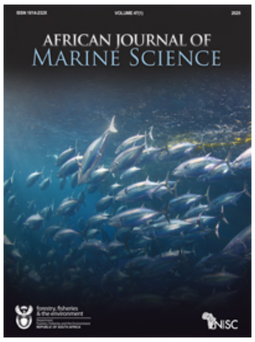

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African Journal of Marine Science

ISSN: 1814-232X (Print) 1814-2338 (Online) Journal homepage: www.tandfonline.com/journals/tams20

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African Journal of Marine Science 2025, 47(1): 1–18
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AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814-232X EISSN 1814-2338
https://doi.org/10.2989/1814232X.2025.2463342

Critical review

Cross-realm biodiversity profile of the South African coastal zone

LR Harris[1]*, JB Adams[1,2], A Dayaram[3,4], LV Dunga[1,3,5], N Job[3], SP Kirkman[1,6], SJ Lamberth[1,7], MC Pfaff[8], JL Raw[1,9], GM Rishworth[1,10], A Robbins[1], KJ Sink[1,3], AL Skowno[3,11], H van Deventer[12,13] and L van Niekerk[1,14]

[1] Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa
[2] Department of Botany, Nelson Mandela University, Gqeberha, South Africa
[3] Kirstenbosch Research Centre, South African National Biodiversity Institute (SANBI), Cape Town, South Africa
[4] Restoration and Conservation Biology Research Group, School of Animal, Plant and Environmental Science, University of the Witwatersrand, Johannesburg, South Africa
[5] Parley for the Oceans – Seas of Good Hope, Cape Town, South Africa
[6] Branch: Oceans and Coasts, Department of Forestry, Fisheries and the Environment, Cape Town, South Africa
[7] Fisheries Research and Development, Branch: Fisheries Management, Department of Forestry, Fisheries and the Environment (DFFE), Cape Town, South Africa
[8] Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[9] Anthesis South Africa, Workshop 17, Ballito Junction Regional Mall, Ballito, Dolphin Coast, South Africa
[10] Department of Zoology, Nelson Mandela University, Gqeberha, South Africa
[11] Department of Biological Sciences, University of Cape Town, Cape Town, South Africa
[12] Council for Scientific and Industrial Research (CSIR), Pretoria, South Africa
[13] Department of Geography, GeoInformatics and Meteorology, University of Pretoria, Pretoria, South Africa
[14] Council for Scientific and Industrial Research (CSIR), Stellenbosch, South Africa
* Corresponding author, e-mail: linda.harris@mandela.ac.za

South Africa's coast is 3 113 km long and includes microtidal shores that experience semi-diurnal tides and mostly high wave energy. From west to east, the cool Benguela Current and the warm Agulhas Current drive steep gradients in climate and environmental conditions, resulting in diverse coastal ecosystem types. Here, we review the biodiversity of South Africa's coastal zone, focusing on the constituent ecosystem types from the terrestrial, freshwater, estuarine and marine realms, and provide a brief overview of cross-realm biodiversity patterns. We also give guidance on coastal boundaries to improve standardisation in this complex area to support assessment, planning and management. The ecologically determined coastal zone currently comprises 193 ecosystem types: 83 vegetation types (e.g. seashore vegetation, strandveld, duneveld, coastal forest); 22 estuary and 3 micro-estuary ecosystem types; and 85 marine ecosystem types (e.g. shores, islands, reefs, kelp forests, bays), with planned inclusion of freshwater types (e.g. coastal lakes, forested wetlands, dune slacks) in the future. Species richness is generally highest along the south and east coasts, with the highest levels of endemism mostly reported for the south coast. The South African coast is a national asset that warrants careful management for long-term sustainability to safeguard its unique biodiversity and many associated benefits for current and future generations.

Keywords: biodiversity patterns, coastal biodiversity, coastal conservation, ecosystem types, endemism, microtidal coast, shoreline

Online supplementary material: Definitions of coastal boundaries and related terms, guidance on which map layers to use, and links to download the spatial data are given in the Supplementary Information, available at https://doi.org/10.2989/1814232X.2025.2463342. A summary table of the 193 coastal ecosystem types is also provided.

