagonite (the precursor of allophane) and Gribnitz et al. (1986) consider that what have been described as clays, organic clays or loamy clays are actually palagonitised fine-grained volcanic ashes, the cold climate and young age of the soils having precluded the formation of clay minerals. According to Gribnitz et al. (1986) the soils of the islands are formed from Holocene ash falls as follows:

- Accumulation of vegetable matter and raw humus on the surface of ash by colonising plants.
- Percolating humic acids stain the immediately underlying ash and mobilise some iron by attacking the palagonitised glass fragments.
- Precipitation of the iron at lower levels as hydroxides, the depth at which this occurs depending on the depth to the water table.

Three features make it difficult to classify the island soils using international systems: their immaturity, the negligible influence of parent material on the profiles, and the marked effect of slight variations in topography and wind exposure on these profiles. Taylor (1955) and Huntley (1971) classified Macquarie and Marion Island soils, respectively, according to the most important factors influencing their development. They regard soils under slope plant communities as high-moor peat and those of mire and bog areas as low-moor peat or fen and bog peat. The red-brown loamy soils of slopes on Marion Island resemble those of well-drained slopes and level ground beneath dry grassland on South Georgia, which have been termed brown soils by Lewis Smith & Walton (1975) since they approximate arctic brown soils.

Conditions such as waterlogging, low temperatures and high acidity lead to substantial amounts of organic acids in the soils. This, with the intensive leaching effect of the high rainfall, will favour podsolisation (Jenny 1941, Kononova 1966) and following most climatic systems of soil classification, the island soils should be predominantly podsolised. However, bleached eluvial horizons are not found in any lowland soil profiles, although Huntley (1971) and Smith (1976a) presented chemical data indicating the presence of an eluviated horizon below, and stained by, the A-horizon in some slope soils. Frequent or permanent waterlogging at or below the soil surface favours gleying and many of the lowland soils are gley (all horizons gleyed or semi-gley) or gleyed (only the lower horizons are so affected). In this respect they are similar to moorland soils of the southwestern Chilean islands which were classified by Papadakis (1969) as gley podsols (eluvial horizons masked by high organic matter content), humic gley soils and peaty soils. Tentatively, slope complex soils on Marion Island may be regarded as gley podsols and those of the mire complex as humic gley soils or, where the organic horizon lies directly on rock, as peat.

Soils under fellfield vegetation on Marion Island are approximately similar to fellfield soils of the northern hemisphere. Noting this similarity, Huntley (1971) referred to the island fellfield soils as rawmark. Taylor (1955) used the terms tundra soils and dry tundra soils when referring to fellfield soils on Macquarie Island. However, although subantarctic fellfield is the vegetation type that most closely resembles tundra vegetation, the well-drained soils under subantarctic island fellfield are actually very different from fellfield soils of northern hemisphere tundra, which are mostly poorly drained, strongly gleyed, mineral soils that overly permafrost.

3.5 Palaeohistory

All studies of geochronology to date have been carried out on Marion Island. Little is known of Prince Edward Island. The oldest K-Ar dates available for the lavas indicate an age of 450 000 ±10 000 years (McDougall et al. 2001). Since the island is only 2° of latitude north of the Antarctic Convergence, past falls in world temperature would have had the effect of shifting the Convergence closer to, and even northwards of, the island (Van Zinderen Bakker 1971). The glaciated surfaces of the old grey lavas and intercalated sediments with glacial characteristics testify to earlier glaciations. Hall (1978, 1981) described three distinct tills of different ages and concluded that during the last 300 000 years the island was subjected to three glacial episodes, each comprising a series of stades and interstades. At many localities the tills are separated by thick sequences of intercalated basaltic lavas and pyroclasts, suggested to have erupted during the interglacials as isostatic response to the removal of the weight of the ice (Hall 1981, 1982). However, although the two most recent periods of effusivity are clearly interglacial, some of the earlier ones seem to have coincided with glacial stages (McDougall et al. 2001).

A temperature drop of at least 3.5°C during the glaciations is indicated from the periglacial evidence (Hall 1978); this supports previous conclusions derived from palynological (Van Zinderen Bakker 1973) and ocean-floor sediment studies (Hays et al. 1976). During the interglacials the temperatures were as high as they are at present (Van Zinderen Bakker 1971). At some localities palaeosols are thought to have formed in the interglacial deposits (Hall 1978). Scott & Hall (1983) found that

organic-rich basal sediments associated with the interglacial deposits contain pollen spectra indicating a vegetation assemblage similar to that found today. Zonation in the pollen profile suggests that during the interglacial phase the ocean shore was close to its present position and that it moved some distance away at the onset of the glacial stage.

Other workers (Kent & Gribnitz 1983, Gribnitz et al. 1986) consider that Hall's palaeosols and tills are tuffs and tuff breccias, i.e. both are volcanogenic rather than glacigenic. They contend that the interpreted stratigraphic successions and the palaeoclimatological deductions of Hall (1978, 1981) are not substantiated. However, morainic deposits occur at many sites on Marion Island and it is not doubted that the island was glaciated in the Quaternary. The ice cover of the last glacial began to disappear rapidly about 12 000 years ago (Van Zinderen Bakker 1973) and the youngest lavas that have been dated (15 000 ±8 000 years BP; McDougall 1971) may have erupted in response to this disappearance. Radiocarbon dating of some mire peats on the island indicates minimum ages of 3 180 ±120 to 4 020 ±65 years BP (Schalke & Van Zinderen Bakker 1971). However, it is certain that many of the lava flows and overlying peat deposits are much younger (Scott 1985, Gribnitz et al. 1986).

4. Flora and Major Vegetation Patterns

The vascular flora of Marion Island consists of 22 native species, 18 introduced species and three species` of unknown status (N.J.M. Gremmen, pers. comm.). Of the alien plant taxa, 12 are still present on the island, but the other six have disappeared. Prince Edward has 21 native and three alien vascular species. A large proportion of the indigenous species has a wide ecological amplitude, and occurs over much of the range of habitats on the islands. There is a much higher diversity of cryptogams; for both islands ca. 100 moss, 42 liverwort and 100 lichen species have been recorded. Mosses and liverworts dominate many of the plant communities. Comprehensive descriptions of the island plant communities have been provided by Huntley (1971) and Gremmen (1981).

Because of the lack of trees and tall shrubs, the island presents a bleak or barren appearance when viewed from offshore. Closer inspection, however, reveals that the vegetation is not so sparse, or even as uniform, as it appears. Huntley (1971) recognised 13 plant communities (he termed them 'noda') based on floristic composition and autecological characteristics of the species. These were grouped into five complexes according to the most important factor controlling their distribution, such as salt spray, manuring, trampling, exposure and drainage. Gremmen's seminal work resulted in a phytosociological classification of the islands' vegetation that includes 41 plant communities. Environmental information (soil depth, moisture content, pH, loss-on-ignition, depth of groundwater, severity of manuring and trampling by animals and of salt spray) was related to floristic composition of the plant communities in order to group them into six community complexes. Subsequently, Smith & Steenkamp (2001) added one more complex.

The complexes are:

- The salt-spray (*Crassula moschata*) complex, restricted to shore-zone areas strongly affected by wind-blown sea spray. On the west coast the belt of salt-spray vegetation extends up to 300 m inland but on the east coast it is restricted to a narrower zone along the tops of coastal cliffs.
- The biotic (*Callitriche antarctica–Poa cookii*) complex, influenced by trampling and manuring by animals. This complex consists of a wide variety of communities, most of which occur on the coastal zone near colonies of seals and penguins. Inland, the influence of surface-nesters and burrowing species is also manifested by the presence of communities belonging to this complex.
- The *Blechnum penna-marina* complex (fernbrake communities) that dominates the vegetation of well-drained lowland slopes.
- The *Acaena magellanica–Brachythecium* complex, which forms at mire and lowland slope sites where there is pronounced lateral subsurface water movement. Communities of springs, flushes and drainage lines belong to this complex.
- The *Juncus scheuchzerioides–Blepharidophyllum densifolium* mire complex, dominated by bryophytes and graminoids and occurring on wet peat.
- The fellfield (*Andreaea–Racomitrium crispulum*) complex which forms in rocky habitats strongly exposed to wind. This complex, consisting of communities of the cushion-forming *Azorella selago*, bryophytes and lichens, dominates the vegetation above 300 m altitude. Fellfield communities also occur at lower altitudes where they exhibit fairly high (up to 60%) aerial vegetation covers.
- Polar desert. An important vegetation type (it covers about 120 km^2 of the 290 km^2 total area of Marion Island, but a much smaller proportion on Prince Edward Island) that was not included in the phytosociological study of Gremmen (1981) and for which there is no published ecological information. It was recognised as a cardinal habitat type on Marion Island by Smith & Steenkamp (2001; see also Smith et al. 2001) who placed it in a polar desert complex. It is the only vegetation type above 550 m altitude on the islands.

Soil moisture and exposure to wind are the most important factors determining variation between plant communities. The wet-sheltered dry, exposed gradient is also associated with a change from organic peat at sheltered sites to mineral soils at exposed sites. The type of plant community which develops at any particular point on the wet-dry gradient is mainly determined by manuring and trampling by seabirds and seals and/or by wind-blown salt spray.

Huntley's (1971) ecological classification and Gremmen's (1981) phytosociological classification implicitly define the terrestrial habitat types that occur on the island according to the main patterns of abiotic and biotic variation in the ecosystem, since both consider the role of the main environmental and biological forcing variables (moisture, exposure, parent soil material, salt spray and manuring and trampling by seals and seabirds) on the island. Canonical correspondence analysis and cluster analysis of soil chemistry and botanical variables for 176 sites on the island recognised 23 habitats in seven habitat complexes in a 'habitat classification' (Smith & Steenkamp 2001) that supports all of Huntley's and Gremmen's conclusions and that closely reflects the between-habitat variation in the relative magnitudes of the main abiotic and biotic forcing variables.

The habitat classification gives a broader grouping (21 habitats) than the phytosociological one (41 communities, plus variants of some communities). However, because it was based on plant types and soil chemistry considerations, rather than just plant species, the habitat groupings can be considered as nodal assemblages of plant communities having vegetation and edaphic affinities. They can thus be considered analogous to the six community complexes of the phytosociological classification since those complexes were recognised on the basis of

ecological and edaphic factors as well as floristic considerations. In this respect, the habitat classification gives a more detailed grouping of sites than the phytosociological scheme. It is also more detailed than Huntley's five nodal ecological complexes. Biotically influenced sites, in particular, are floristically (and edaphically) the most diverse on the island and these are distinguished as seven habitats in three separate complexes, rather than in one complex as in previous schemes. In contrast, the various types of drainage lines (also a floristically and edaphically diverse group) on the island are less finely categorised within the habitat framework than they are by the phytosociological classification. In some respects, the habitat analysis yields a similar dispensation of the drainage lines as does the ecological complex scheme of Huntley (1971) where they are included as two noda, together with mires and bogs, as part of the swamp complex. The main reason for establishing the habitat classification was to provide a framework of structurally and functionally well-defined units against which to detect and evaluate the effects of climate change and human-induced perturbations. Smith et al. (2001) describe the altitudinal distributions of the habitats and provide a scenario of how climate change is expected to affect them.

5. Vegetation Dynamics

5.1 Vegetation Succession

The very small number and wide ecological amplitude of the vascular plant species prevent the development of well-defined, floristically distinctive seral communities. However, a simplistic scheme of vegetation succession is as follows:

Rocky plateaus are colonised by lichens and cushion-forming mosses and dicotyledons (mainly *Azorella selago*). These initiate peat formation and also act as traps for fine, wind-blown volcanic ash. The peaty material fills the crevices and porous structure of the lava and impedes drainage. If the rate of water acquisition by the area is greater than the rate of drainage, bryophyte-dominated bogs develop. Peat accumulation raises the bog surface above the water table and mire-grassland vegetation dominated by graminoids and bryophytes results. Further peat accumulation may make the surface even drier and fernbrake vegetation then develops. However, closed fernbrake on flat, level areas is rare. Dry mire communities dominated by *Blechnum penna-marina, Racomitrium lanuginosum* and *Uncinia compacta* generally represent the culmination of the wet-dry succession on level surfaces.

Where drainage from the fellfield area is unimpeded, the cushion plants develop a stable peat for fernbrake elements to develop. At first these elements may arise epiphytically on, or in the shelter of, the cushions, but eventually extend across the peat to form an open type of fernbrake that is often succeeded by a closed carpet of *Blechnum penna-marina*. This sequence from fellfield to fernbrake occurs predominantly on slopes. On flat plateaus, impeded drainage (caused by peat blocking the drainage channels) diverts the fellfield-fernbrake succession to the one toward mire or bog vegetation.

The pathway of primary succession on cinder cones follows a simple scenario; the lower slopes are less exposed to wind, more stable and climatically less extreme than the upper reaches of the cones and this allows the establishment of *Azorella selago*. Several vascular and cryptogam species grow as epiphytes on the cushions and organic matter built up under the cushions consolidates the scoria. This pattern of colonisation and succession proceeds up the slope (Figure 15.8), and the recent warming of the island is suspected to be increasing the rate at which this is occurring.

At coastal rocky sites subjected to salt spray, the fellfield is dominated by *Azorella selago* and *Crassula moschata*. Peat accumulation in these areas results in a well-developed salt-spray vegetation dominated by *C. moschata* and *Cotula plumosa*. Impeded drainage results in a bog salt-spray community in which *C. moschata* and a few liverwort species occur.

Strong lateral flow of water may modify the vegetation at any level of succession, leading to a group of plant communities characterised, on slopes and stream banks, by the abundance of *Acaena magellanica* in the herb layer and *Brachythecium subplicatum* or *B. rutabulum* in the bryophyte stratum. These communities are associated with drainage lines, water tracks, flushes and springs in slope areas. Drainage lines in mires are characterised by a dominance of *Breutelia integrifolia* and *Bryum laevigatum*.

Animal activities may have a marked influence at any stage of succession. Other than Salvin's Prions (*Pachyptila salvini*), animals seldom establish nests or otherwise exploit fellfield areas, preferring mires and well-vegetated slopes. In the salt-spray zone, sites influenced by animals support luxuriant *Cotula plumosa–Poa cookii* vegetation that is especially characteristic of areas surrounding seal and penguin colonies (Figure 15.9). At mire and bog sites the influence of animals causes the development of wet biotic communities in which coprophilous, trampling-resistant species become established (mainly *Callitriche*

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Figure 15.8 Progressing primary vegetation succession in upslope trend on the northern slopes of Junior's Kop. The green patches on the slope are cushions of *Azorella selago,* with white patches of dry culms of *Agrostis magellanica*.

antarctica and *Montia fontana*). Where fernbrake communities are colonised by burrowing birds, closed tussock grassland dominated by *Poa cookii* develops (Smith 1976b). However, the occurrence and extent of tussock grassland (especially the inland type, the *Leptodontio proliferi–Poetum cookii brachythecietosum rutabuli* of Gremmen 1981) has declined markedly since the early 1970s. For example, tussock grassland occupied 7.8 ha of a 1 040 hectare inland study site on the island's eastern coastal plain in 1971–1972 (Smith 1976a, 1977b). This shrank to 0.9 ha by 1991 (Smith et al. 2001). This observation was made on only ca. 8% of the lowland area supporting closed vegetation but the same trend has been observed over the whole island since 1975 (N.J.M. Gremmen, unpubl. observations of permanent quadrates). Mostly, the inland tussock grasslands have been replaced by closed fernbrake or dwarf-shrub fernbrake. The reason for the shrinkage of tussock grasslands is almost certainly related to the influence of feral domestic cats (*Felis catus*) on burrowing petrel and prion populations at the island during the same period. Cats were introduced to the island in 1949 and their population grew rapidly, by 23% per year; by the mid 1970s it was estimated at ca. 2 100 adults (Van Aarde 1979). Undoubtedly, the cats had a devastating effect on the petrel species of the islands; in the mid-1970s they were eating a minimum of 635 000 petrels and prions each year (Van Aarde 1980). Where petrels and prions burrow into slopes, their guano enriches the soils (Smith 1976b) and this results in a succession to tussock grassland. When the birds disappear, the tussock grassland reverts surprisingly quickly to one of the non-biotically influenced slope communities. In the case of the tussock grassland studied by Smith (1976b), there were 1.2 burrow entrances per square metre in 1972; by 1987 there were no burrows and the area was occupied by closed fernbrake (in the wetter areas by dwarf-shrub fernbrake). With the elimination of cats (the last was killed in 1991; Bester et al. 2000) there are indications that the petrel and prion populations are recovering (Cooper et al. 1995) and it remains to be seen whether this will reverse the shrinkage of the tussock grasslands. Tussock grassland is very common and widespread on Prince Edward Island, where cats were never present.

Another biotic factor that is increasingly affecting the vegetation of the islands, particularly the coastal zone, is the rising population of fur seals. Trampling by these animals has degraded extensive areas of tussock grassland. A similar situation occurred on Bird Island, South Georgia, where fur seals destroyed most of the tussock grassland (Bonner 1985).

5.2. Primary Production, Decomposition and Nutrient Cycling

The subantarctic climate is oceanic and in many respects cool-temperate rather than polar. Hence, the islands do not experience bitterly cold or dry periods and the vegetation growing season is long. Additionally, the plants are all C_3 photosynthetic types that are able to maintain fairly high rates of photosynthesis and growth under the consistently low temperatures. Annual primary production is consequently high, comparable to even the most productive temperate herbaceous plant communities (Smith, 1987a, b). The high annual production results in a substantial annual requirement for nutrients by the vegetation (Smith 1987c, 1988a). There is a paucity of grazers and predators (there are no indigenous herbivorous mammals and insects play only a small role in herbivory), so most of the energy and nutrients incorporated in primary production goes through a detritus chain, rather than a grazing chain. Decomposition, with the concomitant release of nutrients, is overwhelmingly the main bottleneck in nutrient cycling and primary production for most of the plant communities (Smith 1988b, Smith & Steenkamp 1992a). The consistently cool climate, high cloud cover and very high rainfall result in low soil temperatures and excessive soil moisture, both of which restrict microbial activity. That is the reason why peat accumulation (a major determinant of vegetation succession, Section 5.1) is such a conspicuous part of the ecosystems of the islands, at least at lower altitudes where plant growth is possible. Decomposition mediated by soil micro-organisms alone is simply too slow to satisfy the large annual requirement for nutrients by the vegetation. There are large concentrations of soil macro-invertebrates (earthworms, moth larvae, weevils, snails etc.) that, by feeding on plant litter, are responsible for the bulk of energy flow and nutrient cycling on the island (Crafford 1990a, Smith & Steenkamp 1992b). The activities of these animals are strongly temperature-dependent (Klok & Chown 1997, Chown et al. 1997) so, providing nothing else threatens their populations, increasing temperature will result in enhanced rates of litter consumption and hence of nutrient release, allowing the potential for increased primary production due to elevated temperature to be realised. Threats to the soil macro-invertebrates of the islands, and hence to ecosystem functioning, are discussed in Section 7.2.

6. Current Conservation Status of the Islands

The National Parks Act (Act 42 of 1962) does not list Marion or Prince Edward Islands in its schedule of National Parks; neither do the islands enjoy Provincial Nature Reserve status although juristically they are considered as part of the Western Cape. Statutory environmental protection for the islands (to the low water mark) is provided by the Environmental Conservation Act (Act 73 of 1989), in terms of which both islands were proclaimed as Special Nature Reserves on 3 November 1995. The Maritime Zones Act (Act 15 of 1994), Article 54 of the Sea Fishery Act (Act 12 of 1988) and The Fishing Industry Development Act (Act 86 of 1978) afford some control over exploitation of the maritime zone around the islands. Additionally, the Seabirds and Seals Protection Act (Act 46 of 1973) controls the capture and killing of most species of seabirds and seals on the islands and South Africa is an original signatory of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR), which, while not impinging on national sovereignty rights, focuses on conservation and management of marine living resources on and around the islands.

Proclamation of the islands as Special Nature Reserves required the formulation of a Management Plan for the islands, which was published in 1996 (Department of Environmental Affairs and Tourism 1996). The primary aim of the management plan is the conservation and sustained preservation of the islands' unique ecosystems for all people of South Africa and for the scientific community at large. The plan recognises that the Prince Edward Islands are an integral part of South Africa's national heritage and territorial integrity and that a rational and rigorous management of the islands is in keeping with an emerging international ethos and political order that recognises a strong environmental ethic.

A Prince Edward Islands Management Committee (PEIMC) was established to implement the management plan, which contains many provisions and regulations to ensure that activities on the islands take place with the minimum of environmental disturbance. The Management Committee advises the Department of Environmental Affairs & Tourism (DEAT) on planned and existing activities on the islands. A Conservation Officer and Team Leader are appointed to each relief team to the islands and

together they are tasked with the day to day 'management' of the islands in terms of the management plan.

Under the management plan four zones have been designated on the islands. Zone 1 is a service zone that includes the Marion Island meteorological station and a small area surrounding it. Zone 2 is a buffer zone around the station which extends in roughly triangular shape between Trypot Beach, Junior's Kop and Ships Cove. Areas around the field huts are also considered as Zone 2 areas because of limited human impact. The rest of Marion Island is a Zone 3 or wilderness area, with the exception of areas where there are Southern Giant Petrel colonies, Gentoo Penguin colonies, three Wandering Albatross study colonies, and Greyheaded Albatross colonies. These colonies are Zone 4 or protected zone areas. The whole of Prince Edward Island is Zone 4.

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Figure 15.9 King Penguin (*Aptenodytes patagonica*) rookery on Marion Island, surrounded by tussock grassland (*Poa cookii*) vegetation. Light green plants are *Cotula plumosa*.

Entry to these zones is controlled by a permitting system. The permits are issued by DEAT on the advice of the Prince Edward Islands Management Committee. Generally, all visitors to the islands receive permits for Zones 1 and 2. Personnel involved in field research are permitted for Zone 3 and some for work in bird colonies that have Zone 4 status. Other team members may apply for permits to Zone 3 or may accompany research personnel doing field work on the permits of the research personnel involved. Visits to Prince Edward Island take place only with special permission and under strict conditions. These include intensive efforts to reduce the risk of alien introductions to the island.

Collection of any material from the islands, irrespective of the zone in which the collections are carried out, is also regulated by a permit system.

7. Threats to the Islands' Ecosystems

7.1 Implications of Climate Change

A changing climate has implications for the indigenous biota of the islands, especially the terrestrial species, which have all evolved under the cool, humid conditions typical of subantarctic islands. Smith & Steenkamp (1990) proposed some scenarios of the direct effects of warming (and drying) for the biota of Marion Island and there have been a few case studies on particular taxa. Most have concentrated on the ecophysiological responses of particular organisms, or groups of organisms, to abiotic factors such as moisture, light and temperature. For example, Smith & Gremmen (2001) showed that the light/temperature response of photosynthesis in the lichen *Turgidosculum complicatulum* on Marion Island is such that under the prevailing climatic regime the lichen would exhibit near maximal photosynthesis rates for 75% of the photoperiod over the year, if sufficiently hydrated. A model of the photosynthetic response predicts that changes in temperature and radiation by the amounts known to have occurred in the past few decades, and even more drastic changes (temperature up by a further 2°C, radiation up by 10%), would negligibly affect the annual amount of carbon acquired, again provided the thalli remain hydrated. Incorporating hydration/desiccation cycles into the model resulted in a very substantial lowering of annual net carbon exchange. However, attempts to include the increase in aridity known to have occurred at the island since 1971 yielded conflicting scenarios for the effect on annual carbon acquisition, depending on whether atmospheric drying or thallus drying was considered.

Similar studies relating physiological performances to microclimate factors have been carried out on the insects of the islands. For each of the six weevil species of the islands, upper lethal temperature corresponds closely to the maximum microclimate temperature in the habitat of the particular species (Van der Merwe et al. 1997), suggesting that climatic warming might be deleterious to the weevils' survival. Klok & Chown (1997) examined the thermal tolerance and desiccation resistance of larvae of a flightless moth (*Pringleophaga marioni*, the most ubiquitous insect on the islands) and concluded that should the warming trend on the islands continue, it will have a profound negative effect on the moth population, especially if the warming is accompanied by increasing aridity.

It was suggested in Section 3.1 that the climatic change occurring in the subantarctic is associated with changes in sea level (atmospheric and oceanic) circulation patterns, changes that themselves have implications for the biota and ecosystems of the islands. For instance, approximately one million pairs of burrowing petrels and prions occur on Marion Island, and possibly even more on Prince Edward Island. By feeding in the sea and depositing guano on land they represent an important source of marine-derived nutrients and energy (Smith 1976b) and are therefore a major driving force in vegetation succession (Smith & Steenkamp 2001). The birds use atmospheric frontal systems to move between the islands and their feeding areas (Mendelsohn 1981), which may be several hundred kilometres distant, in the surrounding ocean. If atmospheric circulation patterns are changing, then the birds may not be able to reach their usual feeding grounds; alternatively, associated changes in oceanic circulation may move the feeding grounds to other localities. Hence, changing sea level circulation patterns may

be expected to influence the breeding success and population densities of these animals, with obvious implications for nutrient cycling and vegetation succession on the islands. Similar considerations probably apply to the large populations of seals, penguins and albatrosses.

Even the identity of Marion Island (with its sparse, low-growing vegetation devoid of trees, or even shrubs, and an avifauna consisting entirely of seabirds) is challenged by the changes in its climate over the past 30 years or so. In Section 2 it was shown that the most widely accepted definition of 'subantarctic' (at least its terrestrial connotation) is based on a hybrid scheme derived from a vegetation-based classification by Wace (1965) and a climatological classification by Holdgate (1964). The subantarctic region has no months warmer than 8.5°C (considered the lower temperature limit for tree growth) and occurs south of the southern limit of tree or shrub growth (distinguishing it from the cool-temperate zone to the north) and north of the southern limit of closed phanerogamic vegetation (delimiting it from the maritime or low Antarctic to the south). Prior to 1990 Marion Island fitted comfortably into the subantarctic category but in the 1990s mean temperatures for January, February and March were between 8 and 8.5°C. Only slight further warming will put the island into the south cool-temperate zone, a region where the oceanic islands are inhabited by tall shrubs, trees and land birds (even parakeets!).

7.2 *Alien Flora, Alien Animals and Human Influence*

Probably of greater importance than the direct effects of climate change on the biota of the islands, is that a warmer climate will increase the ease with which the island can be invaded by alien species (Bergstrom & Chown 1999). Such invasions, especially by functional groups generally not found on subantarctic islands (e.g. vertebrate and invertebrate predators, mammalian herbivores, particular groups of pathogens), represent by far the greatest threat to the indigenous biota of subantarctic islands. An example of this is the deleterious effect that introduced organisms are having on the Kerguélen cabbage (*Pringlea antiscorbutica*), the only species in its genus, endemic to four subantarctic island groups. The species is the last remaining relict of a once extensive circum-antarctic flora. The distribution of *P. antiscorbutica* on Îles Kerguélen and the Îles Crozet has decreased in the last 25 years due to grazing by introduced rabbits *Oryctolagus cuniculus* (Chapuis 1995). On Marion Island its distribution and abundance has declined alarmingly over the past 25 years for several reasons, all to do with invasive alien biota. The European Slug (*Deroceras caruanae*) was introduced to the island in the mid-1960s (Smith 1992) and the Kerguélen cabbage is one of its preferred food items there. The Diamondback Cabbage Moth (*Plutella xylostella*), a major pest of crucifers worldwide, is also a recent arrival on the island (first discovered in 1986; Crafford & Chown 1990) and *P. antiscorbutica* is its only host plant there. Many stands of the cabbage are severely infected by the moth. *Botryotinia fuckeliana* (conidial state: *Botrytis cinerea*), the causal organism of grey mould rot in crucifers and other vegetable crops, has also reached the island only quite recently (probably through vegetables sent as food for the island personnel; Kloppers & Smith 1998). Many stands of the cabbage have been infected by the fungus, whole plants collapsing into a black slimy residue.

The introduced house mouse (*Mus musculus*) on Marion Island offers a particularly striking example of how profoundly an invasive alien organism can influence the biota and ecosystem of a subantarctic island. House mice on the island feed mainly on soil macro-invertebrates such as moths and weevils (larvae and adults), flies, spiders, earthworms and snails. The mouse population is strongly temperature-limited and is increasing, probably as a result of ameliorating temperatures. Several studies have unequivocally established that house mice are cardinal determinants of the population dynamics of terrestrial macro-invertebrates on the island. Crafford & Scholtz (1987) showed that there are striking differences between Marion Island and Prince Edward Island (which is only 22 km away) in the size, structure and composition of their macro-invertebrate populations (and also in the maximum body size attained by the various species) and ascribed this to the fact that mice do not occur on Prince Edward. The severity of the impact that mice have on their invertebrate prey on Marion Island is illustrated by the fact that mice daily consume between 30 and 107 g of moth (*P. marioni*) larvae per hectare (depending on habitat; Smith et al. 2002), or an average consumption for the island's eastern coastal plain of 65 g per day (Crafford 1990b). This is equivalent to 0.7% of the annual mean biomass of larvae, which take a long time to mature (2 to 10 years; Crafford 1990a, b). Such a high daily consumption rate must have severe implications for an insect with such a long life cycle, especially since almost the whole of it comprises the non-reproductive phase. In the case of weevils, sympatric speciation associated with assortive mating owing to differences in body size is occurring in the *Ectemnorrhinus similis* species complex on the island (Chown 1990), and size-selective predation by mice might be considerably enhancing the rate at which this is taking place (Chown & Smith 1993).

Predation by mice on soil invertebrates directly influences other components of the biota of the island. For example, the Lesser Sheathbill (*Chionis minor*) is the only non-migratory bird species on the island and relies on soil macro-invertebrates as food in winter. Smith & Steenkamp (1990) proposed that escalating predation by mice on soil invertebrates could adversely affect the sheathbill population. Huyser et al. (2000) subsequently reported that between the mid-1970s and mid-1990s the island's sheathbill population decreased by 23%, whereas the one on Prince Edward Island did not change.

More insidious, but probably even more profound than these direct effects of house mice on the biota of the islands, is their influence on ecosystem functioning (primary productivity, decomposition and nutrient cycling). As was stated in Section 5.2, primary production on the island is high, which means that the vegetation has a large annual requirement for nutrients, most of which is met by litter-feeding macro-invertebrates. Increasing temperature is expected to increase productivity and nutrient demand even further. Since soil microbiological processes on the islands appear to be more strongly limited by waterlogging than by temperature (Smith et al. 1993), the increased temperature might not translate into substantially greater rates of nutrient release by soil microbes alone. However, the activities of detritivorous macro-invertebrates, which are responsible for the bulk of energy flow and nutrient cycling on the islands, are strongly temperature-dependent (Klok & Chown 1997, Chown et al. 1997) and increasing temperature will result in enhanced rates of litter consumption and hence of nutrient release, which will allow the potential for increased primary production due to elevated temperature to be realised. An increasing mouse population, through enhanced predation pressure on soil invertebrates, will decrease rates of nutrient cycling and cause imbalances between primary production and decomposition and hence affect, amongst other things, rates of peat accumulation. This, along with more direct effects of mice (e.g. granivory; Chown & Smith 1993) has important implications for vegetation succession and ecosystem structure and functioning on the island.

8. The Future

8.1 Future Research

Biological research on Marion and Prince Edward Islands is financially supported by the South African Antarctic Research Program (SANAP) of the Department of Environmental Affairs and Tourism (DEAT), which until 2003 also co-ordinated and defined the focus and objectives of the research. DEAT, with the Department of Public Works, maintain research laboratories at the meteorological station (Figure 15.10). Smith (1991) provided a synopsis of the directions and priorities of terrestrial biology research on the Prince Edward Islands during the 1970s and 1980s. Since 1990 the focus of the research has been very largely directed toward increasing the ability to rationally manage and conserve the biota and ecosystems of the islands, including predicting the effects of the very marked climate change that is occurring there. Special attention has been given to monitoring and conservation projects, in accordance with national (e.g. requirements for managing Special Nature Reserves) and international (e.g. CCAMLR) obligations. The directives identified by SANAP and against which terrestrial biology research projects carried out between 2000 and 2004 were being evaluated and are being supported by DEAT, were:

- Factors influencing spatial and temporal patterns in biodiversity.
- Indigenous and introduced species: differential responses to environmental change.
- Adaptation, plasticity and response.

In 2003 the research function of SANAP was transferred to the Department of Science and Technology (DST), and is co-ordinated by the National Research Foundation (NRF). Logistics and management of the islands remain the responsibility of DEAT. From 2007 research at the islands will be aligned with the themes of the International Council for Science's *International Polar Year 2007–2008* program (http://www.ipy.org/concept/index.html).

8.2 Development and Conservation Threats

The DEAT is committed to the conservation and preservation of the biota and ecosystems of the islands and in terms of the proclamation of the islands as Special Nature Reserves, the Management Plan must be adhered to in all future research and logistic activities. Two aspects have arisen quite recently that will test that commitment.

The Antarctic is increasingly fascinating tourists and antarctic and subantarctic tourism is growing faster than the average for tourism worldwide. Tourism visits to the Antarctic Peninsula islands, South Georgia and the Falkland Islands, the New Zealand subantarctic islands, Macquarie Island and the French subantarctic islands have increased exponentially over the past 25 years. The Prince Edward Islands have largely escaped this trend, mainly because in addition to being isolated they are not near other sites of tourist interest that can provide alternative possibilities for the tour operator to satisfy clients should the weather be bad during the time that the ship visits them. However, of late there has been an increasing interest in tourism to the islands. In November 2002 the South African supply vessel, the S.A. Agulhas, was chartered to take a large contingent of birdwatchers to both islands, although no one was allowed ashore. There is evidence that two unauthorised tourist landings occurred at Prince Edward in the late 1990s and since 1996 several tour operators have applied to DEAT for permission to visit the Prince Edward Islands and land on Marion Island.

Since the current Prince Edward Islands Management Plan does not explicitly address tourism, the PEIMC recommended to the Minister of Environmental Affairs and Tourism that permission for those visits be denied. However, the PEIMC recognised that pressure for tourism activities at the islands was likely to increase, that such visits would be far more preferable if undertaken under controlled, monitored circumstances, and also that tourism had a positive spin-off in terms of generating income for SANAP and increasing public awareness of the unique nature of the islands and the research and conservation efforts being carried out on them. Accordingly, the PEIMC recommended to the Director General of DEAT that an environmental impact assessment of tourism at Marion Island should be undertaken. A subcommittee of the PEIMC was tasked with the EIA, with the following terms of reference:

- Investigate the possibilities for controlled, limited tourism to Marion Island.
- Undertake an EIA of the impact of tourism at certain sites on the coast of Marion Island between Ships Cove and Trypot Beach.
- Investigate the possibility of construction facilities to house tourists in the event of an emergency, and of erecting structures such as catwalks that would mitigate the impact of people on the biota of the island.

The recommendations of the subcommittee (Heydenrych & Jackson 2000) were that large tours of more than 100 persons not be allowed under any circumstance, but that smaller groups of up to 100 persons may land on Marion Island under a permitting system under an Impact Management Plan to be drawn up by DEAT. Tour visits would be limited to Zones 1 and 2 on Marion Island and no tourism should be allowed on Prince Edward Island. The rest of the recommendations relate to the

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Figure 15.10 Meteorological Station and scientific base on the eastern lowland plain of Marion Island. Large cinder cone behind the station is Junior's Kop.

timing and number of tour ship visits, the size of landing groups, the infrastructure and manpower requirements needed before tourism activities would have an acceptable minimum impact on the ecosystem of the islands, the use of income from tourism to pay for that infrastructure to and monitor the effects of tour visits, and the need for tour operators to have comprehensive insurance against unforeseen circumstances that would negatively impact on the islands, such as oil spills that would require clean-up, search and rescue operations and emergency board and lodging. The subcommittee specifically recommended that no additional accommodation facilities be erected on the island to cater for tourists.

One recommendation of the subcommittee is especially of note—that tourism increases the risk of introducing new alien organisms to the island (see the analysis by Chown et al. 1998 showing very convincingly that increasing numbers of human occupants increase the risk of propagule transfer to an island). Most importantly, the recommendation specifically points out that new introductions might lead to severe impacts on the biota of an island, the costs of mitigation of which might be extremely high. An example is the possible introduction of rats to Marion Island. That would have an enormous impact and the expense of eradication would likewise be enormous, judging from the cost of successful eradications of rats from the much smaller and more accessible islands off New Zealand. An idea of the cost is given by the 1995 estimate made at a workshop on the possibility of eradicating house mice on Marion Island (Chown & Cooper 1995) that the poison bait alone would cost R2.75 million per year, and that the eradication programme would take several years. Added to that is the cost of spreading the bait by air (estimated at 2 000 hours helicopter flying time) and of putting measures in place to reduce the very real risk of poisoning scavenging birds—about two thirds of the skua population on Enderby Island, south of New Zealand, was killed through taking bait put out for rabbits (Torr 1993). Assuming that eradication of rats on Marion Island could be completed in three years, the 2003 estimate of total cost (manpower, bait, helicopter and ship costs) was ca. R37 million. The report of the tourism subcommittee pertinently, and very correctly, points out in its recommendations that such high mitigation costs cannot realistically be claimed from tour operators. The reality is also that South Africa does not have the resources to undertake such an exercise, which means that the introduced rats will become a part of the ecosystem of the island, an ecosystem that will be very different and much less valuable as a laboratory for furthering ecological knowledge and theory.

For this reason the possibility that tourism to the islands might become a non-option is to be welcomed. The Draft National Environmental Management Protected Areas Bill published in 2002 lists three main types of protected areas, Special Nature Reserves, Nature Reserves, and National Parks. Tourism is explicitly stated as one purpose for declaring a protected area as a Nature Reserve or a National Park, but the only stated purposes for establishing Special Nature Reserves are 'to protect highly sensitive, outstanding ecosystems, species, geological or physical features in the area and to make the area primarily available for scientific research or environmental monitoring'.

The second issue that will soon test DEAT's commitment toward the conservation and preservation of Marion Island, in particular, is that construction of a new base station on the island commenced in September 2003. This will take four years and will be followed by the dismantling and removal of the old station. Such activities will involve large numbers of personnel and the importation of a huge amount of material. DEAT and the Department of Public Works (which is carrying out the construction) have undertaken to put all possible measures in place to ensure that the activities do not result in new introductions of alien organisms and that they will be undertaken in a way that reduces environmental disturbance to a minimum. The acid test of the seriousness of their commitment will be the situation in five years' time. If at that time the island possesses a new ultramodern base erected over a wasteland of bare eroded peat and adjacent an urban dump (the site of the current base), and a whole suite of new alien organisms, then DEAT will have failed the test.

9. Definition of Biomes, Vegetation and Mapping Units

Spatial variation of the vegetation of the islands occurs on a very small scale, due to the influence of the hummocky topography formed by the lava flows on aspects such as insolation, shelter from wind, moisture deposition, retention and drainage, and peat accumulation. Except for fellfield and polar desert, large expanses of single vegetation types are quite rare; at low altitudes (<200 m) even very small areas generally contain several vegetation types. For instance, a vegetation map by Gremmen (1981, p. 72) shows 18 plant communities sharing an area of 0.5 ha on Marion Island. Eleven of these are mire communities, two are biotic, two are slopes and one is fellfield. Other than the mires, the rest of the communities occupy patches mostly smaller than 20 m^2. Mapping at the scale of the maps presented here would show the vegetation as mire. Smith (1976c, p. 17) provides a vegetation map for a 1.5 ha area 500 m north of the one in Gremmen (1981), on the same lava flow. There, the vegetation is mapped more coarsely, not according to phytosociological associations. There are four slope vegetation types, one mire type and one fellfield type. Most of the types are represented in more than one patch but the total areas occupied by each type are more or less equal. Together, the four slope types are more extensive than mire or fellfield, so at the scale of the maps here the vegetation would be indicated as slope vegetation. However, between the two sites the lava flow contains a similar-sized site dominated by fellfield and spatially the three sites (mire-dominated, slope-dominated and fellfield-dominated) cannot be depicted separately at the scale of the maps presented here. The particular lava flow extends about 2 km south, 1 km north, and about 4 km inland of the two sites. Overall, this pattern of either mire, slope or (less commonly) fellfield communities being locally dominant is repeated over and over across the lava flow, which is only one of many similar flows that comprise the low altitude region of the island. All that can be said is that the lavas are occupied by a mosaic of slope, mire and fellfield communities.

The situation is even more complex on the coast, since salt-spray plant communities and communities influenced by animals are added to the mosaic. It is only at higher altitudes that more uniform vegetation types (fellfield and polar desert) occur over expanses large enough to be able to delineate them at the resolution of the map. Even there, the transition between fellfield and the mire-slope fellfield mosaic is not a sharp one, nor is the transition from fellfield to polar desert. None of those units can be distinguished on the aerial photographs of Marion Island (there are no photographs for Prince Edward). To compile the maps presented here, the mapping units were delineated on basis of field research (vegetation samples, photographs taken from known locations and other field observations done during on-foot and helicopter-assisted expeditions).

Here we distinguish three groups of vegetation (and mapping) units:

- Marine Macroalgal Vegetation contains only one vegetation (mapping) unit: Subantarctic Kelp Beds. Due to a lack of appropriate field data we do not show this unit on the maps of the islands.
- Subantarctic Tundra. This group corresponds to the extent of Subantarctic Tundra Biome and is found on the islands' lower altitude (<300 m) regions. Vegetation units ST 3, 4, 5 and 6, form an intricate small-scale spatial mosaic. In terms of Gremmen's (1981) classification this mosaic encompasses, respectively, the *Juncus scheuchzerioides–Blepharidophyllum densifolium* complex (mire), the *Acaena magellanica–Brachythecium* complex (slope drainage lines, springs and stream banks), the *Blechnum penna-marina* complex (slope fernbrake communities), and low-altitude representatives of the *Andreaea–Racomitrium crispulum* complex (fellfield). It is not feasible currently to disentangle this mosaic in the form of discrete spatial units at conventional mapping scales. Therefore, in spatial terms (on our map), we summarise vegetation units ST 3, 4 and 5 into a single mapping unit called 'Subantarctic Mire-Slope Vegetation' with the hope of being able to depict them on a more detailed scale at a later stage. The same applies for vegetation units ST 1 and 2, which were mapped together as the mapping unit 'Subantarctic Coastal Vegetation Vegetation'.
- Subantarctic Polar Desert crowns the highest tops of the islands, and on Marion Island descends as low as 100 m in places. It might seem surprising, even paradoxical, to apply the term polar desert to a habitat on a mid-latitude island that receives such a high rainfall, and most vegetation ecologists have tended to avoid using it when describing vegetation formations on subantarctic islands. For instance, Huntley (1971) referred to the vegetation of the habitat as *Ditrichum–Bartramia* montane desert and included it with *Azorella selago* fellfield in a wind desert complex. On other subantarctic islands, vegetation formations corresponding to Marion Island polar desert have generally been considered as fellfield (Taylor 1955, Hughes 1987, Bergström 1998) or included with fellfield as a synusia in a Fellfield Formation (Lewis Smith 1993). However, fellfield (Fjaeldmark, Felsenfluren or Felsentundra) was originally applied to vegetation in which vascular plants, especially cushion-forming ones, are a conspicuous (even important) component of the vegetation. This is certainly not the case for the Marion Island polar desert habitat, which has strong similarities (a barren unstable surface caused by frost-sorting, supporting extremely sparse vegetation dominated by mosses or, more rarely, lichens) to high arctic polar deserts as defined by Aleksandrova (1970) and Bliss (1981). In fact, it is floristically even more polar desert-like than many of the high arctic sites those authors cite as examples, where vascular plants make up a much greater component of the vegetation than is the case for the polar desert habitat on the island. For example, in the polar desert uplands of Devon, Bathurst and Cornwallis islands (all > 75° N in the Canadian North Western Territory), four to six vascular plant species are typical, increasing to eight to 12 at snow flush sites (Bliss 1981). Ten vascular species occur at 900 m altitude on Ellesmere Island (Canadian N.W.T., 82° N), whereas none occur above 800 m on Marion Island. The vegetation of the polar desert habitat on Marion Island thus resembles the most extreme northern hemisphere polar deserts; those dominated by mosses and lichens have been termed 'polar barrens' (Benninghof 1974) or simply 'barrens' (Longton 1998), to distinguish them from fellfield where vascular plants are more important. One only has to examine the photographs in Ochyra & Bednarek-Ochyra (1999) and Figure 15.19 to be convinced of the congruency in equating the Marion Island habitat with polar barrens of theHigh Arctic.

The term 'wind desert' has also been used when referring to the high-altitude vegetation of the subantarctic islands (Taylor 1955, Wace 1965, Huntley 1971) but that is not necessarily a fitting descriptor of the vegetation or the main factors affecting it. This does not imply that wind is unimportant. The polar desert surface on Marion Island, like the polar deserts of the Antarctic and Arctic, is almost totally dominated by physical rather than biological processes, and frost-heaving, frost-sorting and freeze-thaw activity are strong and frequent (at high altitudes, freeze-thaw cycles occur every day of the year; Jan Boelhouwers, pers. comm.). The effect of wind is as much due to its contribution to substrate instability and drying as to its more direct effects on plant growth. In fact, within polar desert there is little correlation between plant cover and shelter from wind, except where the cause of the shelter also contributes to moisture deposition and/or retention.

10. Description of Vegetation Units

Marine Macroalgal Vegetation

AZm 2 Subantarctic Kelp Beds

Distribution On the coast and offshore on the leeward (eastern) side of Marion Island and Prince Edward Island.

Vegetation & Seascape Features Kelp beds are an important and spectacular element of the seascapes of the Prince Edward Islands. They form two well-separated vegetation belts. *Durvillea antarctica* forms a fringing macrophyte belt on the

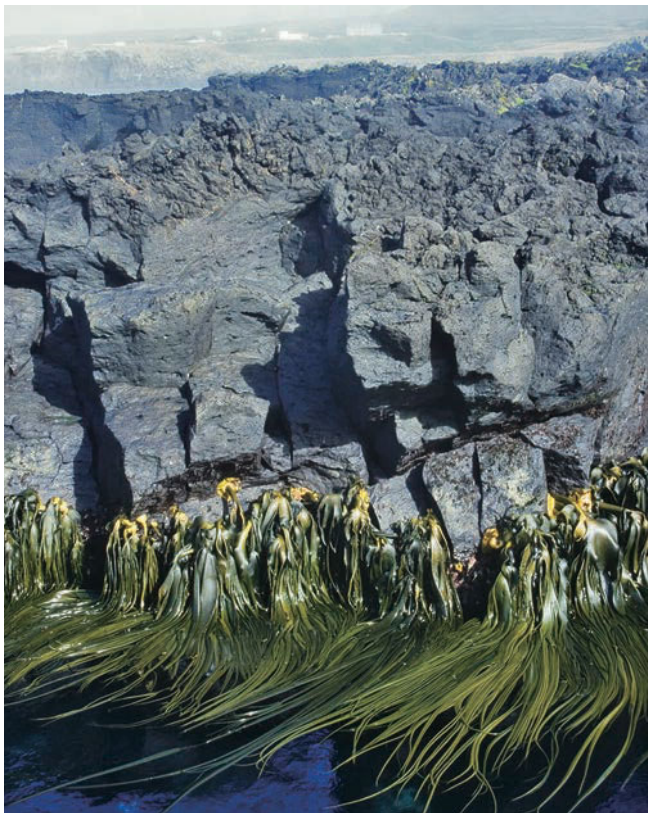

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Figure 15.11 AZm 2 Subantractic Kelp Beds: *Durvillea antarctica* in supra-littoral zone on coastal cliffs formed by head of young lava stream (near the Meteorological Station on Marion Island).

coastal rocks and cliffs. Holdfasts are attached to the rock in the lower littoral zone (De Villiers 1976) and the fronds (up to 8 m long) float freely on the water surface. *Macrocystis laevis* is found further off-shore, forming an interrupted belt up to 150 m broad.

Hydrology & Substrate The coastal cliffs and the sea shelf are built of young Holocene basaltic lavas. The tidal range on Marion Island is 71 cm at springs and 21 cm at neaps. Swell heights on the east coast may reach up to 4 m and as they travel unimpeded in deep water, they extend their energy against the sea cliffs, especially on the west, to lesser extent on the south and north coasts. Both kelp species prefer eastern lee shores (more or less outside the direct influence of roaring west winds and associated wave exposure), but *D. antarctica* occurs all around the island, being seemingly adapted to the relentless and large wave action that produces surf up to 30 m high in places. *M. laevis* forms dense 'kelp forests' of individuals up to 20 m long in water 5 to 20 m deep. It has a uniform distribution of frond-length frequency, suggesting that only the oldest fronds are lost by wave action or senescence. Strong wave action in more shallow water limits the availability of suitable habitat, whereas in deeper water light limits the kelp's growth (De Villers 1976, Attwood et al. 1991). Sea temperature at the island is around 4°C to 5°C in winter and 6°C to 7°C in summer (Mélice et al. 2003). Salinity is 32 to 33 psu (Pakhomov et al. 2002).