Introduction

South Africa's coast is 3 113 km long (Harris et al. 2011) and comprises ecosystem types in the terrestrial, freshwater, estuarine and marine realms, which are strongly connected by cross-realm flows of sediment, fresh water and nutrients, and by winds, waves and tides. The coastal zone comprises diverse assemblages of unique, often endemic species (Harris et al. 2014; Griffiths and Robinson 2016), with constant discoveries of new, endemic coastal species (e.g. Darbyshire and Kara 2024). South Africa's rich biodiversity is world-renowned (Mittermeier et al. 1997; Costello et al. 2010), and the many associated coastal ecosystem services provide a wealth of benefits to people (Harris et al. 2021). A key factor driving many of the outstanding attributes of the South African coastal zone is the country's unique position at the confluence of the Atlantic, Indian and Southern oceans. The complex, regional-scale interactions among these oceans, their currents and the atmosphere, combined with the effects of latitude, topography, wave exposure, substrate types, drainage and climate, give rise to rich terrestrial, freshwater, estuarine and marine biodiversity within a relatively small area.

Most of the literature describing coastal biodiversity in South Africa focuses on single realms (e.g. coastal terrestrial biodiversity: Mucina et al. 2006) or on broad ecosystem groups (e.g. sandy beaches: Harris et al. 2014). The aim of this review is to provide an overview of cross-realm coastal biodiversity in South Africa (i.e. inclusive of the constituent terrestrial, freshwater, estuarine and marine biodiversity). Recognising that entire volumes can be written on coastal biodiversity in South Africa (e.g. Branch and Branch 2018), we focus on the most-salient points that best highlight the ecosystem types and biodiversity patterns that make South Africa's coast a national asset. We also document progress in standardising the concepts, definitions and boundary lines applied in the coastal zone in support of coastal biodiversity assessment, planning and management. Some mention is made of the environmental gradients and physical drivers that are foundational to many of the biodiversity patterns observed, but it is beyond the scope of a single work to review these as well.

Study area

The study area is the South African coastal zone. Although 'coastal zone' is a familiar concept, deciding exactly where it starts and ends is fraught with challenges. There are diverse definitions describing the spatial extent of the coast, with vague terminology introducing complexity and reducing clarity. For example, 'the coastline' is a poor term to use as a coastal boundary, because it denotes an unspecific line on the ground, compared with other terms that refer to specific features, such as the dune base, spring high-tide mark or effluent line (Supplementary Figure S1). There has been a concerted effort in South Africa's biodiversity sector to address these challenges and thereby improve clarity and standardisation in coastal terminology and boundaries to support cross-realm biodiversity assessment (e.g. for determining the status of coastal biodiversity: Harris et al. 2022) and planning (e.g. for identifying priority areas of coastal biodiversity: Harris et al. 2023). Key steps have been creating a seamless, cross-realm map of ecosystem types (Harris et al. 2019) and clearly defining coastal terms, especially those relating to coastal boundaries and delineations (SANBI 2023). In the online supplementary material, we provide a glossary of these and other definitions (Supplementary Table S1), links to map layers of coastal boundaries, and guidance on which maps to use for which purposes. We encourage adopting these conventions and boundary lines as we seek to improve standardisation in this complex, interconnected zone for easier uptake of data and information in biodiversity assessment and planning.

For the purpose of this review, written as part of South Africa's National Biodiversity Assessment (NBA) 2025, the coast is taken to be the ecologically determined coastal zone (EDCZ) (Figure 1), with some additional discussion regarding features that need further research and could be considered coastal ecosystem types in the future. The EDCZ used in the NBA 2018 (Harris et al. 2019, 2021, 2022) has been updated for the NBA 2025 to include new vegetation types (SANBI 2006–2024), with planned inclusion of freshwater ecosystem types in the future, and currently comprises 193 ecosystem types (Figure 1; Supplementary Table S2), as described in the next section.

One of the most-salient drivers of coastal biodiversity in South Africa is the stark difference in ocean currents that create strong environmental and climatic gradients from west to east (Figure 1), which in turn influence species distributions, biogeography and endemism (Lett et al. 2023). Along the west coast, the Benguela Current flows slowly northward, comprising cool water from the South Atlantic gyre (Nelson and Hutchings 1983). Dynamic wind-driven coastal upwelling of cold, nutrient-rich water enhances productivity close inshore on the west coast, in turn driving high biomass of marine species and underpinning key fisheries (Hutchings et al. 2009; Kirkman et al. 2016).

In contrast, the fast-flowing Agulhas Current runs southward along the east coast, bringing warm, nutrient-poor water from the tropical western Indian Ocean, rendering productivity and biomass low in this region. It flows close to the narrow shelf on the east coast, except off the uThukela Bank where the continental shelf is wider. It then moves offshore along the edge of the Agulhas Bank, where it retroflects eastwards into the western Indian Ocean in the Agulhas Return Current, although rings of warm water occasionally break off the point of retroflection, and slowly spin into the South Atlantic (Beal et al. 2011). Upwelling of nutrient-rich subphotic water occurs along the shelf break and at rocky promontories along the south coast, creating an intensive, dynamic mixing region on the broad Agulhas Bank, where there are complex currents that also interact with the Agulhas Current (Jacobs et al. 2022). Given the meeting of the two currents along the south coast, this area is intermediate in terms of temperature and productivity between the Benguela and Agulhas regimes.