Important Taxa (both Macroalgae) *Durvillea antarctica* (d), *Macrocystis laevis* (d).

Remark 1 Mean biomass of *Macrocystis laevis* was estimated at 0.67 kg C m^{-2} and net production at 7.7 g C m^{-2} d^{-1} and 11.5 g C m^{-2} d^{-1} during April and August, respectively (Attwood et al. 1991). Most of the production of *M. laevis* is expected to be exported to the open ocean pelagic system (Attwood et al. 1991).

Remark 2 *Macrocystis laevis* is endemic to the Prince Edward Islands. It was described by Hay (1986); previously it was known as *Macrocystis pyrifera* (De Villers 1976, Gremmen 1981), a species that occurs around many islands in the Subantarctic and cold temperate regions of the Southern Ocean.

Remark 3 This vegetation unit is a subantarctic analogon to the AZm 1 Cape Kelp Beds (see Chapter 14 Coastal Vegetation), dominated by *Ecklonia maxima* and occurring in cold waters influenced by Benguela Current.

References De Villiers (1976), Gremmen (1981), Hay (1986), Attwood et al. (1991), Pakhomov et al. (2002), Mélice et al. (2003).

Subantarctic Tundra Biome

ST 1 Subantarctic Coastal Vegetation

Salt Spray Complex (Huntley 1971). 4.1. *Crassula moschata* Complex (Gremmen 1981). Coastal Salt-spray Complex (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution On the eastern coasts of the islands this vegetation is mostly restricted to within 50 m of the shore but on the northern, western and southwestern coasts it is found further inland, since the predominant wind direction on the islands is northwesterly and southwesterly; on Marion Island ca. 1.5% of the area below an altitude of 100 m, is occupied by salt-spray vegetation.

Vegetation & Landscape Features Herbfields dominated by *Crassula moschata* (sometimes also by *Cotula plumosa* and at very exposed localities, *Azorella selago* co-dominates in a type of coastal fellfield vegetation).

Geology, Soils & Hydrology Mostly on black lava flows, on fibrous, black or dark brown peat that is often saline, being subjected to salt spray and occasional inundation by waves.

Climate The combination of low altitude and coastal location makes the microclimate of vegetation of salt-spray habitats extremely oceanic, with small diurnal and seasonal variation.

Important Taxa Herbs: *Cotula plumosa* (d), *Crassula moschata* (d), *Azorella selago*, *Callitriche antarctica*, *Colobanthus kerguelensis*, *Montia fontana*, *Ranunculus biternatus*. Graminoids: *Agrostis magellanica*, *Poa cookii*. Mosses: *Bucklandiella crispula*, *Calyptichaete apiculata*, *Campylopus clavatus*, *Muelleriella crassifolia*, *Orthotheciella varia*. Liverworts: *Clasmatocolea vermicularis* (d), *Fossombronia australis*, *Plagiochila heterodonta.*

Remarks This vegetation is frequently also influenced by birds, in particular by Rockhopper Penguins (*Eudyptes chrysocome*) and Fur Seals (*Arctocephalus tropicalis*).

References Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001).

ST 2 Subantarctic Biotic Herbfield and Grassland

Biotic Complex (Huntley 1971). 4.2. *Callitriche antarctica–Poa cookii* Complex (Gremmen 1981). 4. Biotic Grassland Complex & 5. Biotic Herbfield Complex (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution Found almost exclusively in coastal areas influenced by trampling and manuring by seabirds and seals. Also inland on slopes supporting colonies of burrowing petrels and on level areas surrounding Wandering Albatross and Giant Petrel nests; on Marion Island ca. 7% of the area at an altitude below

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Figure 15.12 ST 1 Subantarctic Coastal Vegetation: Coastal salt-spray vegetation dominated by *Crassula moschata* (yellow-green plant cover in the left foreground) and *Cotula plumosa* (light green cover in the right foreground and midground) on Marion Island.

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Figure 15.13 ST 2 Subantarctic Biotic Herbfield and Grassland: Vegetation heavily influenced by penguin and seal manuring and trampling at Cave Bay, Prince Edward Island. Tussocks of *Poa cookii* occur on peat pedestals, separated by wallows of a highly organic, eutrophic mud covered with *Callitriche antarctica*. Cave Bay was the site of the annexation ceremony in 1948.

100 m, but less than 1% of that between 100 and 500 m altitude is occupied by biotically influenced vegetation. The largest patches of biotic vegetation are found around large penguin rookeries (Kildalkey Bay, Bullard Beach and King Penguin Bay).

Vegetation & Landscape Features Coastal platforms with numerous depressions supporting *Cotula plumosa*-dominated herbfields and *Callitriche antarctica*-dominated organic mud as well as steep slopes supporting *Poa cookii*-dominated tussock grasslands. Saline habitats influenced by seabirds and seals; overall, species diversity is low.

Geology & Soils The soils are mostly peat with high concentrations of organic and inorganic nitrogen and phosphorus and they may be saline; where trampling is severe the soil surface may be bare and where both trampling and manuring are severe (e.g. seal wallows and penguin rookeries) an anaerobic, almost liquid, organic mud occurs.

Climate The combination of low altitude and coastal location makes the microclimate of salt-spray vegetation extremely oceanic, with small diurnal and seasonal variation. Soils denuded of vegetation through trampling can reach high surface temperatures (up to 35°C) on sunny days.

Important Taxa (*Aliens) Herbs: *Callitriche antarctica* (d), *Cotula plumosa* (d), *Montia fontana* (d), *Sagina procumbens** (d), *Azorella selago*, *Ranunculus biternatus*. Graminoids: *Agrostis stolonifera** (d), *Poa annua** (d), *P. cookii* (d), *Agrostis magellanica*, *Juncus scheuchzerioides*. Mosses: *Brachythecium rutabulum* (d), *Leptodontium gemmascens*, *Schizymenium campylocarpum*. Liverworts: *Clasmatocolea vermicularis* (d), *Fossombronia australis*, *Lophocolea randii*, *Lophozia cylindriformis* var. *australis*, *Marchantia berteroana*.

Remark 1 Twenty-nine bird and three seal species use the islands to breed and moult. Most of the birds, and the Subantarctic Fur Seal, occur in large numbers and have a significant impact on the vegetation, through trampling and manuring. Tussock grasslands occur around King Penguin (*Aptenodytes patagonicus*) and Macaroni Penguin (*Eudyptes chrysolophus*) rookeries and Elephant Seal (*Mirounga leonina*) wallows and are often pedestalled, the tops of the 30–100 cm peat pedestals are occupied by *Poa cookii* and their bases by *Cotula plumosa* or *Callitriche antarctica*, sometimes also *Montia fontana* and *Poa annua*. Areas occupied by Rockhopper Penguins (*Eudyptes chrysocome*), Gentoo Penguins (*Pygoscelis papua*), Crozet Cormorants (*Phalacrocorax atriceps*) or Fur Seals (*Arctocephalus tropicalis* and *A. gazella*) are generally occupied by vegetation dominated by *C. plumosa* and *P. cookii*. Inland slopes where burrowing petrels (10 species) or prions (two species) occur are also dominated by *P. cookii*, generally with *Acaena magellanica* and *Brachythecium rutabulum* in the understorey. In mires, Wandering Albatross nests are generally surrounded by vegetation dominated by *P. cookii* and also often containing other nitrophilous plants (*Callitriche antarctica, Montia fontana, C. plumosa* and *P. annua*) that are not normal constituents of mire vegetation.

Remark 2 Biotic vegetation, because of the disturbance through trampling and probably also the nutrient-enriched soils, is readily invaded by alien plant species, especially *Agrostis stolonifera, Sagina procumbens, Poa annua* and *P. pratensis*.

Remark 3 Liverworts are infrequent components of vegetation influenced by seabirds or seals; the notable exceptions are *Marchantia berteroana* and *Clasmatocolea vermicularis*.

References Huntley (1971), Smith (1978c), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001).

ST 3 Subantarctic Mire

Swamp Complex p.p. (Huntley 1971). 4.4. *Juncus scheuchzerioides–Blepharidophyllum densifolium* Complex (Gremmen 1981). 6. Mire Complex (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution Mire vegetation is found in most lowland areas, being most extensive below 200 m, but found up to 400 m altitude. On Marion Island approximately 30% of the area below 100 m and approximately 3% of that between 100 and 300 m is occupied by mire vegetation; the largest mires on Marion Island are found on the coastal plain between Repetto's Hill and Long Ridge, inland of East Cape, Macaroni Bay and on the western coastal plain between Kleinkoppie and Kampkoppie.

Vegetation & Landscape Features Flat or only slightly sloping localities are dominated by conspicuous graminoids *Agrostis magellanica, Juncus scheuchzerioides, Uncinia compacta* and an abundant bryophyte flora (about 60 species). In wetter areas the dominating liverworts and mosses include *Blepharidophyllum densifolium*, *Clasmotocolea humilis, Sanionia uncinata* and *Distichophyllum fasciculatum*, while in drier mires *Jamesoniella colorata* and *Racomitrium lanuginosum* are prevalent and *Blechnum penna-marina* also occurs. In mires where there is pronounced lateral flow of water *Bryum laevigatum* and *Breutelia integrifolia* (sometimes also *Brachythecium subplicatum*) dominate.

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Figure 15.14 ST 3 Subantarctic Mire: Mire dominated by *Agrostis magellanica* and *Breutelia integrifolia* formed in a basin inland of Hendrik Fisher Kop on Marion Island.

Geology, Soils & Hydrology Mire vegetation occurs on both the older grey and younger black lava flows and overlies highly organic, generally waterlogged, peat which may be up to 2.5 m deep; since most of the mires receive water from surrounding areas as well as directly from rainfall, they are not ombrotrophic in the strict sense. However, most lateral water movement occurs at the bottom of the profile and the high rainfall leads to downward leaching and acidic upper horizons; the vegetation is effectively out of contact with the lower horizons and not influenced by mineral soil or water that has been in contact with mineral soil of surrounding areas. The vegetation relies on nutrients in rainfall (and to a lesser extent on biological nitrogen fixation) and so the mires can be regarded as ombrotrophic. In their hydrology and vegetation physiognomy subantarctic mires closely resemble raised bogs and blanket bogs of the northern hemisphere.

Climate High moisture content of mire peat dampens the already small diurnal soil temperature fluctuations. Freezing of the top layer (1–2 cm deep) of peat or bryophyte mat is a regular occurrence in autumn, winter and spring, even at low altitudes.

Important Taxa (*Aliens, [S]Submerged or floating macrophytes in lakes and tarns) Graminoids: *Agrostis magellanica* (d), *Juncus scheuchzerioides* (d), *Uncinia compacta* (d), *Agrostis stolonifera**[S] (aquatic form). Herbs: *Ranunculus biternatus* (d), *Acaena magellanica*, *Azorella selago*, *Blechnum penna-marina*, *Limosella australis*[S], *Lycopodium magellanicum*, *Montia fontana*, *Potamogeton nodosus*[S], *Sagina apetala**. Mosses: *Breutelia integrifolia* (d), *Bryum laevigatum* (d), *Distichophyllum fasciculatum* (d), *Ptychomnion densifolium* (d), *Racomitrium lanuginosum* (d), *Sanionia uncinata* (d), *Campylopus clavatus*, *Catagonium nitens*, *Plagiothecium ovalifolium*. Liverworts: *Blepharophyllum densifolium* (d), *Jamesoniella colorata* (d), *Clasmatocolea humilis* (d), *Lepidozia laevifolia* (d), *Fossombronia australis*, *Cryptochila grandiflora*, *Jensenia pisicolor*, *Leptoscyphus expansus*, *Lophozia cylindriformis*, *Metzgeria decipiens*, *Plagiochila heterodonta*, *Riccardia multifida*, *R. pinguis*, *Symphyogyna marionensis*. Lichen: *Peltigera polydactyla.*

Biogeographically Important Taxa (endemics of Kerguélen Floristic Province) Herb: *Ranunculus moseleyi* (on Marion only, but not recorded since 1987). Mosses: *Campylopus austrostramineus, C. subnites*. Liverworts: *Andrewsianthus carinatus*, *A. lancistipus*, *A. marionensis*, *Diplophyllum marionense*, *Metzgeria grollei*, *M. marionensis.*

Remark 1 Many ponds, crater lakes and tarns occur on the islands. Most are small (< 400 m^2 in area) and, except for the crater lakes which are found in the craters of some cinder cones, all are less than 1 m deep. The bottom is generally volcanic ash mixed with organic matter. Benthic algal felts occur in some, especially the smaller ones which are protected from the scouring effects of wind-driven wave action. The most common plants are *Ranunculus biternatus*, *Agrostis magellanica, A. stolonifera*, and *Juncus scheuchzerioides*. Rarer, and found only on the bottom of ponds and tarns, are *Limosella australis* and *Ranunculus moseleyi*. Bryophytes are uncommon on the bottoms of ponds and tarns (*Drepanocladus aduncus* is sometimes found there) but very abundant around the edges, especially *Sanionia uncinata*. The wettest mires have standing water on the surface and are probably more correctly considered as pools. They are dominated by *Agrostis magellanica, Juncus scheuchzerioides, Ranunculus biternatus* and *Sanionia uncinata*. Small streams are common on the islands, especially Marion Island. *Agrostis stolonifera* (submerged form) is the only vascular plant, and *Schistidium falcatum* the main bryophyte, that establish in stream beds.

Remark 2 The mires occur on both islands as an intricate, small-scale mosaic with fernbrakes and low-altitude fellfield. Ecotones between mire and fernbrake, and between mire and fellfield, are a significant component of the slope-mire (and some fellfield) mosaic.

References Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001).

ST 4 Subantarctic Drainage Line and Spring Vegetation

Swamp Complex p.p. (Huntley 1971). 4.3. *Acaena magellanica–Brachythecium* Complex (Gremmen 1981). 3. Slope Complex p.p., incl. 3.5. Slope Drainage Line and Streambank Habitat & 3.6. Spring and Flush Habitat (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution This vegetation occurs on both islands up to 400 m altitude (rare above 300 m).

Vegetation & Landscape Features On slopes with impeded drainage, in sheltered depressions and drainage lines of slopes, also on the banks of streams—vegetation dominated by the suffrutex *Acaena magellanica* and mosses (mostly *Brachythecium rutabulum, B. subplicatum* and *Sanionia uncinata*).

Geology, Soil & Hydrology Common on younger black lava and also on the sides of horsts formed by older grey lava, e.g. southern slopes of Skua Ridge. Soils are wet peat, sometimes with substantial volcanic ash.

Climate The complete plant cover restricts diurnal soil temperature fluctuations and the soils have never been observed to freeze.

Important Taxa (*Aliens) Graminoids: *Agrostis stolonifera** (d), *Poa cookii* (d). Herbs: *Acaena magellanica* (d), *Blechnum penna-marina*, *Montia fontana*, *Pringlea antiscorbutica*,

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Figure 15.15 ST 4 Subantarctic Drainage Line and Spring Vegetation: Moss-rich (*Breutelia integrifolia*, *Bryum laevigatum*) spring mire with abundant *Agrostis magellanica* at the Van den Boogaard River below Tafelberg on Marion Island.

best developed and show the greatest horizon differentiation of all the soils of the islands, and show some evidence of podsolisation; a dark brown or black A-horizon made up mainly of plant litter overlies a yellow-brown or yellow-grey loamy clay that sometimes contains red plinthic layers. The lower horizons of the soils are often gleyed.

Climate The *Blechnum penna-marina* fronds (10–18 cm long) are tightly packed vertically to form a thick carpet that protects the soil from insolation and radiative heat loss at night. Diurnal temperature variation is very small and the soils have never been observed to freeze.

Important Taxa Graminoids: *Agrostis magellanica*, *Poa cookii*, *Uncinia compacta*. Herbs: *Blechnum penna-marina* (d), *Acaena magellanica*, *Azorella selago*, *Grammitis poeppigiana*. Mosses: *Brachythecium rutabulum*, *Campylopus introflexus*, *Distichophyllum fasciculatum*, *D. imbricatum*, *Isopterygiopsis pulchella*, *Leptodontium gemmascens*, *Plagiothecium ovalifolium*, *Racomitrium lanuginosum*, *Sanionia uncinata*. Liverworts: *Acrobolbus ochrophyllus*, *Blepharophyllum densiflorum*, *Clasmatocolea humilis*, *Fossombronia australis*, *Jamesoniella colorata*, *Jensenia pisicolor*, *Lepidozia laevifolia*, *Leptoscyphus expansus*, *Lophocolea randii*, *Lophozia cylindriformis*, *Metzgeria decipiens*, *Plagiochila heretodonta*.

Biogeographically Important Taxa (endemics of Kerguélen Floristic Province) Herbs: *Elaphoglossum randii*, *Polystichum marionense*. Liverwort: *Symphyogyna marionensis*.

References Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001).

Ranunculus biternatus. Mosses: *Brachythecium rutabulum* (d), *B. subplicatum* (d), *Sanionia uncinata* (d), *Breutelia integrifolia*, *Leptodontium gemmascens*, *Orthotheciella varia*, *Philonotis polymorpha*. Liverwort: *Lophocolea randii*.

References Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001).

ST 5 Subantarctic Fernbrake Vegetation

Slope Complex (Huntley 1971). 4.5. Blechnum penna-marina Complex (Gremmen 1981). 3. Slope Complex p.p. (incl. Habitats 3.1 to 3.4) (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution Extremely common on both islands, occurs up to 300 m altitude but rare above 200 m. On Marion Island approximately 24% of the area below 100 m, and approximately 10% of that between 100 and 300 m, is occupied by fernbrake vegetation.

Vegetation & Landscape Features Almost all slope communities are dominated by the fern *Blechnum penna-marina*. Closed fernbrake, the climax slope community, consists of an almost pure carpet of the fern; an open fernbrake is found in more exposed or rocky localities, where the fern is co-dominant with *Azorella selago* and cushion-forming mosses; in wetter habitats on less steep slopes, graminoids (especially *Uncinia compacta, Poa cookii* and *Agrostis magellanica*) and bryophytes such as *Jamesoniella colorata* and *Racomitrium lanuginosum* occur, but the vegetation is still overwhelmingly dominated by *B. penna-marina*.

Geology & Soils Mainly on black lava flows, rare on grey lava. Soils are the

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Figure 15.16 ST 5 Subantarctic Fernbrake Vegetation: Lowland area on the eastern side of Marion Island showing the mosaic of fernbrake (dark green vegetation on slope) dominated by *Blechnum penna-marina* and mires (light green and brown flat areas in between the fernbrakes) dominated by graminoids *Agrostis magellanica, Juncus scheuchzerioides* and *Uncinia compacta* and liverworts such as *Jamesoniella colorata* and *Blepharidophyllum densifolium*.

ST 6 Subantarctic Fellfield

Wind Desert Complex p.p. (incl. *Azorella selago* fjaeldmark) (Huntley 1971). 4.6. *Andreaea–Racomitrium crispulum* Complex (Gremmen 1981). 2. Fellfield Complex (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution On both islands, dominant between 200 and 550 m altitude, although fellfield does occur at lower altitudes at exposed areas. On Marion Island ca. 33% of the area below 100 m, 72% of that between 100 and 500 m, and 15% of that above 500 m, is occupied by fellfield. Fellfield occupies around 46% of the total surface area of the island.

Vegetation & Landscape Features Dominated by *Azorella selago*, and frequently also by cushion- and ball-forming mosses. Several species grow on the *A. selago* cushions. By far the most common is *Agrostis magellanica* which may be co-dominant with *A. selago* in low-altitude fellfield. Crustose lichens are common. Total vegetation cover is from 5% to 50%, often more at lower altitudes.

Geology & Soils Fellfield occurs on both black and grey lava flows but is more common on the latter. Soils are more mineral than soils of any of the other vegetation types of the islands. They are generally skeletal but some are quite deep and consist of a matrix of organic matter (derived from *A. selago*) and volcanic ash.

Climate Fellfield occurs on rocky ridges and slopes that are very exposed to wind—this, with the sparse vegetation cover, means that the surface soil is subjected to frequent freeze-thaw cycles. On clear days soil surface temperature can rise to 15°C above air temperature.

Important Taxa ([A]Only in fellfield at altitudes below 250 m): Herbs: *Azorella selago* (d), *Acaena magellanica*[A], *Blechnum penna-marina*, *Colobanthus kerguelensis*, *Grammitis poeppigiana*, *Hymenophyllum peltatum*, *Lycopodium saururus*[A]. Graminoid: *Agrostis magellanica* (d). Mosses: *Andreaea acuminata*[A] (d), *A. acutifolia* (d), *Ditrichum strictum* (d), *Bartramia patens*, *Bucklandiella crispula*, *Catagonium nitens*, *Guembelia kidderi*, *Hypnum cupressiforme*, *Kiaeria pumila*, *Philonotis scabrifolia*, *Racomitrium lanuginosum*. Liverworts: *Herzogobryum vermiculare*, *Jensenia pisicolor*, *Jungermannia coniflora*, *Lepidozia laevifolia*, *Metzgeria decipiens*, *Plagiochila heterodonta*.

Biogeographically Important Taxa (endemics of Kerguélen Floristic Province) Moss: *Valdonia microcarpa*. Herb: *Colobanthus kerguelensis*.

Remark 1 The terms 'Fjaeldmark' (Warming 1887), 'Felsenfluren' or 'Felsentundra' (Schimper & Von Faber 1935) were originally applied to polar vegetation that is sparse and in which vascular plants, especially cushion-forming ones, are a conspicuous (even important) component of the vegetation. Here, the English equivalent 'Fellfield' (Warming 1909) is used.

Remark 2 Overall, fellfield occupies a smaller proportion of the total area of the mire-slope-fellfield mosaic than do mire or slope communities but its importance increases with altitude up to the upper limit of the mosaic, which is between about 200 and 250 m altitude depending on aspect and exposure. On grey lava horsts that extend to, or almost to, the coasts (Long Ridge, Skua Ridge, Stoney Ridge, Kerguélen Rise) these are dominated by fellfield with patches of very wet mire vegetation. They are here mapped as fellfield.

References Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001), Le Roux & McGeogh (2004), Le Roux et al. (2005).

ST 7 Subantarctic Cinder Cone Vegetation

Distribution On both Marion (approximately 130 cones) and Prince Edward Islands (14 cones).

Vegetation & Landscape Features Cinder cones are a prominent landscape feature. Most of them have no vegetation, but where the scoria is relatively stable, some sublithic mosses and hepatics (protected by the top layer of scoria fragments) may occur.

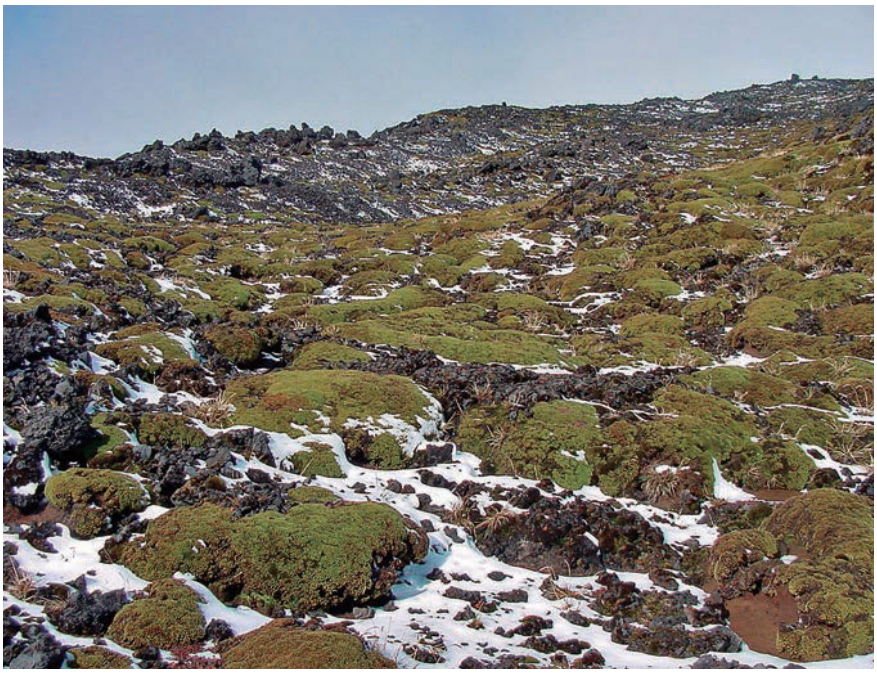
Geology Holocene cones of red volcanic ash (scoria) are a prominent feature on both islands, representing the centres of explosive eruption of the younger black lavas. The scoria consists of vesicular fragments from cm to dm in size, mostly loose but in some places welded into layers.