These contrasting ocean currents, together with the varied topography of the mainland, and enhanced by the Coriolis effect, contribute to vastly different climates, rainfall patterns and freshwater flows across South Africa. The Benguela Current helps to create the low-rainfall Namib Desert, which extends northwards from the Northern Cape Province of South Africa through to Namibia and southern Angola. Consequently, the far northwestern coast of South Africa is arid, with 40–250 mm mean annual precipitation (MAP) largely occurring in winter. Farther south, around Saldanha, the coast is also arid, with 200–400 mm MAP that is mainly cyclonic. Sea fog is prevalent along most of the west coast, transporting water and nutrients from the ocean to the arid lands. The Western Cape Province predominantly experiences a winter rainfall regime (MAP: 170–1 600 mm) from cold fronts, which transitions to a more aseasonal coastal rainfall pattern (MAP: 260–1 200 mm) along the southeastern coast (Mucina et al. 2006). Summer rainfall (MAP: 836–1 900 mm)

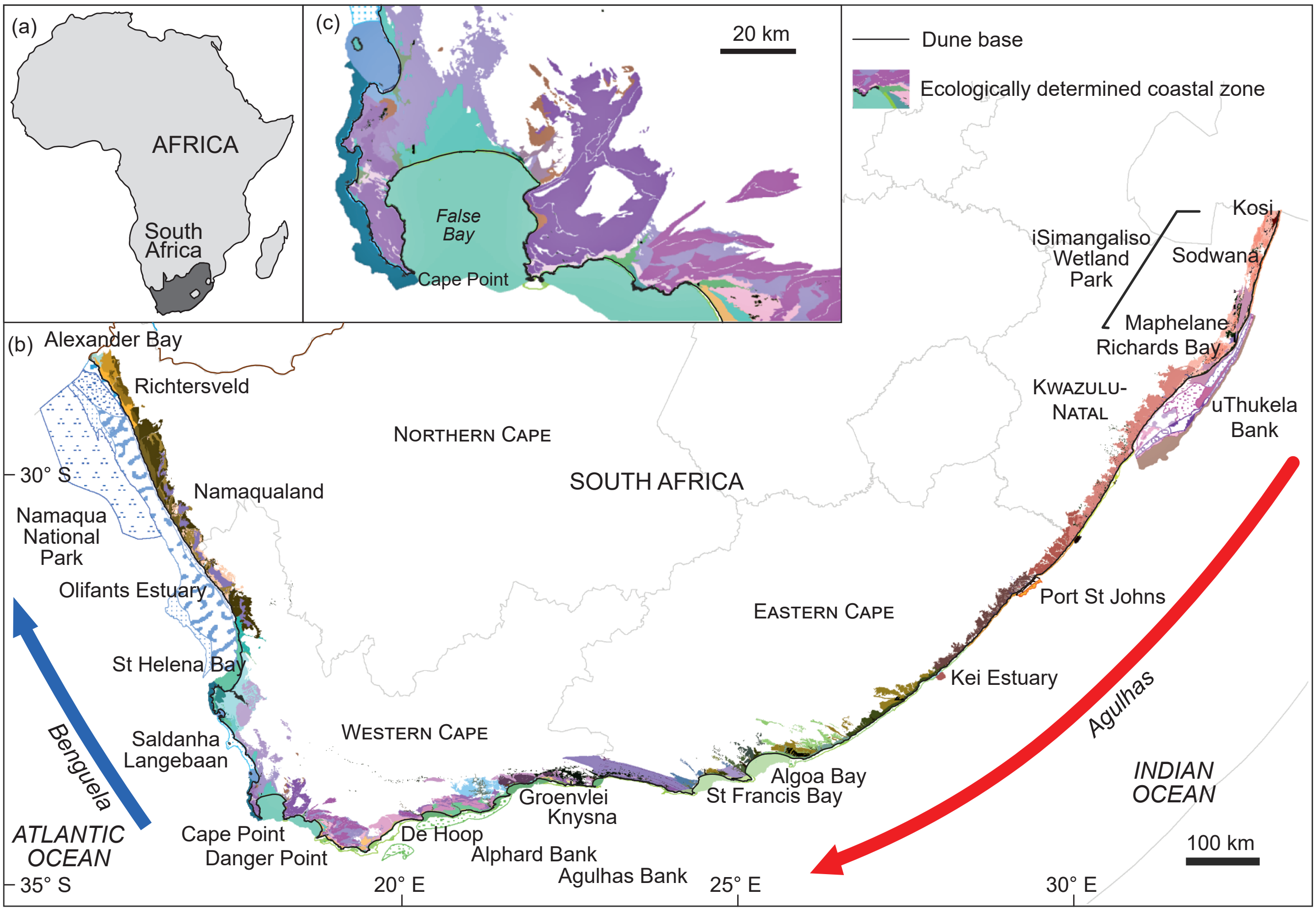

Figure 1: (a) Location of the study area (South Africa). (b) The ecologically determined coastal zone, comprising 193 ecosystem types (see Supplementary Table S2), annotated with the major ocean currents and salient place names mentioned in the text. (c) Coastal ecosystem types in False Bay and surrounds

dominates the subtropical to tropical east coast, where tropical cyclones also contribute to the resupply of aquifer-dependent regions (Mucina et al. 2006). The incidence of frost is very low (~1 day year^{-1}) along the arid west coast, low (~3 days year^{-1}) along the southwest coast, and absent along the east coast (Mucina et al. 2006).

Coastal ecosystems

Coastal terrestrial ecosystem types

The National Vegetation Map (Mucina and Rutherford 2006; Dayaram et al. 2019) has been recently updated (SANBI 2006–2024) to include, *inter alia*, five new types of vegetation with strong fynbos affinities in areas previously described as strandveld along the south coast (Cowling et al. 2023). Because the EDCZ includes whole ecosystem types, Harris et al. (2019) established criteria by which vegetation types could be defined as coastal (having purely coastal descriptions of the vegetation type, and/or >95% of their extent within 2.5 km of the shore) or semi-coastal (coastal affinities mentioned in the description of the vegetation type, and/or >70% of their extent within 10 km of the shore). Applying these criteria to the National Vegetation Map 2024 (SANBI 2006–2024), South Africa now has 52 coastal vegetation types and 31 semi-coastal vegetation types that are included in the EDCZ (Figure 1; Supplementary Table S2).

Coastal vegetation (primarily seashore vegetation, strandveld, duneveld, dune thicket, and coastal forest types) occurs from sea level up to ~450 m; farther inland, semi-coastal vegetation (mostly thicket and fynbos ecosystem types) can reach elevations over 1 600 m in some places, such as in mountainous fynbos systems. Coastal terrestrial ecosystem types are outside the influence of tidal floods (but with a few exceptions, such as seashore vegetation), but are still under the direct influence of the sea through exposure to salt spray and fine airborne sediments (Mucina et al. 2006). Eight of the nine terrestrial biomes in South African are represented in the EDCZ (i.e. all except grasslands).

Dunes and seashore vegetation

Although there are some sections of the coast where rocky cliffs comprise the backshore (Figure 2e), the South African shores are largely backed by sand dunes that support the four seashore vegetation types: Natal, Cape, Namaqua and Namib. These vegetation types are generally dominated by a single pioneer-like species (e.g. *Scaevola*) (Figure 2f),


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Figure 2: The South African coast comprises a large variety of features and ecosystem types, including: (a) foredunes, (b) parabolic dunes, (c) transgressive dunes, (d) barrier dunes, such as the last remnants of the headland-bypass system across Cape Recife, and (e) cliff-backed shores. Terrestrial vegetation types: (f) seashore vegetation, (g) duneveld, (h) coastal thicket, and (i) coastal forest. Freshwater ecosystem types: (j) freshwater forested wetlands (swamp forests), (k) coastal lakes (e.g. Groenvlei), and (l) dune slacks. Estuarine ecosystem types: (m) river mouths (e.g. uThukela), (n) a variety of estuary types, and associated estuarine habitats, such as (o) mangroves. Marine ecosystem types: (p) dissipative, (q) intermediate, and (r) reflective sandy beaches, (s,t) shingle shores, (u) boulder shores, (v,w,x) mixed shores, (y) Namaqua, (z) Agulhas, and (aa) Natal rocky shores, (ab) microbialites, (ac) islands, (ad) kelp forests, (ae) temperate reefs, (af) coral reefs, (ag) coastal muds, and (ah) the 11 bays (white stars). Image credits: (d,q) Google Earth; (j) Heidi van Deventer; (m) Ezemvelo Scientific Services; (o) Janine Adams; (t,u) Amanda Robbins; (y,z,aa), Maya Pfaff; (ab) Gavin Rishworth; (ac) Andrea Thiebault; (ad,ae,af) Geoff Spiby; (ag) ACEP Deep Connections; (ah) annotated Google Earth image; all other photographs by Linda Harris