Climate The macroclimate of cinder cones is harsh due to wind exposure but the sublithic microclimate (high humidity and, on sunny days, warm temperatures) is favourable for bryophyte growth.

Important Taxa ([S]Sublithic) Mosses: *Catagonium nitens*[S], *Ditrichum conicum*, *D. strictum*, *Hypnum cupressiforme*[S]. Liverworts: *Acrobolbus ochrophyllus*[S], *Herzogobryum vermiculare*[S], *Lepidozia laevifolia*[S], *Metzgeria decipiens*[S], *Plagiochila heterodonta*[S]. Herbs: *Azorella selago* (d), *Colobanthus kerguelensis*, *Hymenophyllum peltatum*, *Pringlea antiscorbutica*.

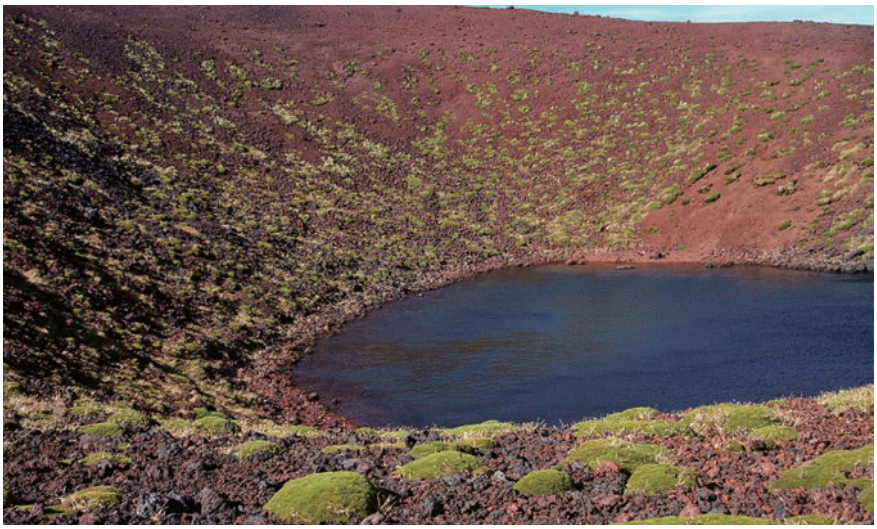
Remarks Gremmen (1981) considers this cryptic vegetation found on some cinder cones as a part of the fellfield (the *Andreaeo acutifoliae–Racomitrietum crispuli hypnetosum cupressiformis*).

Reference Gremmen (1981).



V.R. Smith

Figure 15.17 ST 6 Subantarctic Fellfield Vegetation: *Azorella selago* (large, green cushions) fellfield above Tafelberg on Marion Island, with *Ditrichum strictum* (small olive-green cushions) and the grass *Agrostis magellanica*. Peat and volcanic ash deposits are built up under the *Azorella* cushions.



L. Mucina

Figure 15.18 ST 7 Subantarctic Cinder Cone Vegetation: Sparse fellfield (with *Azorella selago* and *Agrostis magellanica*) and oligotrophic lake in the cinder-cone crater of Junior's Kop on Marion Island.

Polar Desert Biome

PD 1 Subantarctic Polar Desert

Wind Desert Complex p.p. (incl. *Ditrichum–Bartramia* montane desert) (Huntley 1971). 7. Polar Desert Complex (Smith & Steenkamp 2001, Smith et al. 2001).

Distribution On Marion Island polar desert occupies ca. 10% of the area below 300 m altitude, 32% of that between 100 and 500 m, and 98% of that above 500 m.

Vegetation & Landscape Features Mosses are the dominating plant group in this vegetation (*Andreaea acutifolia, A. regularis, Bartramia patens, Bucklandiella orthotrichacea, B. valdon-smithii*, *Dicranella gremmenii, Ditrichum strictum, D. subaustrale, Grimmia kidderi, Notoligotrichum australe, Philonotis scabrifolia* and *Valdonia microcarpa*). The moss cover is generally less than 2%; it may reach up to 50% or more in localities where snow-melt accumulates but such sites are very localised (seldom more than 2 or 3 m^2) and they are surrounded by large expanses (sometimes tens of hectares) of bare rock with only an occasional cushion-forming moss or crustose lichen. *Azorella selago* is the only vascular plant in the habitat but is infrequent, rarely attaining more than 2% cover and then only at altitudes below 650 m. It is absent above 800 m; lichens are mainly crustose forms and are much less common than in the fellfield habitats of lower altitudes (only a few have been identified).

Geology & Soils Polar desert is found mainly on the black lava flows since they are the dominant flows in the higher regions of the islands. There are no soils in polar desert; sometimes a thin, grit-like layer of volcanic ash occurs under and between the rocks, or the habitat may be found on large expanses of unconsolidated deposits of pebble-sized scoria with only the occasional rock or boulder on the surface; the scoria show various relict and active periglacial features and polar desert is dominated by physical, rather than biological, processes.

Climate Polar desert has the most extreme microclimate on the islands. The tops of the scoria layer are frozen almost every morning and the almost total absence of plants allows the same layer to reach high temperatures during periods of extreme sunshine. The free drainage and wind-drying (see notes below) make polar desert the driest habitat on the islands.

Important Taxa Mosses: *Ditrichum strictum* (d), *Andreaea acutifolia*, *A. regularis*, *Bartramia patens*, *Bucklandiella orthotrichacea*, *Guembellia kidderi*, *Hymenoloma antarcticum*, *Notoligotrichum australe*, *Philonotis scabrifolia*. Lichens: *Pannaria dichroa*, *P. hookeri*, *Placopsis bicolor*, *P.* cf. *cribellans*. Herb: *Azorella selago.*

Biogeographically Important Taxa (endemics of Kerguélen Floristic Province) Mosses: *Bucklandiella valdon-smithii*, *Dicranella gremmenii*, *Ditrichum subaustrale, Valdonia microcarpa.*

Remarks In terms of area, fellfield and polar desert are the dominant habitats on the two islands, perhaps less so in the case of Prince Edward due to its much lower topography. Truly, if any vegetation types can be said to be archetypical of Marion and Prince Edward Islands, it is the two—fellfield and polar desert—that most closely resemble northern hemisphere tundra vegetation, and not the luxuriant coastal plant communities which have so far enjoyed the lion's share of biological investigations at the islands.

References Huntley (1971), Gremmen (1981), Smith & Steenkamp (2001), Smith et al. (2001).

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Figure 15.19 PD 1 Subantarctic Polar Desert on the high plateau of Marion Island with mostly black scoria overlying permanent ice. Vegetation is extremely sparse, comprising a few cushion-forming moss species.

11. Credits

The introductory text to the chapter as well as most of the descriptions of the vegetation units were written by V.R. Smith, who also produced the first version of the vegetation map. L. Mucina contributed by shaping the concepts of some vegetation units to the lists of species and by describing vegetation units (ST 3, PD 1 and AZm 2) and by introducing some changes to the original map after a joint excursion with V.R. Smith to Marion Island in April–May 2004. Most of the photographs were supplied by V.R. Smith, some by L. Mucina.

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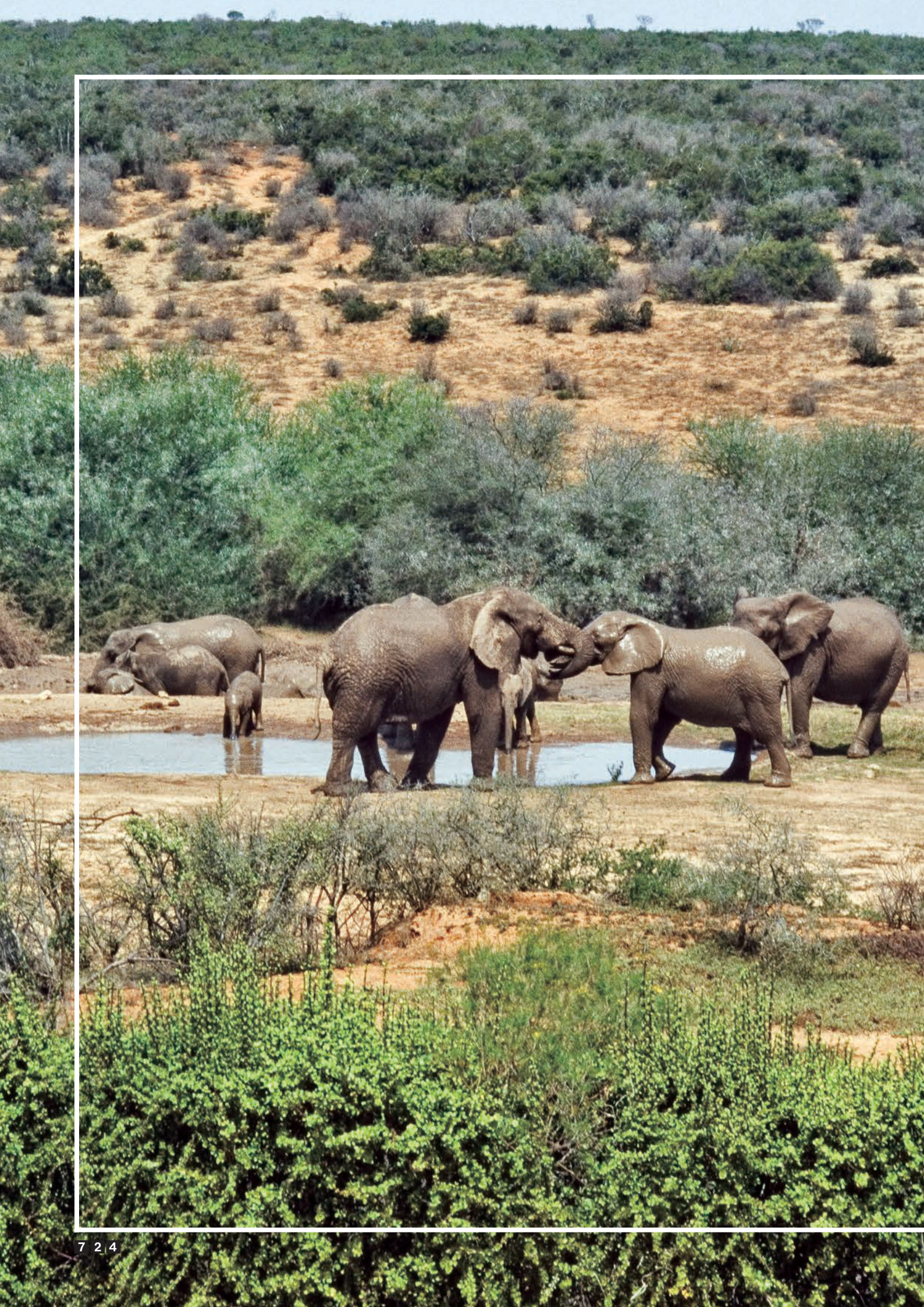

Ecosystem Status and Protection Levels of Vegetation Types

16

Mathieu Rouget, Zuziwe Jonas, Richard M. Cowling, Philip G. Desmet, Amanda Driver, Bulelwa Mohamed, Ladislav Mucina, Michael C. Rutherford and Leslie W. Powrie

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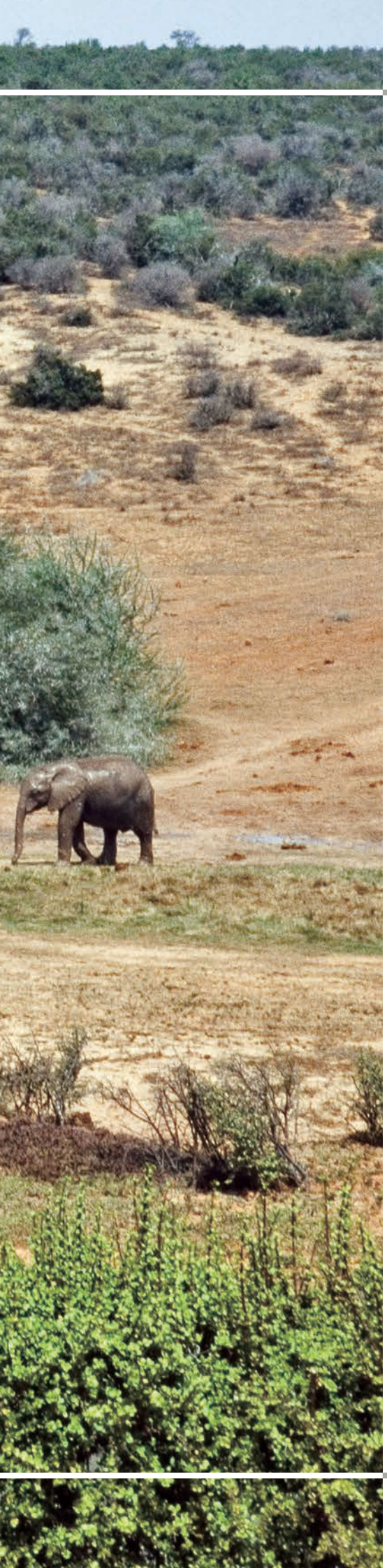

L. Mucina

Figure 16.1 The pride of South African nature conservation is the extensive and well-functioning network of statutory and private reserves and parks. One of the largest parks in the country–the Greater Addo Elephant National Park in the Eastern Cape–supports the last (albeit thriving) Cape population of African elephant (*Loxodonta africana*).

1. Introduction

The southern African region has a long conservation history—some of the first protected areas in the world were established in South Africa in the late 1880s. However, these were proclaimed with a strong focus on protecting hunting grounds and with limited concern for conserving biodiversity (Pringle 1982). As in many parts of the world, marginal areas unsuitable for agriculture or other land uses were set aside for conservation. Areas were proclaimed as protected areas for maintaining populations of large mammal species, for securing forest in the light of future afforestation, and for maintaining water catchments. In some instances, such conservation efforts had some detrimental effects on the vegetation (e.g. 'veld-improvement' or provision of water sources for the protection of large game; Rebelo 1992). A more detailed history of conservation areas and conservation planning is described in Rebelo (1997).

The protected area network has gradually increased over the last century to reach 7.93 million ha (6.25% of the land area) in 2005 (Figure 16.2). Most of the expansion occurred in the 1920s and 1930s through the addition of the Kruger National Park and then Kalahari Gemsbok National Park (today part of the Kgalagadi Transfrontier Park), and in the last 25 years. However, because biodiversity conservation was not the main rationale in selecting protected areas, the result is a protected area network that is not representative of the region's biodiversity.

Several reports (here referred to as conservation assessments) have highlighted the bias in protection levels across the region. The first assessment of the adequacy of protected areas in preserving South African vegetation types was realised in the 1970s (Edwards 1974). This assessment called for the protection of 5% of each vegetation type in formal reserves. Over the last 15 years, conservation assessments have evolved from ad hoc decisions to scoring approaches and lately to systematic approaches considering the issues of biodiversity representation and persistence. Recently, conservation planners have become more mindful of the challenges of implementing planning outcomes, resulting in innovative planning approaches that are implementation-oriented from the outset (Driver et al. 2003).

The approach used most often in South Africa (including in this assessment) to identify priority areas for conservation is referred to as systematic conservation planning (see Margules & Pressey 2000 and Driver et al. 2003 for more details). Systematic conservation planning is based on three key principles:

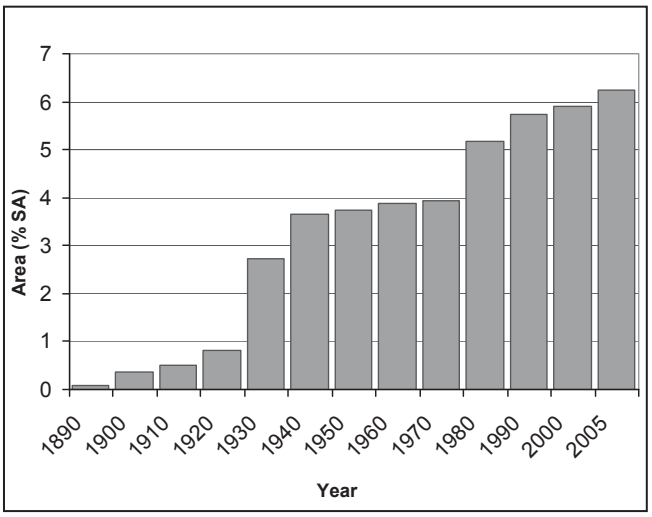

Figure 16.2 Expansion of protected area network (statutory and nonstatutory protected areas) in South Africa (SA) from 1890 to the present.

- The need to conserve a representative sample of biodiversity pattern, such as species and habitats (the principle of representation).
- The need to conserve the ecological and evolutionary processes that allow biodiversity to persist over time (the principle of persistence).
- The need to set quantitative biodiversity-based targets that tell us how much of each biodiversity feature should be conserved in order to maintain functioning landscapes. These targets should ideally be based on best available science, rather than on arbitrarily defined thresholds (such as 10% of all features).

In many parts of the world and especially in southern Africa, current conservation assessments include a wide array of features: various biodiversity features (biodiversity pattern, e.g. species and habitats and ecological and evolutionary processes), land use opportunities and constraints in order to lay the basis for successful implementation. For example, considerable attention is given to the use of conservation assessments in land use planning, extending biodiversity conservation beyond formally protected areas.

Through the series of conservation assessments (starting with Edwards 1974), several conservation priority areas have been identified such as the Cape lowlands, the central Grassland and the Succulent Karoo (Edwards 1974, Greyling & Huntley 1984, Jarman 1986, Rebelo 1997). However, the implementation of new protected areas or conservation measures has been limited to a certain extent (e.g. Jarman 1986, Rebelo 1994). Recently, major regional planning initiatives have been undertaken or are under way to implement conservation programmes, for example in the Cape Floristic Region (C.A.P.E.), the Succulent Karoo (SKEP), the Albany Thicket Biome (STEP), and in several South African provinces such as KwaZulu-Natal, Gauteng and Mpumalanga. Some of these have led to large multi-sectorial conservation programmes involving partnerships between government, civil society and the private sector.

As a signatory of the Convention on Biodiversity, South Africa is obliged to produce a National Biodiversity Strategy and Action Plan (NBSAP), which is currently being developed. The conservation assessment, which follows below, forms part of the spatial component of South Africa's first NBSAP. Systematic conservation planning methods used were based on comprehensive spatial information of biodiversity pattern and ecological processes, biodiversity targets, and current and future land use patterns. This provided an up-to-date assessment whose products are geared towards implementation, each accompanied by a set of guidelines and recommendations (see Driver et al. 2005).

Our assessment is in threefold. Firstly, we review the ecosystem status of the vegetation of South Africa, Lesotho and Swaziland, assessing the spatial pattern of current habitat transformation and relating this to biodiversity targets set for each vegetation type. Secondly, we review the adequacy of the current protected area network in representing all vegetation types. Conservation priorities are then identified on the basis of ecosystem status, protection levels and irreplaceability. The Prince Edward Islands were not subject to this analysis due to their status of Special Reserve (see chapter on Vegetation of subantarctic Marion and Prince Edward Islands).

The NBSAP biodiversity assessment used a relatively coarse-filter approach designed to identify areas that require a finer-scale assessment (if this has not already been done). Terrestrial conservation priority areas were identified on the basis of many biodiversity features including species (endemic and threatened

plants and animals), ecological and evolutionary processes (such as biota migration along the escarpment) and habitats (vegetation types) (Rouget et al. 2004). Here we focused on conservation priorities identified using vegetation types only, a reasonable surrogate for many biodiversity features in southern Africa (Lombard et al. 2003)[1].

2. Patterns of Current Habitat Transformation

Human activities can impact on areas of natural vegetation in various ways, from minor degradation to total conversion. Loss of natural habitat as a result of land uses such as agriculture, forestry, mining and urban development, remains the single most important threat to biodiversity (Wilcove et al. 1998). In southern Africa, and other developing regions, the natural vegetation is often partially degraded (albeit not completely cleared) by livestock grazing, soil erosion often following too frequent fires or by invasion by alien plants. Given the fact that approximately two thirds of southern Africa is used for extensive livestock farming, grazing is likely to have an important impact on the natural vegetation. However, mapping grazing impact over large areas is complex, especially in arid areas, and not enough spatial information is currently available to provide a proper assessment of grazing impacts on southern African vegetation types. This assessment focuses on irreversible loss of natural habitat as a result of croplands (including plantations), urban and rural settlements, mining and roads. The extent of alien plant invasions and habitat degradation was excluded due to lack of appropriate data at a national scale (see Box A). For this purpose, we used the National Land Cover (NLC), a comprehensive data source derived from 1996 satellite imagery (Fairbanks et al. 2000). We acknowledge that, due to the lack of spatial data on grazing impacts, as well as the fact that the NLC is not up to date, the impacts of human activities on the natural vegetation are far greater than is reflected here.

About 16% of the vegetation in South Africa, Lesotho and Swaziland has been irreversibly transformed (croplands: 14%, urban areas: 1.1%, roads: 0.5% and mines: 0.1%) (see Figure 16.3). Most habitat transformation has occurred in Gauteng, the Cape lowlands and the eastern seaboard, resulting in considerable differences in the spatial extent of habitat transformation between biomes and vegetation types. Fynbos and Grassland are the two biomes most severely impacted upon by human activities; almost 30% of their original extent is now covered by cropland, urban areas, mines or roads (Table 16.1). In contrast, only 5% of the Succulent Karoo and Nama-Karoo Biomes has been irreversibly transformed. Only two vegetation types have lost more than 90% of their original extent, and 11 more than 75% (Table 16.2). The large majority of vegetation types still comprise extensive areas of natural vegetation (although they could be heavily grazed or invaded by alien plants): 326 vegetation types (74.8%) still have 75% or more of their original extent intact.

Except for a few vegetation types, South Africa, Lesotho and Swaziland appear to have been marginally impacted by irreversible habitat transformation. However, habitat transformation is underestimated due to inaccuracies in mapping land uses and the lack of spatial information on habitat degradation. In many parts of southern Africa, it has been reported that habitat degradation due to alien plant invasion, overgrazing and harvesting of natural resources (wood, flowers, medicinal plants) had a far more extensive impact on vegetation than the transformation of natural habitat (Hoffman & Ashwell 2000; Box A). Degree of habitat fragmentation and alien plant invasion within vegetation types could not be taken into account (but see chapter on Vulnerability).

Pattern of habitat transformation among vegetation types can be used to crudely identify conservation priorities. Vegetation types that are already modified should ideally receive more conservation efforts than those relatively free of human activities because the former are currently more vulnerable to habitat fragmentation and degradation. For heavily transformed vegetation types, this could represent the last opportunity to conserve remaining fragments of natural vegetation and their associated species. However, other factors should be taken into consideration for identifying conservation priorities: biodiversity targets and protection levels (see below).

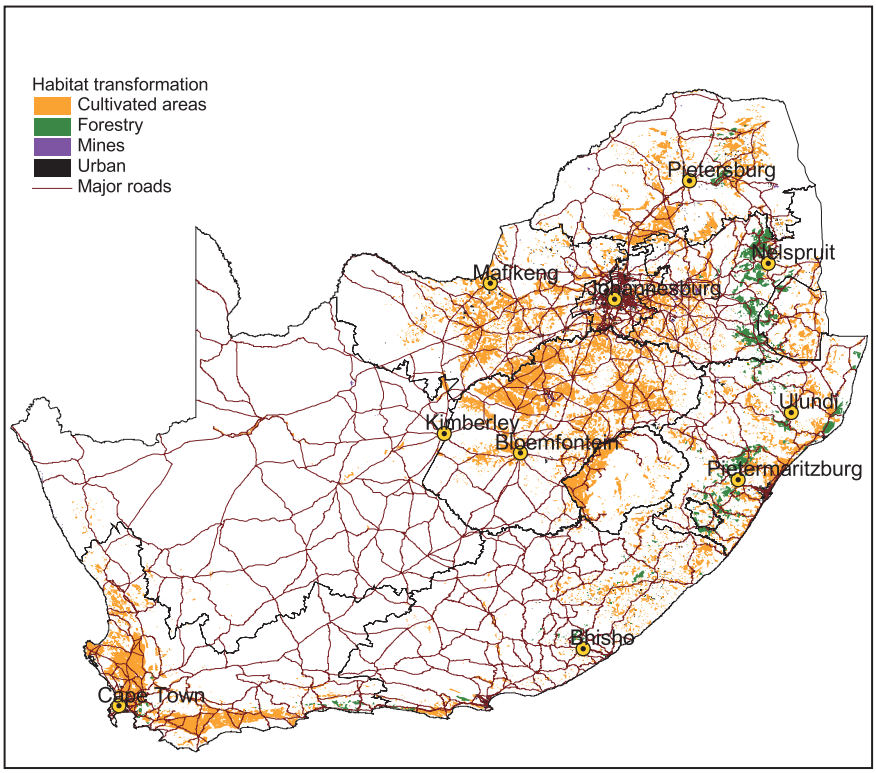

Figure 16.3 Extent of irreversible habitat transformation (cultivated areas, forestry plantations, mines, urban areas and roads) in South Africa, Lesotho and Swaziland. This map does not take habitat degradation, for example due to grazing or alien plant invasions, into account.

[1] The spatial components of the NBSAP also included freshwater, marine and estuarine conservation assessments using systematic conservation planning methods (for more on the spatial component of the NBSAP, please see Driver et al. 2005).

3. Setting Biodiversity Targets

Targets are an integral part of contemporary conservation planning, implementation and monitoring. Systematic conservation planning is dependent on explicitness, accountability and defensibility in identifying priority conservation areas (Margules & Pressey 2000). As a part of this, conservation targets underpin this process as they provide a clear purpose for conservation decisions, lending them accountability and defensibility (Pressey et al. 2003). Targets are basically quantitative interpretations of broad conservation goals that are established in policy, by experts, implementing agencies or other stakeholders (Margules & Pressey 2000, Pressey et al. 2003). For example, a conservation agency may specify that it wishes to conserve at least 10% of each vegetation type and three populations of each endangered species within its jurisdiction. Consequently, targets also provide a benchmark against which to measure the success of conservation action.

Table 16.1 Habitat transformation and protected status of biomes and azonal vegetation in South Africa, Lesotho and Swaziland. Only statutory reserves (national parks, provincial and local authority reserves) were considered.

Biome or azonal units	Area (km²)	% Total area	% Remaining	% Protected
Albany Thicket Biome	29 127.547	2.30	88.02	6.06
Azonal Vegetation	28 979.583	2.29	78.13	4.59
Desert Biome	7 166.443	0.57	99.16	14.56
Forests	4 731.407	0.37	94.08	16.73
Fynbos Biome	83 946.257	6.62	68.79	10.10
Grassland Biome	354 593.501	27.97	64.96	1.68
Indian Ocean Coastal Belt	14 282.489	1.13	50.71	1.54
Nama-Karoo Biome	248 278.626	19.59	97.65	0.61
Savanna Biome	412 544.091	32.54	77.06	8.75
Succulent Karoo Biome	83 283.976	6.57	94.64	2.93

Table 16.2 The ten vegetation types most impacted by irreversible habitat transformation (croplands, urban areas, mining and roads).

Vegetation type	Remaining (ha)	% Remaining	% Protected
Lourensford Alluvium Fynbos	491.1	8.88	4.2
Swartland Shale Renosterveld	47 369.9	9.58	0.5
Swartland Silcrete Renosterveld	1 015.9	10.17	0.6
Central Rûens Shale Renosterveld	27 004.0	13.42	0.4
Western Rûens Shale Renosterveld	16 545.4	13.90	0
Eastern Rûens Shale Renosterveld	53 161.2	19.20	0.4
Cape Flats Sand Fynbos	10 511.5	19.27	0.1
Elgin Shale Fynbos	5 817.5	20.82	5.9
Swartland Granite Renosterveld	20 259.2	21.38	0.6
Rûens Silcrete Renosterveld	4 644.6	22.14	0.1

Table 16.3 The range of conservation targets estimated for vegetation types and summarised per biome and azonal vegetation. Targets were estimated using the species-area relationship with the goal being the area required to represent 75% of species that occur within a vegetation type.

Biome or azonal units	Targets (%)		
	Average	Minimum	Maximum
Albany Thicket Biome	19.0	19	19
Nama-Karoo Biome	19.6	16	21
Indian Ocean Coastal Belt	25.0	25	25
Savanna Biome	19.9	16	25
Grassland Biome	24.9	23	28
Azonal Vegetation	24.7	16	34
Desert Biome	32.0	28	34
Succulent Karoo Biome	24.7	16	34
Fynbos Biome	28.0	23	36
Forests	62.3	30	100

So how can we set biologically meaningful quantitative conservation targets for Southern African vegetation types? While there are some studies dealing with a range of species (e.g. Travaini et al. 1997), minimum viable population (e.g. Burgman et al. 2001), meta population (e.g. Lindenmayer & Lacy 1995), genetic diversity (e.g. Ferguson et al. 1998), community (e.g. Prins et al. 1998), habitats (e.g. Turner et al. 1999) or ecosystem (e.g. Noss 1996) targets, there is generally a paucity of work dealing specifically with targets for vegetation types.

The widely used 10% target, recommended by IUCN, when applied to our vegetation types implies that all are equal in terms of their species diversity, abundance and distribution. Most would agree that this is certainly not the case. Desmet & Cowling (2004) discuss a more biologically relevant method for setting targets for vegetation types using the power form of the species-area relationship (SAR). The SAR describes in mathematical terms the basic observation that one observes more species as one samples a larger area. Using Equation 1 it is possible to predict the number of species observed if a given percentage of a vegetation type was sampled, provided that the z-value for the vegetation type was known:

Equation 1: $S = A^z$

Here S and A denote the proportion of species and area rather than absolute values. This equation can be reordered to address conservation targets to determine the proportion of area of a vegetation type required to represent a given percentage of species:

Equation 2: $A = z\sqrt{S}$ or $\log A = \log S/z$

Published z-values for biotas range between approximately 0.1 and 0.4 (Rosenzweig 1995). Although this range in the exponent is small, the nature of the power curve means that for a species target of 75% (i.e. we wish to represent 75% of species occurring in this vegeta-

tion type within a reserve network), the area target for the vegetation types ranges from 5% to 48%, respectively (Desmet & Cowling 2004).

SKEP and STEP projects all used vegetation survey data (phytosociological relevés) to estimate the z-values for Succulent Karoo vegetation types. The same method was used here to estimate z-values for all southern African vegetation types. The details of the method used to develop the conservation targets for South African vegetation types is discussed in more detail in Desmet & Cowling (2004) and Rouget et al. (2004).

Relevé data for South Africa were obtained from three geo-referenced phytosociological relevé databases, comprising over 17 000 relevés. There are more phytosociological datasets available for the region but these have either not been captured or geo-referenced.

For South African vegetation types, estimates of z-values range between 0.13 and 0.25. After considerable discussion it was decided that the goal for statutory reserves should be to represent at least 75% of species that occur in a vegetation type within at least one or more statutory reserves. Using Equation 2 this goal translates to conservation targets ranging between 11% and 30%, respectively (see Table 16.3). For forest vegetation types the targets were based on those set for the Forest Assessment Process (Berliner & Benn 2004) and not the species-area approach. Targets for forests range between 30% and 100%. As would be expected, areas of the country rich in endemic species or high levels of plant species diversity such as Fynbos, Succulent Karoo and some Grassland Biome vegetation types have higher representation targets (i.e. require more area to represent the same overall proportion of plant species). Some rare vegetation types such as forests also have high targets.

4. Ecosystem Status

The identification of conservation priorities, at a vegetation type level, should take into consideration at least the following factors: plant species diversity and turnover, habitat transformation and protection levels. Ecosystem status takes into account the first two, species diversity and turnover (through biodiversity targets), and habitat transformation. Ecosystem status aims at identifying threatened ecosystems (here vegetation types). It draws on the Red List classification scheme developed by the IUCN and borrows the familiar terminology applied to species, such as critically endangered (CR), endangered (EN), vulnerable (VU) and least threatened (LT). Focusing conservation efforts on threatened species is crucial for maintaining biodiversity. However, only conserving the natural habitats in which species occur will ensure species persistence. The identification of threatened ecosystems is aimed at addressing this. The recognition of threatened ecosystems by international organisations such as the IUCN and national governments could prove to be a very powerful conservation tool. It is envisaged that specific land use restrictions will be enforced in threatened ecosystems. In South Africa, the new Biodiversity Act (10 of 2004) provides for the Minister of Environmental Affairs and Tourism to list threatened ecosystems. Threatening processes in these ecosystems will be listed in terms of the National Environmental Management Act (107 of 1998) as activities that require environmental assessment.

Although the Biodiversity Act in South Africa allows for the listing of threatened ecosystems, it does not specify a standard approach for identifying them. The approach proposed here focuses on the retention of ecosystem functioning (such as pollination, nutrient cycling) and plant species diversity at the landscape scale. Vegetation types were classified based on the extent of remaining area (currently not transformed) of each

Box A: The extent of habitat degradation in South Africa

At least 8% of South Africa, Lesotho and Swaziland is invaded by alien plants (Versfeld et al. 1998). Over 700 alien plant species have become naturalised, 120 of which are considered as major invader plants, invading natural habitat (Nel et al. 2004). It is not clear whether some vegetation communities are more resilient to plant invasions than other, but some vegetation types have been heavily invaded. This applies to fynbos vegetation, thicket and highveld grassland (Rouget et al. 2002).

Loss of plant cover, change in species composition and bush encroachment are the major forms of habitat degradation in South Africa (Hoffman & Ashwell 2000). Loss of plant cover is the most important degradation problem in grasslands in the higher-rainfall eastern part of the country. Change in species composition occurs mostly in the dry west. Habitat degradation due to removal of woody species is widespread in shrubland and savanna woodland of the Limpopo Province (see Figure A1).

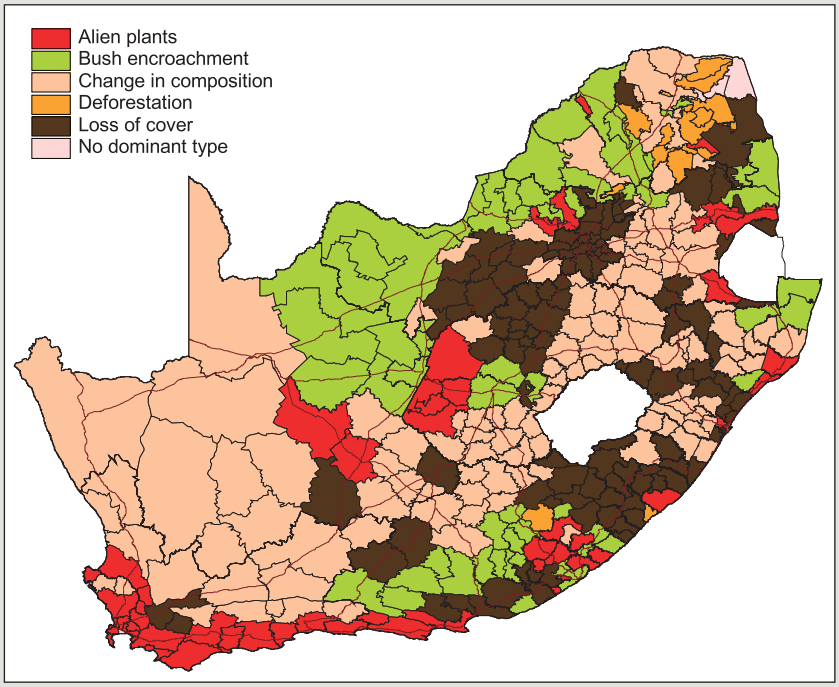

Figure A1 Types of habitat degradation perceived to be the first priority concern in each of the 367 magisterial districts—excluding Lesotho and Swaziland (from Hoffman & Ashwell 2000).

vegetation type in relation to its biodiversity target and thresholds for ecosystem functioning (see Figure 16.4). We recognise that our approach is very simplistic and that many other factors should be taken into account (such as habitat degradation). This represents one of the first attempts towards deriving an objective and defensible method for the identification of threatened ecosystems. It does not preclude the identification of additional threatened ecosystems based on, for example, an assessment of habitat degradation, when further spatial information becomes available. Similar assessments were conducted in the subtropical thicket biome (Cowling et al. 2003, Pierce et al. 2005) and in the United States based on the same factors (Noss et al. 1995).

Critically endangered vegetation types have been transformed to such an extent that the remaining habitat is less than that required to represent 75% of species diversity (i.e. the biodiversity target); in other words, one would expect species loss to take place in such vegetation types. Endangered vegetation types have lost up to 40% of their original extent and are exposed to partial loss of ecosystem function. Vulnerable vegetation types have lost up to 20% of their original extent, which could result in some ecosystem functions being altered (Figure 16.4). No significant disruption of ecosystem functioning is assumed in least threatened vegetation types, which still possess more than 80% of their original extent intact.

The status of two vegetation types could not be determined, namely Cape Vernal Pools and Pitketberg Quartz Succulent Shrubland (due to their small extent). Out of 433 vegetation types assessed, 19 are critically endangered, 53 endangered, 69 vulnerable and 292 least threatened.

Table 16.4 Critically endangered vegetation types in South Africa, Lesotho and Swaziland. These were identified based on extent of habitat transformation and biodiversity target. For all of them, the percentage of remaining natural habitat is less than the required biodiversity target set to represent 75% of the plant species present in each vegetation type.

Vegetation type	Biome or azonal units	Remaining area (%)	Target (%)	Protected (%)
Lourensford Alluvium Fynbos	Fynbos Biome	7	27	4.2
Swartland Shale Renosterveld	Fynbos Biome	9	27	0.5
Swartland Silcrete Renosterveld	Fynbos Biome	10	27	0.6
Central Rûens Shale Renosterveld	Fynbos Biome	13	30	0.4
Western Rûens Shale Renosterveld	Fynbos Biome	14	30	0
Elgin Shale Fynbos	Fynbos Biome	18	29	5.9
Cape Flats Sand Fynbos	Fynbos Biome	19	25	0.1
Eastern Rûens Shale Renosterveld	Fynbos Biome	19	32	0.4
Swartland Granite Renosterveld	Fynbos Biome	20	27	0.6
Rûens Silcrete Renosterveld	Fynbos Biome	22	32	0.1
Peninsula Shale Renosterveld	Fynbos Biome	23	25	18.7
Swartland Alluvium Fynbos	Fynbos Biome	25	27	1.7
Woodbush Granite Grassland	Grassland Biome	26	27	0
Cape Lowland Alluvial Vegetation	Azonal Vegetation	31	32	0.7
Swamp Forest	Forests	95	100	100
Mangrove Forest	Forests	96	100	46.9
Lowveld Riverine Forest	Forests	97	100	100
Sand Forest	Forests	98	100	100
Ironwood Dry Forest	Forests	100	100	100

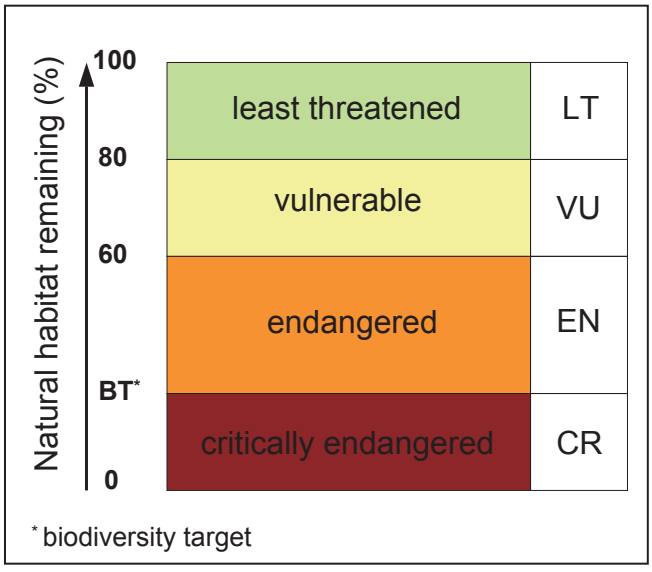

Figure 16.4 Classification of vegetation types into four levels of ecosystem status based on % of remaining untransformed area and the biodiversity target.

Due to the spatial bias of habitat transformation in South Africa, Lesotho and Swaziland (see Figure 16.3), critically endangered vegetation types, with the exception of forest types, are mostly concentrated in the Western Cape Province of South Africa (Figure 16.5). The forests and the Fynbos Biome have the greatest proportion of critically endangered vegetation types (see Figure 16.6). The Desert, Nama-Karoo and Succulent Karoo Biomes have the highest proportion of least threatened vegetation types. The grasslands have been considerably impacted by habitat transformation, and as a result, most of the grassland vegetation types are classified as endangered or at least as vulnerable (Figure 16.6). Critically endangered vegetation types are listed in Table 16.4.

It is unlikely that we have overestimated the ecosystem status of any vegetation type. However, the ecosystem status for some vegetation types is likely to be underestimated as habitat degradation was not taken into account. Many vegetation types currently classified as least threatened are degraded to a large extent. A more detailed spatial assessment of the extent of habitat degradation in southern Africa is required in order to derive a more accurate ecosystem status of vegetation types.

5. Protection Level

Currently, 6.25% of South Africa, Lesotho and Swaziland is under protection. This includes statutory reserves (national parks, provincial and local authority nature reserves) and nonstatutory reserves (such as mountain catchment areas and private nature reserves) with a much less secure conservation agreement. The conservation estate consists of 465 statutory protected areas (representing 77% of the total protected area) and 508 non-statutory protected areas (Figure 16.7). Only few protected areas are greater than 100 000 ha; most of them are between 1 000 and 10 000 ha (Figure 16.8). The implications of the size

of protected areas for conserving biodiversity have been discussed elsewhere (Schwartz 1999; see Rebelo 1997 for a review on southern Africa) and will not be addressed here. While concern has been raised that small protected areas might be inadequate for maintaining large-scale processes (such as natural fire regimes), they do play an important role in conserving some of the last remaining fragments of lowland vegetation types.

In assessing the protection levels of vegetation types, it would be ideal to include some measure of management effectiveness within protected areas. However, it is unlikely that we will ever have a national dataset that provides widely endorsed information of this kind. In the absence of information about management effectiveness, legal status and ownership must suffice as a way of distinguishing categories of protected areas.

With only 6.2% of the land protected, most of South Africa, Lesotho and Swaziland is not adequately conserved (Figure 16.9). As biodiversity and protected areas are not uniformly distributed in the landscape, huge gaps appear in the protected area network. In terms of biome representation, the Forest, Fynbos and Desert are the most protected biomes (in terms of percentage of total area), while the Nama-Karoo and Grassland are the least protected biomes (Table 16.1). An assessment of the protection levels of each vegetation type in relation to their biodiversity targets reveals that 116 vegetation types have no form of protection at all (Figure 16.9). It is important to note that this assessment focuses on representation of biodiversity pattern, and that larger areas will be required for conserving critical ecological and evolutionary processes. Furthermore, an additional 79 vegetation types, with only < 5% of their biodiversity target protected, are hardly protected. More than 300 vegetation types have less than half of their biodiversity target conserved in statutory protected areas. Only 65 vegetation types have their biodiversity targets met in statutory protected areas, including 24 types of Fynbos, 24 of Savanna and seven of Grassland.

In order to meet the biodiversity targets for all vegetation types, at least an additional 215 000 km^2 would have to receive some form of conservation action. This amounts to 20% of the remaining natural habitat in South Africa, Lesotho and Swaziland.

Protection level can and should inform priorities for the establishment and expansion of protected areas. Based on the principle of representation, vegetation types not adequately represented in the current protected area network should receive priority attention. However, we need to note strongly that the establishment of formal protected areas is not the only form of conservation action possible. Especially in vegetation types that are highly fragmented, conservation action may include, for example, working with industry and local government to ensure conservation-friendly land use in priority areas. Used in conjunction, measures of ecosystem status and protection level are very useful for identifying priority vegetation types in need of conservation action of some kind. Ecosystem status tells us which vegetation types are most threatened, while protection level tells us which vegetation types are least protected. For example, it is clear that the Knysna Sand Fynbos or the Rûens

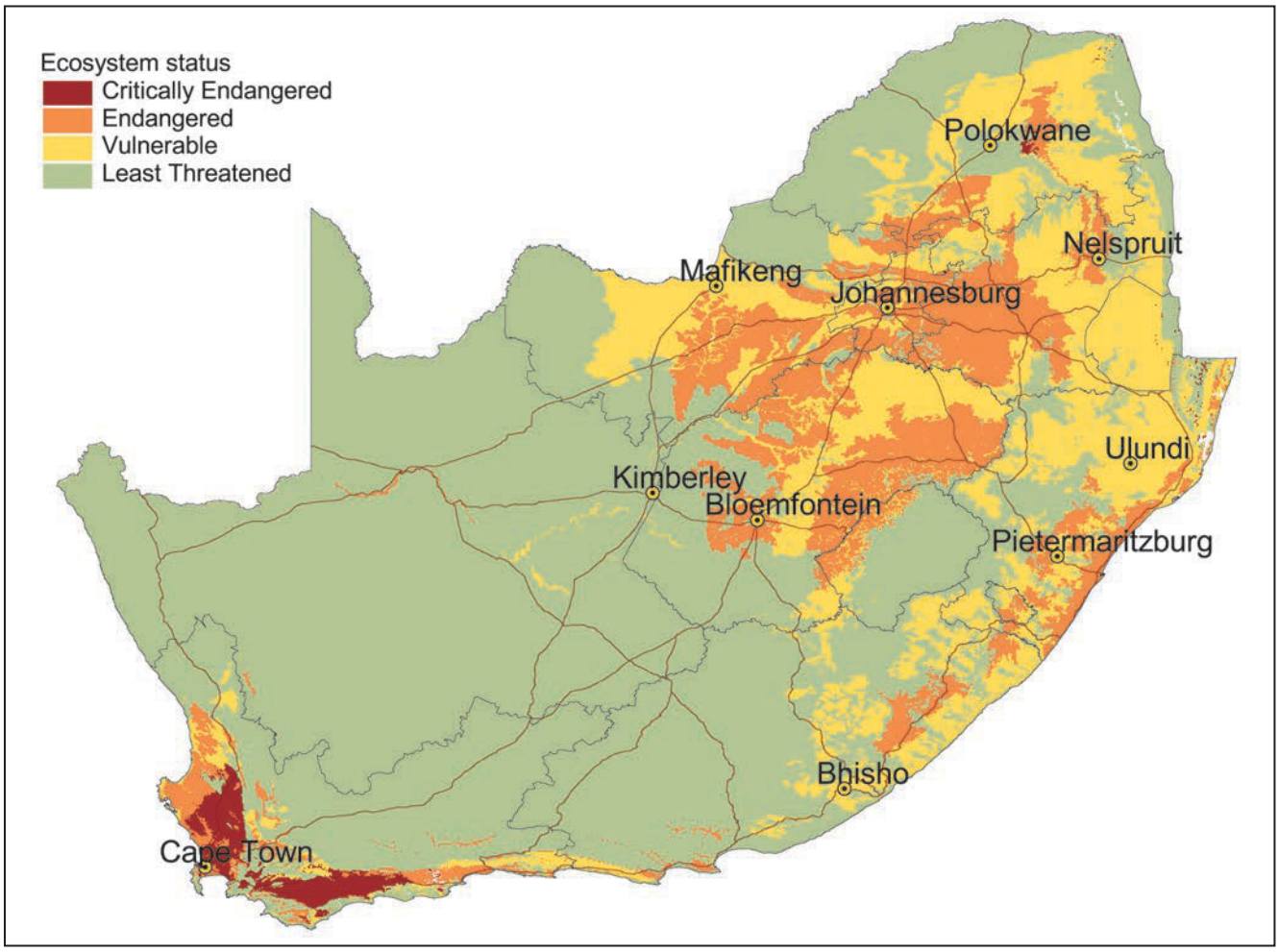

Figure 16.5 Ecosystem status of vegetation types. Vegetation types were classified into critically endangered (CR), endangered (EN), vulnerable (VU) and least threatened (LT) based on habitat transformation pattern and biodiversity targets.

Silcrete Renosterveld, which are critically endangered *and* not represented in the current protected area network, have not received adequate conservation efforts.

However, while the implementation of conservation plans can take quite some time and when conservation budgets are limited, scheduling of conservation actions becomes important. It has been proposed that scheduling should consider a measure of conservation value and vulnerability to future land use pressures (What is the likelihood of losing this area of natural vegetation in the near future?) (Pressey & Taffs 2001; see chapter on Vulnerability).

6. Conservation Priorities

Setting conservation priorities is a complex task (see Box B). One has to integrate biodiversity pattern and process as well as consider future pressures due to other land uses. Few conservation

Box B: Species or land class biodiversity features?

Conservation targets can be divided into two broad categories based on the scale of biodiversity surrogate targeted (Pressey et al. 2003). Coarse-filter approaches set targets for features such as vegetation types, ecosystems or land-classes. Fine-filter approaches use species or populations as the focal feature for conservation action. While the two approaches are complementary, for most regions limitations in species distribution datasets obligate the use of coarse-filter surrogates (Lombard et al. 2003).

Vegetation or land-class maps, such as this vegetation map, have the advantage of covering the entire landscape, thereby eliminating the inherent spatial and taxonomic bias of species datasets (Lombard et al. 2003). There are limitations when using such maps. Firstly, reserve selection using the coarse-filter approach is likely to protect many species for which records are deficient or are yet to be discovered. However, unless complementary fine-filter information is incorporated in the process, other species, especially rarer ones, are likely to be missed (Kirkpatrick & Brown 1994; Lombard et al. 2003). Secondly, the spatial, land-class compositional or process requirements of certain species are unlikely to be satisfied unless specifically targeted. Thirdly, land classes do not explicitly target natural processes. These need to be targeted separately if biodiversity is to persist (Cowling et al. 1999; Cowling & Pressey 2001).

These problems are compounded by problems relating to scale. Targets framed as percentages of countries or regions can be achieved while failing to protect the natural features most urgently in need of protection (Pressey et al. 2003). Large regions are heterogeneous in terms of biodiversity and potential for anthropogenic transformation. Conservation areas have often been relegated to the least useable portions of regions, thereby avoiding areas where past impacts on biodiversity have been greatest and future threats are most serious (Pressey et al. 2000, Scott et al. 2001). This is true even of regions with overall percentages under formal protection equal to or greater than 10%. Also, coarse-scale maps do not capture all possible land-class combinations, so even if vulnerability over the whole area is low, certain landscape biodiversity features (e.g. rare vegetation types or habitats) can fall through the cracks. These issues can be addressed by mapping at finer scales and with improved mapping techniques (Ferrier et al. 2002). Targeting better mapped land types with classes that are more homogeneous in terms of biodiversity and land use potential, limits the potential for conservation action to miss capturing all biodiversity (Bedward et al. 1992). To this end the new vegetation map represents a more fine-scale interpretation of the vegetation patterns, and more broadly, biodiversity patterns encountered within Southern Africa.

Mindful of these limitations, it must be accepted that for most areas on this planet, land-class maps of some sort will be the primary biodiversity feature used for conservation and land use planning.

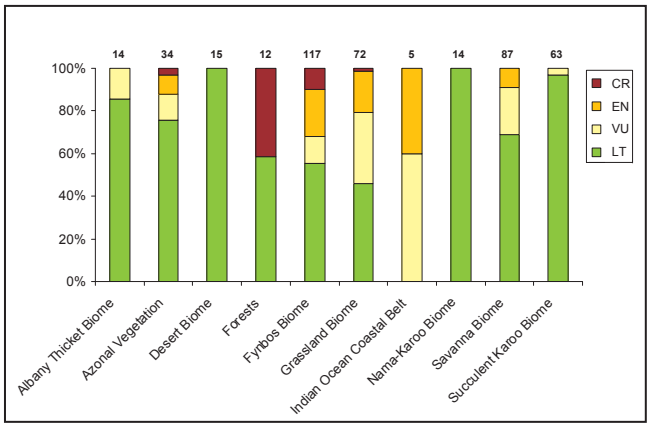

Figure 16.6 Proportion of critically endangered (CR), endangered (EN), vulnerable (VU) and least threatened (LT) vegetation types per biome. The number of vegetation types present in each biome and in azonal vegetation is indicated on top of the bars.

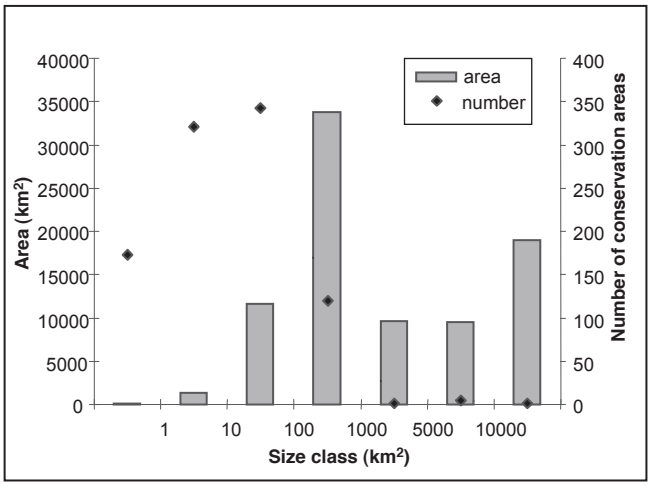

Figure 16.8 Size-class distribution of the protected area network for South Africa, Lesotho and Swaziland.

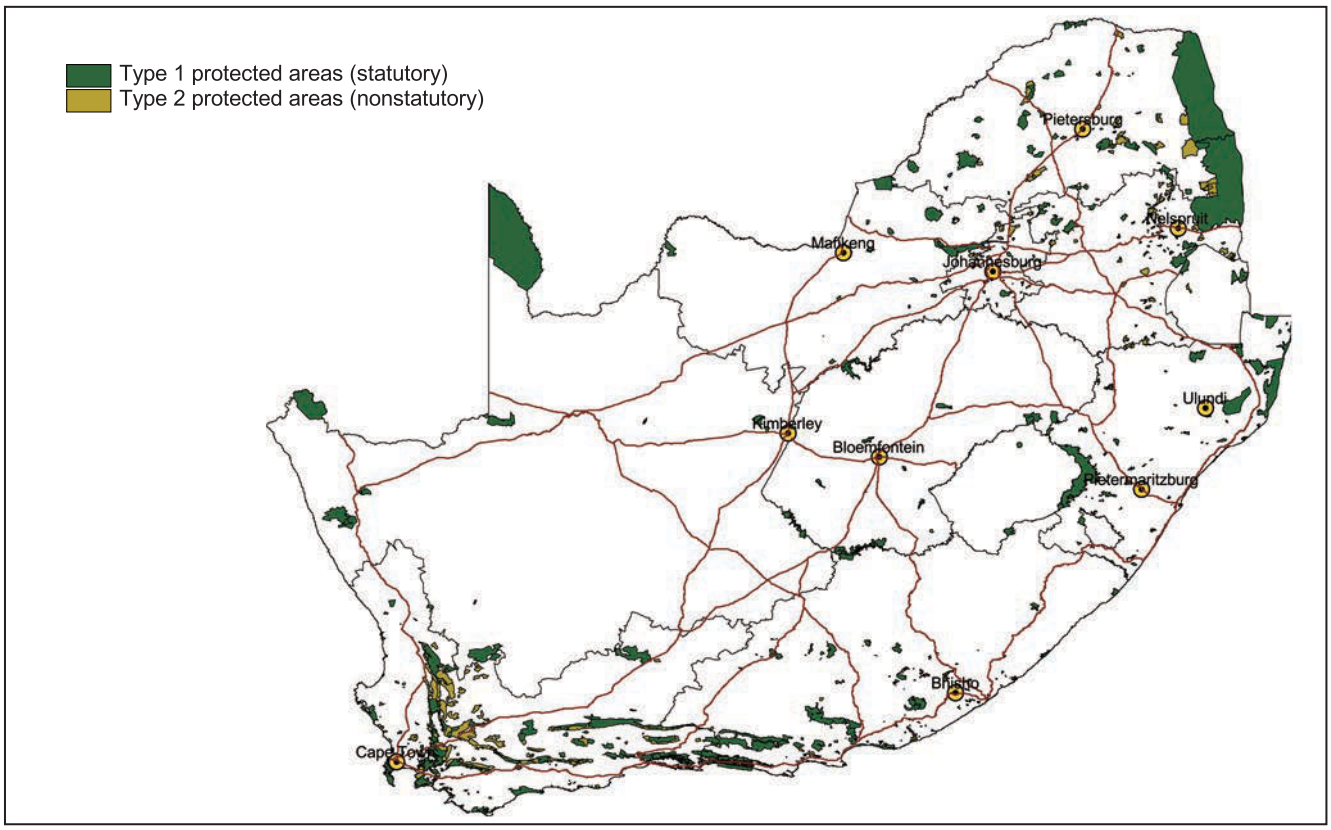

Figure 16.7 Protected area network in South Africa, Lesotho and Swaziland. Protected areas are classified into two types: statutory (type 1) and nonstatutory (type 2) based on ownership and legal status.

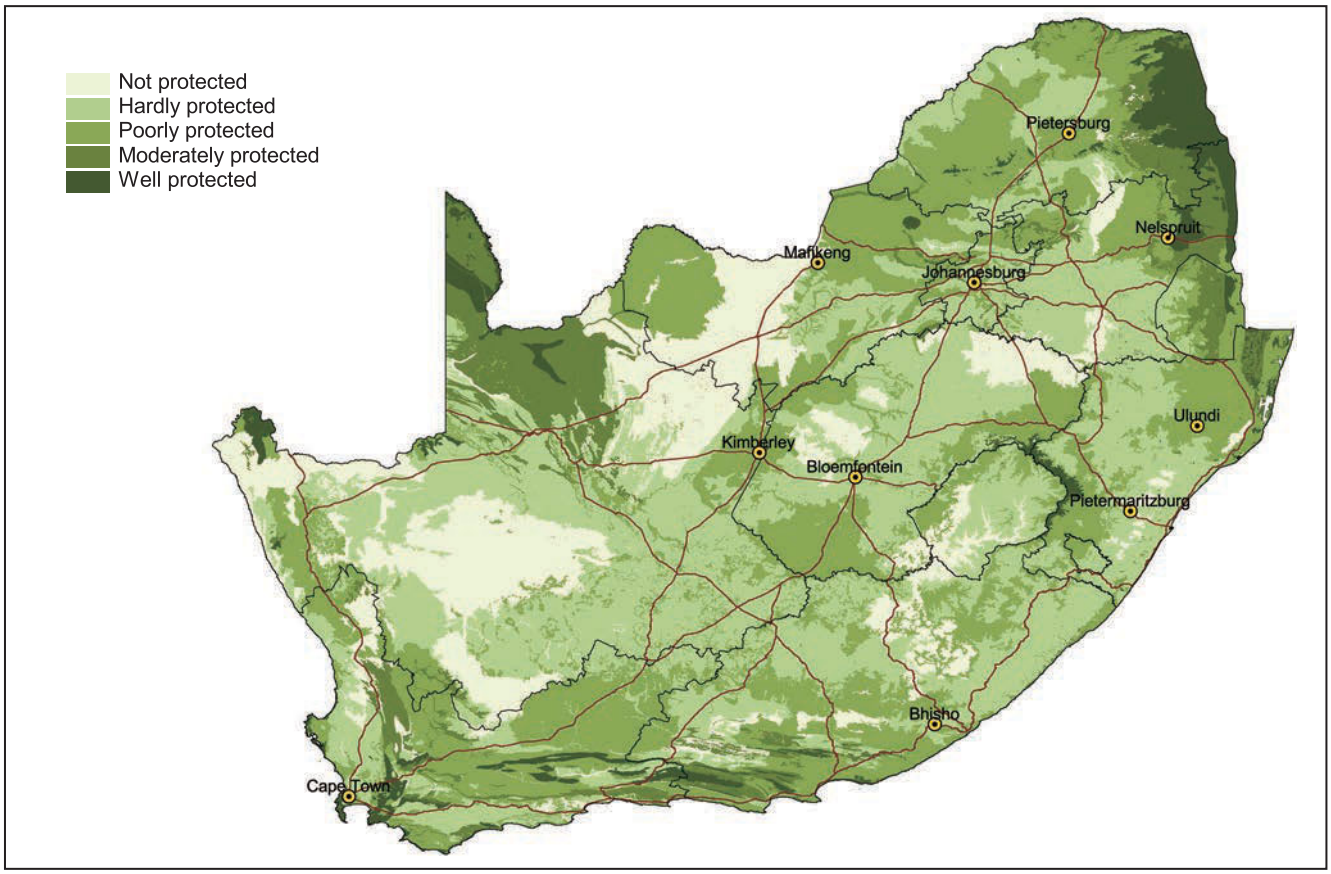

Figure 16.9 Protection levels of vegetation types based on the proportion of biodiversity target set for each vegetation type represented in statutory protected areas. Not protected (0% of biodiversity target protected in statutory protected areas), hardly protected (< 5% of the biodiversity target protected), poorly protected (< 50% of the target protected), moderately (< 100% of the target protected), well protected (biodiversity target protected in statutory protected areas).

assessments have managed to do this successfully. Trade-offs tend to occur as areas required for achieving pattern and process often do not overlap. Therefore different geographical priority areas can be identified by focusing on habitats, species of special concern or biodiversity processes.

In the National Spatial Biodiversity Assessment (NSBA, see Driver et al. 2005), due to the mismatch of scale between the various analyses (e.g. ecosystem status at the vegetation type scale, habitat irreplaceability at a sixteenth-degree scale, species irreplaceability at a quarter-degree scale), all analyses could not be combined into one overall 'irreplaceability' measure. A scoring system was developed whereby each separate analysis (e.g. ecosystem status, species irreplaceability) was scored. This enables one to combine all these analyses and identify priority areas for habitat, species and processes. Multi-criteria approaches, when used in conservation assessments, have been criticised because they are often not systematic and do not satisfy the principle of representation or persistence. The products of the NSBA (ecosystem status, protection levels of ecosystems, analysis of species of special concern, and national-scale ecological processes) are systematic and fulfil the goals of representation and persistence. The NSBA simply used a scoring approach for prioritising areas based on systematic conservation assessment products. As there is a potential danger of mixing criteria of different kinds together in a scoring approach, priority scores (and priority areas) were first identified for habitat, species and process separately, and then combined to identify overall priority areas. The priority areas thus identified are also priority areas for habitat, species or process, and not an area averaging medium score for all criteria.

Here we focus on priority areas identified for habitat only (i.e. vegetation types). One should bear in mind that other areas might be crucial for maintaining ecological and evolutionary processes (see Figure 16.10), or for species representation.

We combined three analyses to identify priority areas for habitat: ecosystem status, protection levels and irreplaceability (see Box C). Irreplaceability quantifies the contribution of a site to achieve biodiversity targets, in other words, to ensure the representation of biodiversity features (Ferrier et al. 2000). Irreplaceability values range from 0 (site not required to achieve biodiversity targets) to 1 (irreplaceable site, target cannot be achieved without it). We calculated irreplaceability values based on biodiversity targets set for vegetation types, wetlands and estuaries (see Box C). We used sixteenth-degree squares (approximately 4 400 ha) to calculate irreplaceability.

Ecosystem status was scored from 0 to 100 as follows: critically endangered vegetation types were assigned a score of 100; endangered vegetation types, 75; vulnerable vegetation types, 50; and least-threatened vegetation types, 25. Protection levels of ecosystems were scored as follows: well-protected vegetation types (100% or more of the target is achieved in statutory protected areas) were assigned a score of 0; nonprotected vegetation types, 100; and for other vegetation types, the score was 100 minus the percentage target achieved in statutory protected areas (e.g. if a vegetation type has 10% of its biodiversity

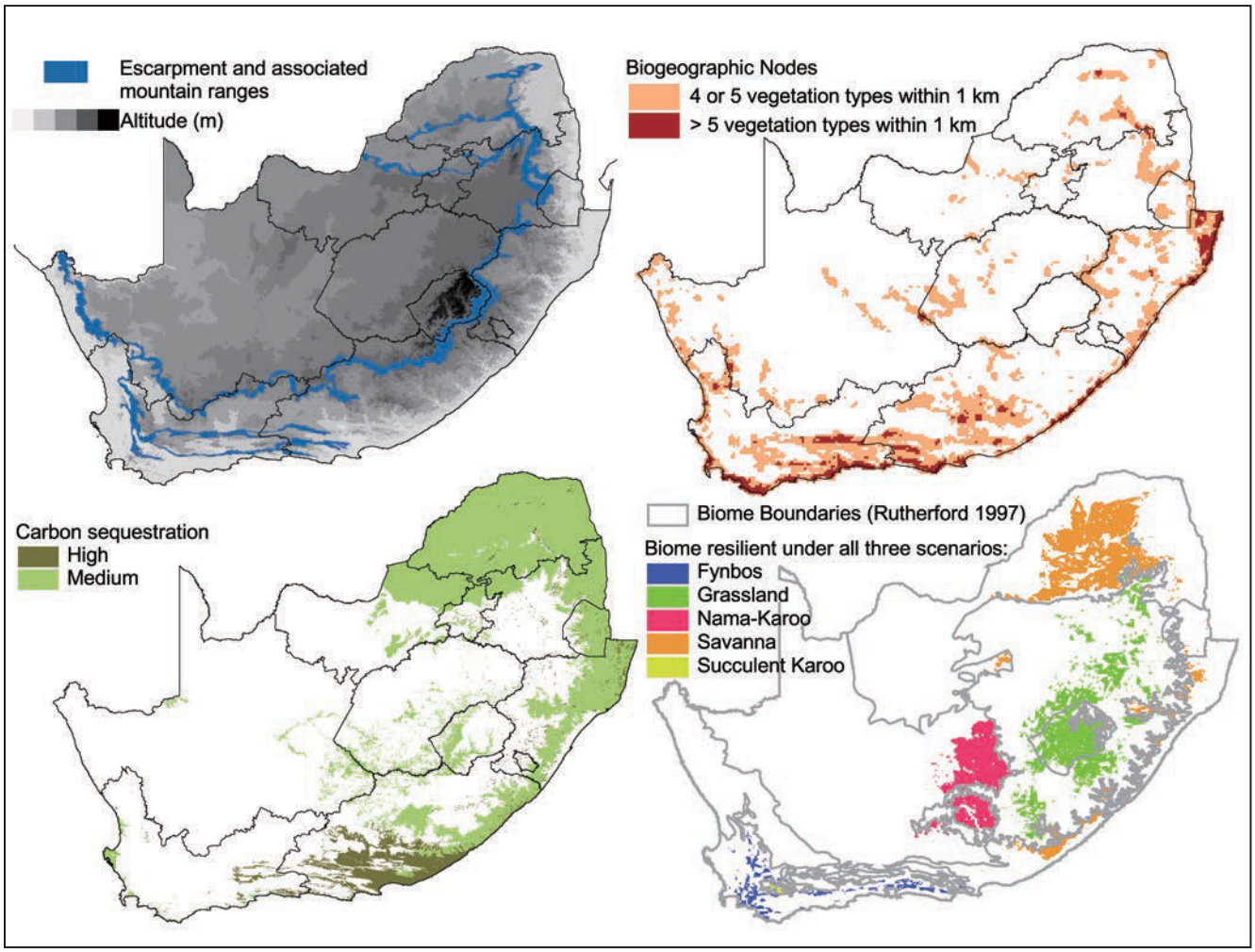

Figure 16.10 National-scale ecological processes, represented by (a) the Great Escarpment and associated mountain ranges, (b) biogeographic nodes, (c) carbon sequestration areas and (d) areas of biome resilience to climate change.

Box C: Irreplaceability analysis for vegetation types, estuaries and wetlands

The concept of representation underpins most conservation assessments (Margules & Pressey 2000, Driver et al. 2003). Conservation planners seek to identify areas that will represent an appropriate sample (defined by the biodiversity targets) of each biodiversity feature. Irreplaceability quantifies the contribution of a site to achieve biodiversity targets, in other words, to ensure the representation of biodiversity features (Ferrier 2002). Irreplaceability values range from 0 (site not required to achieve biodiversity targets) to 1 (irreplaceable site, target cannot be achieved without it).

The irreplaceability measure applies to sites (and not directly to biodiversity features).

Based on vegetation types (and estuaries and wetlands from a separate study, see table below), we calculated irreplaceability values for the 31 130 planning units using the software C-Plan (Ferrier et al. 2000).

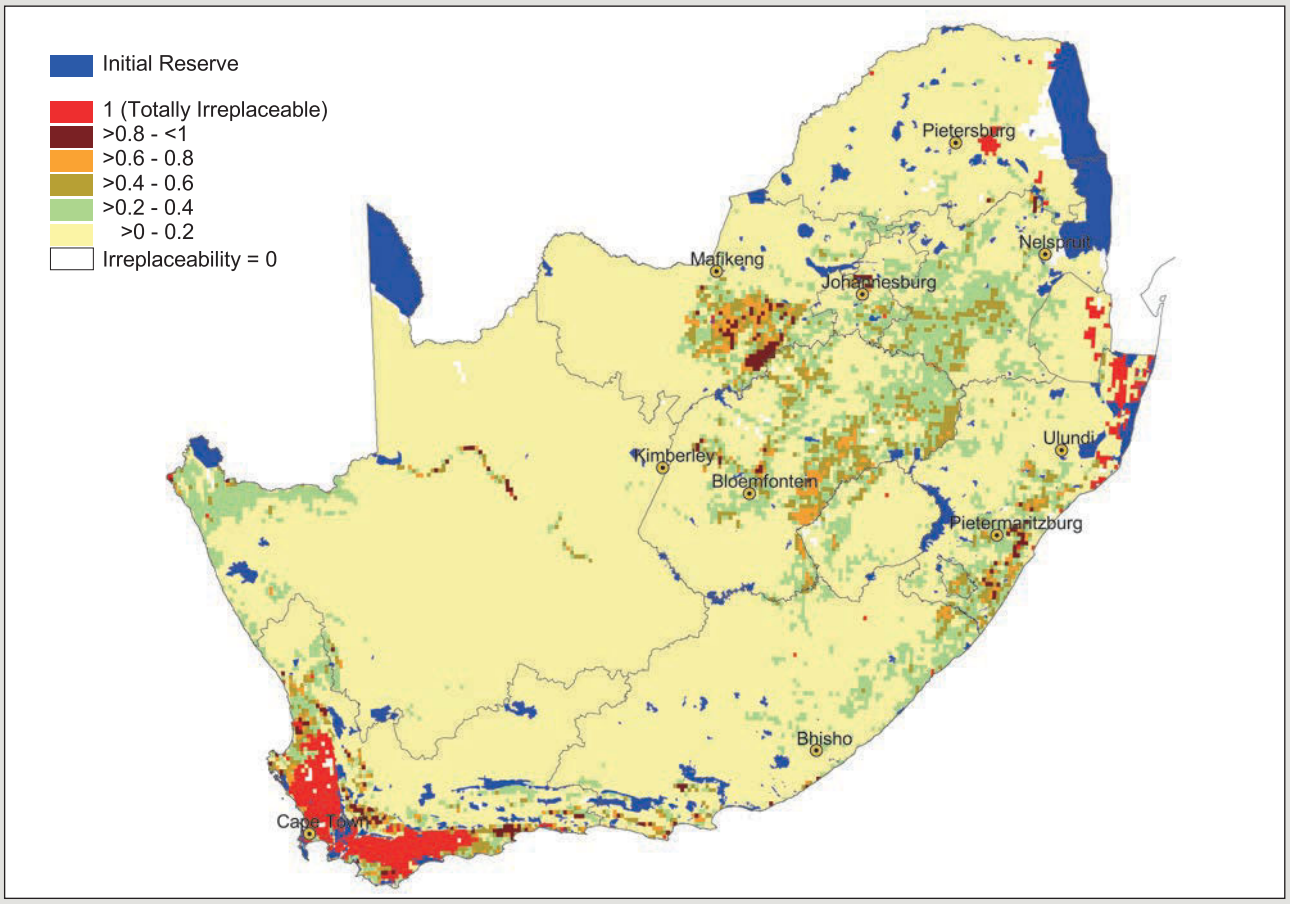

Figure C1 Irreplaceability pattern for vegetation types, estuaries and wetlands.

Most of South Africa's land surface appears to have low irreplaceability values (< 0.4), meaning that there are still many options for achieving biodiversity representation targets for many vegetation types (or estuaries or wetlands) (Figure C1). 790 sites representing 1% of South Africa's remaining habitats are irreplaceable. A further 0.6% has high irreplaceability values (> 0.8). A site could be irreplaceable for two reasons: (a) severe habitat transformation has reduced the amount of remaining habitat close to the target (the case for critically endangered vegetation types); and/or (b) the biodiversity target is quite high (the case for some forest or estuary types). Options to achieve biodiversity targets are limited in places where habitat transformation has been most severe (see Figure C1 and compare it with Figure 16.3). In other words, our ability to achieve biodiversity representation targets is influenced more by habitat transformation than the biodiversity target itself.

List of biodiversity features included in the irreplaceability analysis (SANBI, South African National Biodiversity Institute; DEAT, Department of Environmental Affairs and Tourism)

Biodiversity feature	Source	Number	Target range
Vegetation types	SANBI	438 types	12–100% of original area
Estuaries	DEAT	16 types	At least 3 or 20% of each type
Wetlands	DEAT	17 types	At least 3 or 20% of each type
Wetlands & estuaries of significant importance	DEAT	1 type	100%

target achieved in statutory protected areas, the score was 90). For habitat irreplaceability, we applied the following score to each planning unit: 100 × irreplaceability value.

Due to different scales, all layers were converted to a grid of sixteenth-degree cell size to match the planning unit layer. Each cell was assigned a score for ecosystem status, protection levels and irreplaceability. These three scores were averaged and ranged from 0 to 100 (maximum score for all three criteria). Priority areas for habitat conservation were defined as cells where the average score was greater than 60.

Figure 16.11 shows the priority areas identified for conserving biodiversity at the habitat level. Three main priorities emerged: the Cape lowlands (lowland part of the Southwest Fynbos Bioregion, and the West Coast Renosterveld and East Coast Renosterveld Bioregions), the central grasslands (Mesic Highveld and Dry Highveld Grassland Bioregions), and part of the Indian Ocean Coastal Belt and the Sub-Escarpment Savanna Bioregion in KwaZulu-Natal. Most of the Nama-Karoo Biome appears least transformed. However, this could be due to the lack of fine-scale spatial information on habitat degradation.

These habitat priority areas differ from those identified on the basis of species distribution pattern or ecological processes (see Driver et al. 2005). On the basis of habitat alone, the Succulent Karoo and the Albany Thicket do not emerge as a priority. However, both are national priority areas identified by the National Spatial Biodiversity Assessment (Driver et al. 2005).

7. Conclusion

What are the implications of these results for conservation action in South Africa, Lesotho and Swaziland? Perhaps the main implication is that conservation action cannot be limited to the establishment or expansion of 'traditional' large protected areas. Clearly, protected areas represent a major conservation instrument and we need more (in the Grassland Biome for example), but they might not be appropriate in every situation. The remaining natural habitat in critically endangered and endangered ecosystems is likely to be fragmented and situated in a matrix of productive agricultural, industrial and urban land uses, making the establishment of protected areas impractical. This means that the conservation sector needs to engage proactively with industry, civil society and local government in areas where there are concentrations of critically endangered and endangered ecosystems. Curtailing further loss of natural habitat in these areas, and the associated loss of ecosystem functioning and species, will involve making the case to major land users and decision-makers that retention of biodiversity is part of maintaining national ecological infrastructure. It could involve the development of industry-specific biodiversity guidelines, in close partnership with industry bodies, to guide decisions about how land is used and managed. The incorporation of spatial biodiversity priorities into land use planning and environmental assessment processes at municipal and provincial level can provide a powerful way to protect critically endangered and endangered ecosystems.

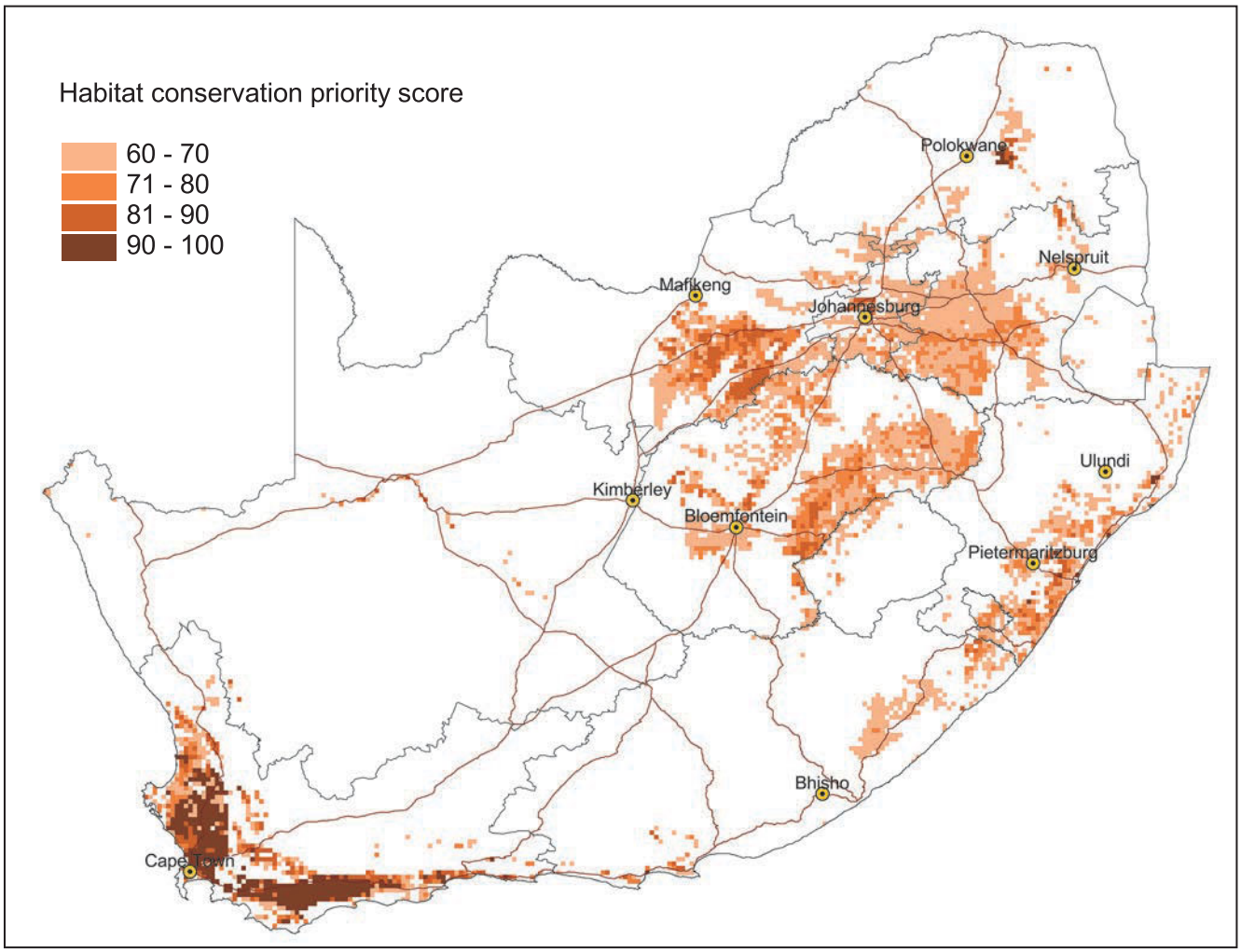

Figure 16.11 Priority areas for conserving habitat based on ecosystem status, protection levels and irreplaceability surface. The colour gradient refers to the priority score.

8. Credits

The unpublished version of the vegetation map used for this analysis was provided by M.C. Rutherford and L. Mucina. The GIS data were provided by L.W. Powrie. Some tables and figures were adjusted for presentation by L.W. Powrie. The National Land Cover was provided by the CSIR, and information on protected areas by DEAT and all provincial conservation agencies. Biodiversity targets were calculated by P.G. Desmet and R.M. Cowling. Most analyses were performed by Z. Jonas and M. Rouget. B. Mohamed assisted with some GIS analysis. M. Rouget was the lead author and R.M. Cowling, P .G. Desmet and A. Driver provided substantial input and editing on earlier drafts. P.G. Desmet wrote the section on targets. L. Mucina and M.C. Rutherford provided final editorial comments. Valuable scientific and technical input was received from conservation planners who were involved in the National Spatial Biodiversity Assessment.

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Vulnerability Assessment of Vegetation Types

17

Zuziwe Jonas, Mathieu Rouget, Belinda Reyers, Bulelwa Mohamed, Michael C. Rutherford, Ladislav Mucina and Leslie W. Powrie

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Figure 17.1 A small patch of shale fynbos surrounded by expanding upmarket suburbs in Gordon's Bay (Western Cape) at the foot of the Hottentots Holland Mountains. Populations of two local proteoid endemics (*Leucospermum bolusii* and *Paranomus spicatus*) share this vacant lot with other rare fynbos flora.

L. Mucina

1. Introduction

Humans have transformed almost half of the world's land surface area into agriculture and urban systems (Chapin et al. 2000). The most severe biodiversity loss occurs when a natural ecosystem is converted to an artificial system (Geneletti 2003). This does not only affect ecosystems by altering their composition and processes, but also has important consequences for water supply and other ecosystem services upon which humans depend (Kunin & Lawton 1996, McCann 2000). Land conversion can be due to several causes, e.g. agriculture, urbanisation, road development and deforestation. When the land is converted from a natural or semi-natural state to one of these forms of land cover, many species are unable to persist (Dale et al. 1994) as a result of direct and indirect loss of habitat.

Mapping expected future loss of natural habitat or ecosystem function can be very useful in scheduling implementation of conservation actions. Focusing first on areas of high biodiversity value that are also highly vulnerable to future habitat loss or degradation is usually recognised as the most effective way to minimise biodiversity loss (Pressey 2004).

South Africa is one of the top 25 countries in the world in terms of biodiversity (WCMC 1992), with a greater part of its biodiversity occurring on agricultural land than in current conservation areas. Due to the expansion of cropland or urban areas, some of that biodiversity will be lost in the near future (Wessels et al. 2000).

Few studies done at different scales have outlined the land use pressures in South Africa (Wessels et al. 2003). This assessment focuses on the potential loss of natural habitat due to habitat transformation and degradation processes, which will threaten the biodiversity of the area. These processes can be land use-related where untransformed areas with a high suitability to a particular land use (e.g. cultivation, afforestation) are highly vulnerable. In these areas, not only natural habitat will be lost, but the species composition can also be completely altered. Alternatively these processes may be linked to the modification or degradation of biodiversity pattern and processes of an area (e.g. alien invasion and habitat fragmentation). These processes may not necessarily lead to complete loss of natural habitat, but do modify the composition of an area sufficiently to threaten ecosystem function.

We refer to the potential loss of natural habitat or ecosystem function defined above as vulnerability. In this assessment, two classes of vulnerability are referred to as *land use vulnerability* (population growth, land capability—dryland agriculture, afforestation and mining) and *degradation vulnerability* (habitat fragmentation and alien plant invasion). Vulnerability was summarised for each vegetation type.

The objective of this chapter is to describe the relationship between biodiversity pattern (defined by 433 of the 435 mainland vegetation types—two were too small for analysis), landscape structure and land use pressures in natural habitats of South Africa and to interpret this relationship in terms of vulnerability.

2. Approach

In this assessment we used several databases (see Box A) to quantify the vulnerability of vegetation types to a suite of future pressures in order to identify vegetation types of concern. We mapped and quantified land use vulnerability based on land capability, afforestation potential, mining potential and population growth. We also mapped and quantified degradation vulnerability based on habitat fragmentation and alien plant invasion. Fine-scale habitat degradation (related to over-grazing, bush encroachment, over-harvesting of natural resources) has not been mapped comprehensively for South Africa. The only information available was the assessment done by Hoffman & Ashwell (2000) at a district level. Due to the coarse scale, this could not be used for assessing the degradation status of vegetation types. However, such information can be used at the scale of the priority areas identified by the National Spatial Biodiversity Assessment (Driver et al. 2005).

All the vulnerability layers were rasterised using a 100 m cell size. For each vulnerability type, vulnerability was scored from 0 (not vulnerable) to 100 (highly vulnerable). Each layer thus had a very low vulnerability class (0–25), a low vulnerability class (25–50), a medium vulnerability class (50–75) and a high vulnerability class (75–100). Care was taken to ensure that all re-scaled values represented the original vulnerability classes well.

In order to produce one layer on vulnerability across the country, we needed to combine these various datasets. All the datasets, with the exception of the mining potential, were continuous datasets and could therefore be combined arithmetically. Combining multiple threats raises several challenges, e.g. whether an area susceptible to more than one threat is more vulnerable than one susceptible to only one threat.

We produced two sets of vulnerability indices. One was an average vulnerability score for each 100 × 100 m grid cell across the country based on all vulnerability layers. This product would thus highlight areas vulnerable to a large number of future pressures. For areas currently untransformed within each vegetation type, we calculated the average score for each vulnerability type (degradation and land use). The degradation vulnerability layer was derived using the average per grid cell of the alien plant invasion and habitat fragmentation layers (see later in Habitat Fragmentation section). Land use vulnerability was derived using the average per grid cell of the land capability, afforestation and population change layers. An overall vulnerability index was calculated by averaging land use and degradation vulnerability. Vulnerability to climate change was not considered.

The second was a map of all areas in the country, which are highly vulnerable to any threat. This highlights highly vulnerable areas irrespective of the number of pressures. The raster layers produced for each type of vulnerability were used to extract areas of high vulnerability to any pressure. Pixels with a vulnerability of higher than 75 for afforestation, land capability, mining, population change, habitat fragmentation and alien plant invasion were extracted and combined to produce maps of high future pressures. Vulnerability to land use and to habitat degradation were differentiated.

In order to identify the degree of vulnerability of each vegetation type, we then summarised the average vulnerability value and the percentage of the natural area under high pressure per vegetation type.

3. Land Use Vulnerability

3.1 Land capability

Land capability reflects the land suitability to crop production and also to other less intensive uses such as pasture, natural grazing, forestry and wildlife (see Figure 17.2). Land capability was modelled based on soil and terrain features and climate of an area. Low nutrient status was not considered a limitation,

Box A: Description of the databases used to derive vulnerability layers in South Africa.

Several databases on vulnerability are available in South Africa at a national scale. These databases were investigated and either selected for the analysis or discarded based on characteristics in the database. Table A1 provides a list of these databases and reasons for their selection or rejection.

Table A1 Various datasets used in the vulnerability assessment.

Database	Source	Description	Limitations	Used
Land use vulnerability				
Land capability	ARC (ISCW)	Total suitability for use, in an ecologically sustainable way, for crops, grazing, woodland and wildlife	Mapped at a broad scale	Yes
Grazing potential	CSIR	Areas which have the potential to support a similar number of herbivores per unit land area	Does not imply pressure unless poorly managed	No
Afforestation	CSIR	Potential for pine and eucalypt species based on bioclimatic variables	Only mapped for some provinces (LP, MP, KZN, EC, WC)	Yes
Mining	Council for Geoscience	Mapped mineral deposits, fields, layers and provinces	Categorical data	Yes
Population growth	StatsSA	Change in population density per municipality from 1996 to 2001 census products	Broad units of municipalities	Yes
Degradation vulnerability				
Fragmentation				
Landscape resistance	NLC	Incorporates connectivity and surrounding land uses		Yes
Extent of natural habitat	NLC	Area of untransformed habitat		Yes
Fragment size	NLC	Size of remaining habitat		Yes
Plant invasion	SANBI/ CSIR	Numbers of alien invasive species that could occur in a region		Yes
Degradation	Hoffman & Ashwell (2000)	Soil and vegetation degradation per magisterial district	Very broad units for vegetation analysis	No

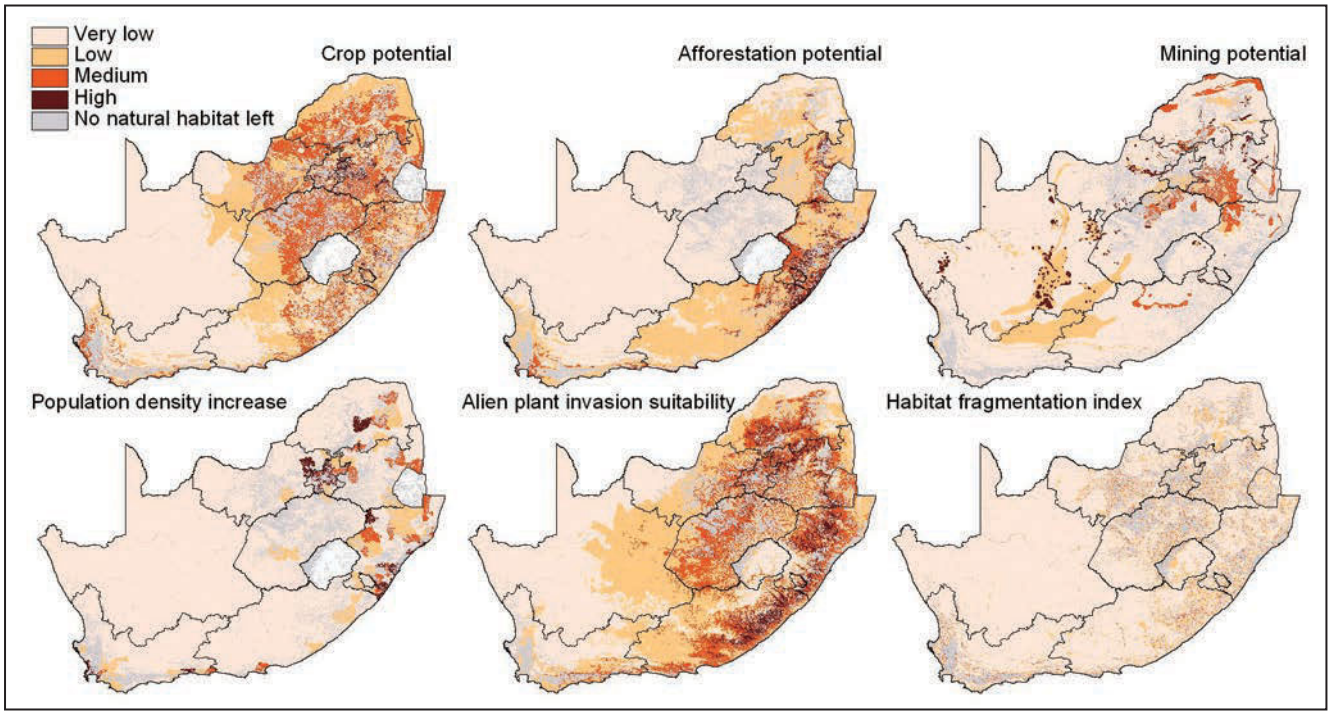

Figure 17.2 Vulnerability to future land use change (crop potential, afforestation potential, mining potential, population density increase) and habitat degradation (alien plant invasion suitability and habitat fragmentation index) in South Africa.

since it is assumed that inherent nutrient deficiencies/toxicities will be rectified by appropriate liming and/or fertilisation. The land capability classification system applies only to rain-fed agriculture. Land suited to crop production is also suited to other less intensive uses such as pasture, natural grazing, forestry and wildlife. Most of the conversion of natural habitats with a high agricultural production potential to cultivated areas took place in the last 50 years and has considerably reduced the extent of several vegetation types. These vegetation types are mostly communities of the Grassland Biome (Macdonald 1989) and Renosterveld shrublands of the Western Cape, which presently occupy a fraction of their original range (Heydenrych & Littlewort 1995).

Land capability potential, averaged per vegetation type, varies quite considerably. Out of 433 vegetation types, 189 vegetation types have very low land capability; 180 vegetation types, low; 64 vegetation types, medium; and no vegetation types have high land capability. The top six vegetation types that are under medium land capability pressure include the Eastern Highveld Grassland, Tembe Sandy Bushveld, Swartland Alluvium Renosterveld, Maputaland Wooded Grassland, Western Maputaland Sandy Bushveld and Makatini Clay Thicket.

3.2 Afforestation Potential

Afforestation is the planting of trees for commercial purposes, usually on land supporting non-forest veld types, e.g. grassland or fynbos. Afforestation potential maps were modelled using fuzzy tolerance models, based on bioclimatic parameters. The bioclimatic factors used in these models were soil, rainfall and temperature (Fairbanks 1995). Although these maps were only generated for five provinces in South Africa, these provinces were found to coincide well with the areas suitable for wood production across southern Africa and thus the layer could be used in a national assessment. Each 1 km^2 grid was assigned an average suitability value for pine and eucalypt species. These values ranged from 0 (low suitability) to 100 (very high suitability) (Figure 17.2).

Natural habitats most severely affected by current afforestation include wetlands, grasslands, fynbos and indigenous forests (Heydenrych & Littlewort 1995). Based on this afforestation model (see Figure 17.2), 238 vegetation types have very low afforestation potential; 136 vegetation types, low; 52 vegetation types, medium; and seven vegetation types have a high afforestation potential. The top six vegetation types highly threatened by afforestation are the Pondoland-Ugu Sandstone Coastal Sourveld, Mangrove Forest, KwaZulu-Natal Sandstone Sourveld, Southern KwaZulu-Natal Moist Grassland, Midlands Mistbelt Grassland and Northern Escarpment Afromontane Fynbos.

3.3 Population Density Change

Due to the lack of data on urban and peri-urban sprawl in South Africa, we decided to use the change in population density as an indicator of human pressure. Data from the national censuses in 1996 and 2001 were used for this purpose. Both datasets were aggregated to the municipality level from the original enumerator areas. The difference in population between the two census periods was used to calculate the change in population density. This change in density is mostly related to the movement of people across the country towards urban areas, as well as natural population growth. Each municipality was thus assigned a value of the change in population density, which ranged from 19 to 356 people per km^2 and re-scaled from 0 to 100 (Figure 17.2).

From this assessment, 343 vegetation types occur in areas with very low population growth, 71 vegetation types in areas with low population growth, 12 in areas with medium population growth and seven in areas with high population growth. The top six highly threatened vegetation types are the Egoli Granite Grassland, Peninsula Granite Fynbos, Peninsula Shale Renosterveld, Peninsula Sandstone Fynbos, Lourensford Alluvium Fynbos and Cape Flats Sand Fynbos.

3.4 Mining Potential

No layer was readily available for mapping mining potential; Box B describes how we used mining resource field to map and categorise mining potential. Mining potential was determined based on the accuracy of the deposit mapping, its size, and the type of commodities. For example, areas of high mining potential consist of large mines/deposits or mineralised fields for 13 economically important commodities (Figure 17.2).

Mining potential is concentrated in few parts of the country (such as the West Coast) with only 2.1% of the whole country (1.8% of the untransformed natural habitats) under high mining potential.

Due to its categorical nature, mining potential could not be averaged per vegetation type. Instead we calculated the percentage of the untransformed area of each vegetation type of high mining potential. There are 195 vegetation types with no mining potential. A total of six vegetation types have 50% of their natural area occurring in medium mining potential areas and another four have 50% of their natural area occurring in high mining potential areas (see Table 17.1). The vegetation types most vulnerable to mining are: Namib Seashore Vegetation, Richtersveld Coastal Duneveld, Northern Escarpment Dolomite Grassland and Subtropical Seashore Vegetation.

Box B: Mining potential in South Africa.

The mining dataset was obtained from the Council for Geoscience.

It includes mineral points subdivided into two types, namely mines and mineral deposits. Mines can be dormant mines, continuously producing (active) mines, abandoned mines and intermittently producing mines. The mineral deposits can be exploited or unexploited. The dataset also contains information on mineralised fields (areas of high concentration of commodity) and mineralised provinces (broad areas where a given commodity occurs) as well as mineralised layers (veins of high concentration of commodity–linear feature).

Mines and deposits were buffered by 500 m and the mineralised layers by 1 000 m (less accurate).

The mining potential was determined based on the accuracy of the deposit mapping, its size and the type of commodities.

We considered four types of deposit mapping (arranged from high spatial accuracy to low):

- Mines and deposits (500 m radius).
- Mineralised layers (1 km buffer).
- Mineralised fields (high concentration of commodity).
- Mineralised provinces (broad area where commodity occurs).

The commodities were classified into two groups, namely economically important and other minerals. The minerals of economic importance (13) were obtained from the website of the Council for Geoscience. Table B1 lists the 13 minerals of economic importance in South Africa.

Table B1 Minerals of economic importance in South Africa.

Mineral	Symbol
Gold	Au
Platinum Group Metals	Pt
Diamonds (alluvial & kimberlite)	Da, Dk
Chromite	Cr
Manganese	Mn
Vanadium	V
Titanium	Ti
Zirconium	Zr
Antimony	Sb
Aluminum Silicates	Al
Coal	C
Fluorspar	F
Vermiculite	Vm

Table B2 illustrates how we classified mining potential into three categories: high, medium and low. We associated areas where an economically important commodity (such as gold) occurs in large deposits/mines, or where a mineralised field/layer of such commodity was mapped.

Table B2 Criteria used to map mining potential in South Africa.

Category	Type	Commodity
High	Large deposits/mines OR Mineralised fields/layers	Economically important
Medium	Medium mines OR Mineralised provinces	Economically important
	Large deposits/mines	Other
Low	Small deposits/mines OR Mineralised layers/fields/ provinces	Any

Table 17.1 Top vegetation types with high or medium mining potential in South Africa, ranked from the highest to the lowest potential. Percentage of the vegetation type area with high and medium mining potential is shown.

Vegetation types	% High	% Medium
Namib Seashore Vegetation	100	0
Richtersveld Coastal Duneveld	76	0
Northern Escarpment Dolomite Grassland	66	0
Subtropical Seashore Vegetation	53	0
Arid Estuarine Salt Marshes	49	0
Namaqualand Seashore Vegetation	0	0
Wakkerstroom Montane Grassland	0	90
Nwambyia-Pumbe Sandy Bushveld	0	84
Eastern Highveld Grassland	0	71
Springbokvlakte Thornveld	0	61
Soweto Highveld Grassland	0	60
Delagoa Lowveld	0	53

4. Degradation Vulnerability

4.1 Habitat Fragmentation

We considered three elements to derive the habitat fragmentation layer at landscape level. These were the surrounding land use (matrix resistance), the average fragment size and connectivity (distance between natural fragments). The first aspect is based on the assumption of different species movement to land cover types, by relating the species movements between different land use types to the resistance value. Landscape resistance thus represents the difficulty of a species to cross a certain land use type (Nikolakaki 2004). The approach is described in Box C. An overall habitat fragmentation index was derived by averaging the three aspects (Figure 17.2).

From this assessment, 244 vegetation types occur in areas with very low habitat fragmentation, 171 vegetation types in areas with low habitat fragmentation, 16 in areas with medium habitat fragmentation and two in areas with high habitat fragmentation. Highly fragmented vegetation types (last quartile of overall habitat fragmentation index) are listed in Table 17.2. The analysis of average fragment size separated vegetation types that are naturally fragmented (i.e. very small fragment size but high percentage extent) from those that have been fragmented due to anthropogenic change (i.e. very small fragment size and low percentage extent). For example, vegetation types such as Northern Afromontane Forest are naturally fragmented.

Table 17.2 Total number of highly fragmented vegetation types (11). Habitat fragmentation was quantified in terms of extent of habitat fragmentation (extent value), resistance to species movement (resistance value) and average fragment size (fragment size). The overall habitat fragmentation index ranged from 0 (not fragmented) to 85 (highly fragmented).

Vegetation types	Extent value	Resistance value	Fragment size	Overall index
Lourensford Alluvium Fynbos	91.0	82.7	80.5	84.8
Swartland Silcrete Renosterveld	96.7	57.0	72.7	75.5
Cape Lowland Alluvial Vegetation	90.4	43.4	57.5	63.8
Rûens Silcrete Renosterveld	93.9	40.8	56.4	63.7
Saldanha Granite Strandveld	85.0	45.9	56.9	62.6
Swartland Shale Renosterveld	85.0	43.2	57.4	61.9
Western Rûens Shale Renosterveld	82.0	44.0	59.3	61.7
Eastern Rûens Shale Renosterveld	82.0	43.9	58.9	61.6
Swartland Alluvium Renosterveld	79.0	46.2	57.6	60.9
Central Rûens Shale Renosterveld	84.0	42.1	56.3	60.8
Knysna Sand Fynbos	87.0	40.8	53.9	60.6

Box C: Habitat fragmentation.

1. Resistance Layer

The land cover map (including roads) was reclassified to reflect resistance to species movement. The types that allow minimal resistance were given a value of 0 (e.g. natural areas), while other types offer a greater resistance (Table C1). The layer was aggregated to 1 km distance in order to average the resistance value for fragments that are within the prescribed dispersal distance (1 km) using Grid Analyst in Arc View GIS. This produced a resistance layer with values ranging from 0 to 100. The cut-offs used for resistance values were as follows: 0–25, very low; 25–50, low; 50–75, medium; 75–100, high. We summarised the resistance values per vegetation type to classify vegetation types into four categories of habitat fragmentation in terms of resistance to species movement using equal interval categories.

Table C1 Land use classification based on the estimated landscape resistance value. Note: estimated resistance values were not species-specific.

Land use types	Landscape resistance value
Forests & Woodlands	0
Thicket & Bushland	0
Grassland	0
Wetlands	0
Waterbodies	25
Degraded land	50
Minor roads	50
Cultivated land	75
Forest plantation	75
Mines & Quarries	85
Major roads	85
Urban/Built-up Land	100

2. Extent of Habitat Transformation

To derive the extent of habitat transformation, we reclassified the NLC layer into natural and transformed areas (where natural areas = 0 and transformed areas = 1). The layer was then aggregated to 1 km using a sum method to calculate the percentage of habitat transformation within 1 km blocks. Values ranged from 0 (natural 1 × 1 km block) to 100 (transformed 1 × 1 km block). The layer was then summarised per vegetation type, which were reclassified into four categories of habitat fragmentation in terms of habitat transformation extent using equal interval categories.

3. Fragment Size

A unique value was assigned to each fragment of natural habitat per vegetation type (using the Arc Info command 'region group'). We then determined the area of each fragment of natural vegetation per vegetation type. The average fragment size was calculated for each vegetation type. We re-scaled the average fragment size value from 0 (average fragment size: 22 641 ha) to 100 (average fragment size: 1 ha). We reclassified vegetation types into four categories of habitat fragmentation in terms of fragment size using equal intervals.

4. Habitat Fragmentation Index

The overall habitat fragmentation index was derived per vegetation type. We averaged the values obtained for resistance to species movement, extent of habitat transformation and average fragment size. Vegetation types were then classified into four categories (very low, low, medium and high) of habitat fragmentation using equal intervals.

4.2 *Alien Plant Invasion*

We quantified alien plant invasion potential based on an assessment of the climatic correlates of distribution of 71 important invasive alien plants (Nel et al. 2004, Rouget et al. 2004). We assumed that alien plant species would have the potential to spread in areas identified as climatically suitable by a climatic envelope model (see Box D). Figure 17.3 illustrates the approach for three species. The index derived (re-scaled from 0 to 100) relates to the potential number of invader plants. This was then summarised per vegetation types and categorised into four categories.

A total of 157 of the vegetation types have low invasion potential where fewer than five species can invade, and five vegetation types have high invasion potential, being potentially suitable for more than 25 of the invader plants.

Box D: Mapping alien plant potential.

Climate Envelope Models (CEMs) are very useful at a broad scale to develop a general picture of where species are most likely to invade, especially in this region with marked climatic gradients. In this study, we used a variant of CEMs based on an oblique ellipse model, which calculates the Mahalanobis distance to the 'optimal' climate conditions. Such models are supported by the niche theory which assumes the existence of optimal environmental conditions for a species and that any deviation from this optimum is associated with a lower climatic suitability. These models are an improvement on traditional CEMs in that a continuous range of climatic suitability values can be equated with probability of occurrence. We derived climatic suitability surface for 71 major invader plants.

Preliminary analyses suggested that the relative importance of climatic factors was species-specific, making it difficult to identify a few 'generic' climatic variables that could be applied for all our species. We therefore reduced the large number of possible explanatory variables to three components (principal component axes 1, 2 and 3) using Principal Component Analysis (PCA). The first three components of the resulting PCA explained over 95% of the initial variation, based on the seven climatic variables with the greatest influence on plant species distribution. We then used these three climatic indices to derive the CEMs. We assumed that alien plant species would have the potential to spread in areas identified as climatically suitable by the CEMs. Rouget et al. (2004) describe the approach in more detail. Ideally, CEMs for alien plants should also be based on their bioclimatic occurrence in their continent of origin (Rutherford et al. 1995) and any other areas of the world where they are invasive.

Species potential distributions were derived on a grid of 1-minute resolution. We quantified alien plant invasion potential by calculating the number of alien plants that could potentially invade each 1-minute cell (i.e. for which the climate is suitable). The index was re-scaled from 0 to 100.

Most species are currently confined to 10% or less of the region, but could potentially invade up to 40%, based on their climatic envelope. Depending on the species, between 2% and 79% of the region is climatically suitable for species to invade, and some areas were suitable for up to 45 invader plants. Over one third of the major invader plants considered here have limited potential to substantially expand their distribution.

The number of potential invaders was then averaged per vegetation type to produce an index of alien plant invasion potential per vegetation type. This was classified into four categories (very low, low, medium and high) based on equal intervals.

5. Overall Vulnerability of Vegetation Types

Not all the vegetation types of the country are affected by land use pressures and degradation (Figure 17.4) in the same way. Out of 433 vegetation types, 207 vegetation types have a very low overall vulnerability index. A total of 217 vegetation types have a low overall vulnerability index. However, nine vegetation types have a medium overall vulnerability index (i.e. average greater than 50 for all vulnerability types).

The six vegetation types that are the most likely to be affected (based on the combined vulnerability index of land use and degradation) are (in decreasing order): Lourensford Alluvium Fynbos, Knysna Sand Fynbos, Algoa Sandstone Fynbos, Cape Flats Sand Fynbos, Egoli Granite Grassland and KwaZulu-Natal Sandstone Sourveld. Table 17.3 lists the three most threatened vegetation types for each land use and degradation pressure.

One can also analyse vulnerability in terms of the areas highly vulnerable to any land use or degradation pressure (score >75 for one or more of the six vulnerability types considered).

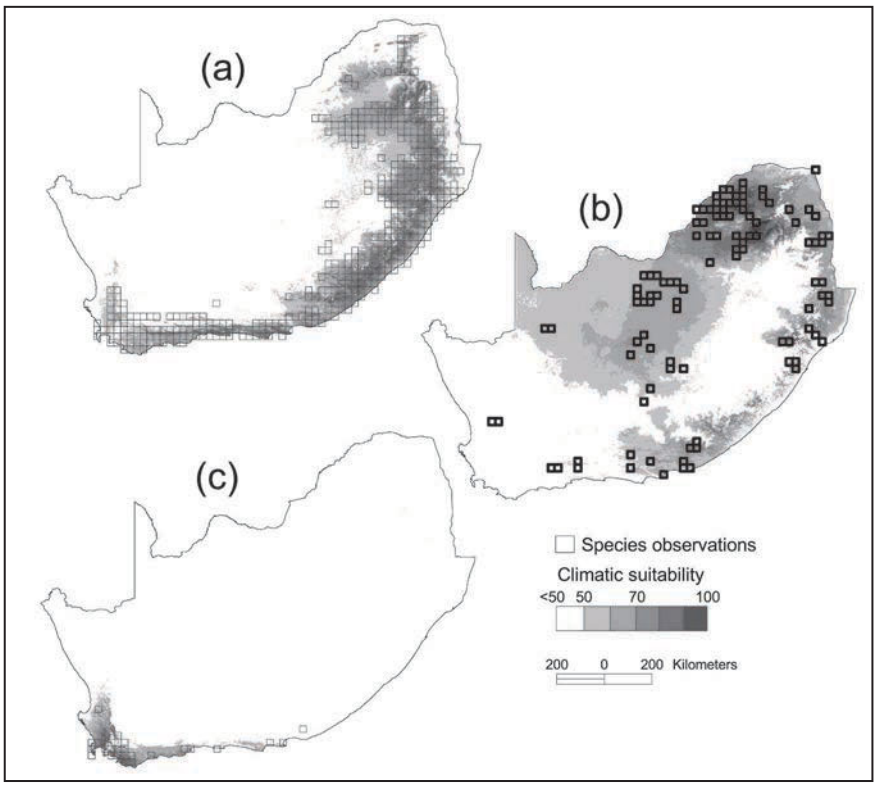

Figure 17.3 Species presence observations and climatic suitability derived from climatic envelope models for three characteristic species in South Africa, Lesotho and Swaziland: (a) *Acacia mearnsii*, a very widespread and abundant invader; (b) *Opuntia stricta*, a widespread and common invader; and (c) *Hakea drupacea*, a localised and abundant invader (from Rouget et al. 2004).

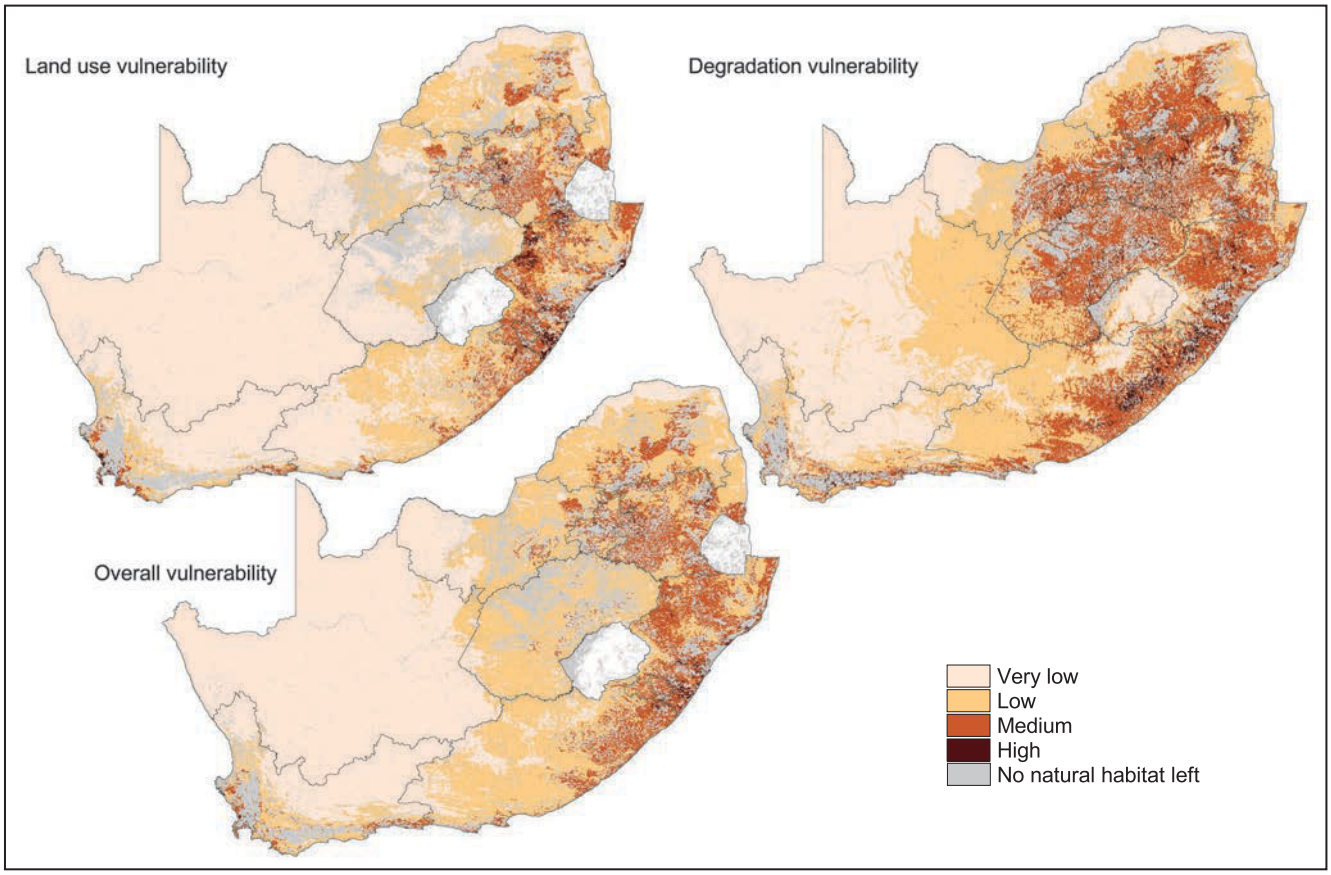

Figure 17.4 Average vulnerability of land use pressure, habitat degradation and overall vulnerability.

Table 17.3 Top three highly vulnerable vegetation types for both land use and degradation pressures as well as for overall vulnerability.

Vulnerability	Vegetation type 1	Vegetation type 2	Vegetation type 3
Land use	Mangrove Forest	Cape Flats Sand Fynbos	Cape Flats Dune Strandveld
Land degradation	Lourensford Alluvium Fynbos	Cape Lowland Alluvial Vegetation	Rûens Silcrete Renosterveld
Overall vulnerability	Lourensford Alluvium Fynbos	Knysna Sand Fynbos	Algoa Sandstone Fynbos

Regarding land use pressure only, the most threatened vegetation types (i.e. irrespective of the number of pressures) are in the Northern Cape coastal belt and localised parts of the interior of the province, central parts of Limpopo Province, parts of Gauteng, the coastal and mostly the southern parts of KwaZulu-Natal, the northeastern Eastern Cape and the lowlands of the Western Cape (Figure 17.5). In these terms, the most vulnerable vegetation types are the Cape Flats Sand Fynbos, Cape Flats Dune Strandveld, Lourensford Alluvium Fynbos, Peninsula Granite Fynbos, Peninsula Shale Renosterveld, Peninsula Sandstone Fynbos and Namib Seashore Vegetation (not identified as a vulnerable vegetation type based on the average overall vulnerability index).

Regarding degradation vulnerability only, Figure 17.6 highlights areas of high vulnerability to habitat fragmentation and/or alien plant invasion. This highlights 12 vegetation types most vulnerable to habitat degradation, including most of the Cape Lowlands vegetation types.

Predicting vulnerability to future land use pressures can be complex, but we found that the current extent of habitat transformation can serve as a broad predictor of vulnerability. The combined vulnerability index (see Figure 17.4) was correlated with the current extent of habitat transformation (Figure 17.7). For example, the Lourensford Alluvium Fynbos with 91% of its vegetation transformed has a high vulnerability index (vulnerability score of 61). However, there are many outliers where a vegetation type is either highly transformed with a low vulnerability index or vice versa. The land use vulnerability score was poorly correlated with the percentage of current habitat transformation.

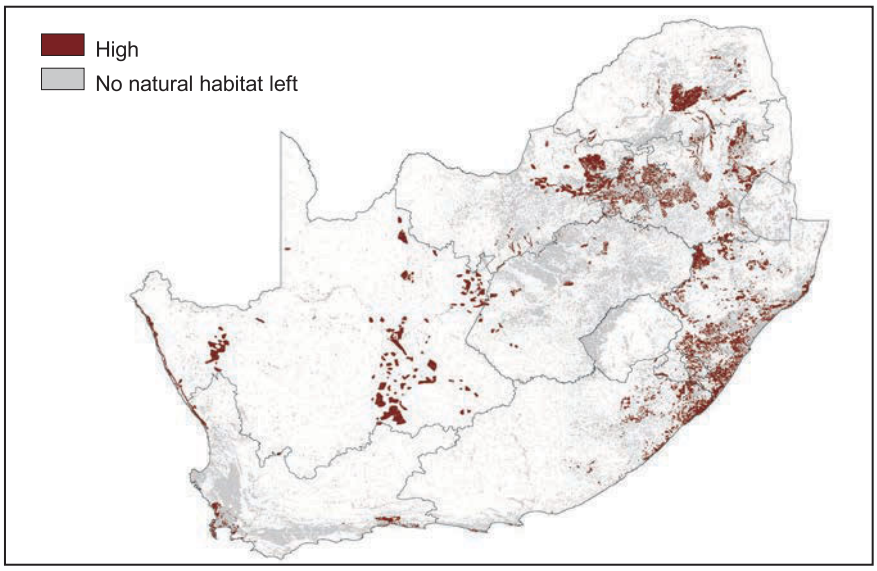

Figure 17.5 Areas of high future land use pressure based on land capability, afforestation, population growth and mining potential.

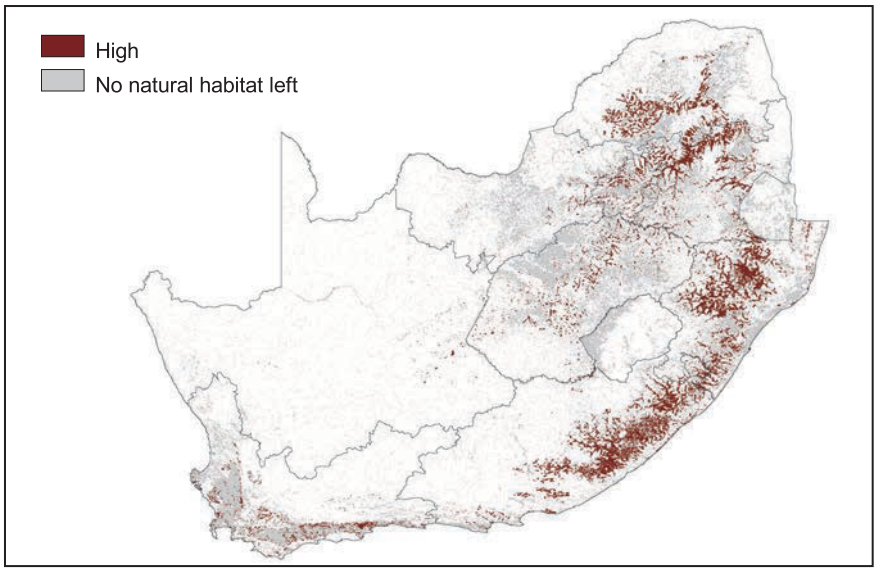

Figure 17.6 Areas of high degradation vulnerability to habitat fragmentation and alien plant invasion.

6. Conclusion

Recently, the National Spatial Biodiversity Assessment (Driver et al. 2005) quantified the current status of vegetation types. This revealed that 19 vegetation types are critically endangered, in other words ecosystem functioning has been severely disrupted by habitat transformation and such vegetation types could experience species loss. This also indicated that 53 vegetation types are endangered, 69 are vulnerable and 292 are least threatened.

Although the current ecosystem status highlights that 67% of the vegetation types are currently least threatened, our analysis of future vulnerability to land use pressures and degradation suggests that many vegetation types could experience further loss of habitat and/or loss of ecosystem functioning. The conservation challenge is now to identify which vegetation types should require immediate conservation efforts in order to mitigate the impacts of future land use changes. We recommend that vegetation types under high land use pressure but currently not transformed and/or not protected should receive conservation attention.

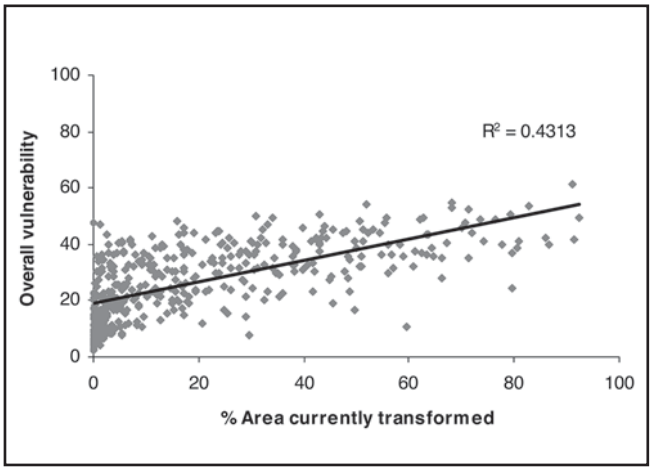

Figure 17.7 Relationship between the current habitat transformation and combined vulnerability (land use and degradation) in South Africa.

7. Credits

The unpublished version of the vegetation map used for this vulnerability analysis was provided by M.C. Rutherford and L. Mucina. The GIS data were obtained from L.W. Powrie. The layer of land capability, afforestation potential and population density was provided by B. Reyers and was requested from different sources. Z. Jonas and M. Rouget created the layer of mining potential and habitat fragmentation index. M. Rouget provided the layer of alien plant invasion. Z. Jonas, B. Mohamed and M. Rouget did the analysis. Z. Jonas was the lead author, M. Rouget and B. Reyers provided substantial input and editing on early drafts. L. Mucina and M.C. Rutherford provided final editorial comments. Valuable scientific and technical input was provided by conservation planners involved in the National Spatial Biodiversity Assessment.

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