and are often accompanied by grasses, herbs and dwarf shrubs. Between dunes, dune slacks supporting salt-tolerant pioneer species can form where the groundwater is close to the surface (covered in more detail below) (Mucina et al. 2006). South Africa has some remarkable dune systems, including the largest mobile coastal dunefield in the Southern Hemisphere at Alexandria in Algoa Bay (Figure 2c), and some very tall vegetated dunes, such as at Groenvlei (201 m high) and at Maphelane in iSimangaliso Wetland Park (183 m high) (Tinley 1985). Tinley (1985) described the full variety of coastal dunes in southern Africa, which are generally summarised into four main types (McLachlan and Defeo 2018): foredunes, parabolic dunes, transgressive dunes and barrier dunes (Figure 2a–d).

The types of dunes that form along the shore depend on many variables (Tinley 1985), such as: wind regime, sand supply, shoreline orientation and configuration, rainfall regime, plant colonisation, sea conditions (wave action and longshore drift), and estuary mouth dynamics. Most of South Africa's barrier dunes have been artificially stabilised and developed (McLachlan and Burns 1992; McLachlan et al. 1994), such that they are effectively an extinct dune type in South Africa. The foredunes are also highly disturbed, often replaced with coastal development, and are often heavily trampled, even within protected areas. The parabolic dunes and transgressive dunes tend to be more intact than the other two dune types, although trampling has led to dune blowouts in some places. Additional research is needed to determine whether the seashore vegetation types should be split further into sub-types based on the type of sand dune on which they grow.

Strandveld, duneveld, dune thicket, and coastal thicket, forests and fynbos

The strong gradients in climate from the arid west coast to the mesic east coast are reflected in the types of plants and, therefore, vegetation types that comprise the terrestrial portion of the EDCZ. In the northwest, from Alexander Bay to the Richtersveld, low-growing (<1-m tall shrubs with spinescent grasses and succulent dwarf shrubs), sparsely vegetated plains with gently undulating hills dominate the topography of the arid west coast. This area includes the most dense and diverse lichen fields in southern Africa (Jürgens and Niebel 1991), and although vegetation is sparse, beta diversity can be high. Sparse vegetation continues into Namaqualand on the strandveld coastal peneplains, with mobile and semi-mobile dunes, and occasional sand plumes from hairpin parabolic dunes (Tinley 1985). Namaqualand strandvelds are dominated by erect and creeping dwarf succulent and non-succulent shrubs, spiny grasses with wind-adapted leaves, and annual flowering herbs. Dunevelds (Figure 2g) farther inland include slightly taller shrubs (sometimes sclerophyllous), grasses, restioids and geophytic herbs with large floral displays. The Namaqualand sandy dune plumes are dominated by the only known case of non-fire-maintained proteaceous fynbos communities.

Along the more topographically diverse Western Cape coast, the vegetation becomes progressively denser in response to the more Mediterranean climate. Inland coastal vegetation in the west is moderately taller, with proteoid, ericaceous and restioid shrubs and grassy shrublands, and thickets farther east. Fire is an important natural process, and milkwood *Sideroxylon inerme* forests occur in fire-protected areas. Vegetation along the south coast is moderately tall (1–4 m) on dunes, with strong fynbos elements and components of thicket (Figure 2h), including short to tall shrubs and trees, grasses, lianas, vines, and many geophytic herbaceous and succulent forbs that may be a reflection of ancient landscapes (Cowling et al. 2023). Fynbos tends to occur on drier slopes, while thicket densification occurs on swales and lower dune slopes (Cowling and Hoffman 2021).

Vegetation grows denser and taller (10–15 m in some woody stands) along the remainder of the wetter subtropical east coast. Undulating hills grade from subtropical thicket to flatter peneplain systems dominated by subtropical coastal forests, freshwater forested wetlands and mangrove forests (Adams and Rajkaran 2020; van Deventer et al. 2021). Dune-stabilising coastal forest with a well-developed understorey forms dense stands (Figure 2i), which are abundant in endemic species (e.g. six endemic genera, one endemic family, and relict occurrences of *Encephalartos* cycads).

Coastal freshwater ecosystem types

There has been recent debate as to which freshwater features qualify as 'coastal'. This reveals an important research gap that needs to be filled to address systematic typing and mapping of truly coastal freshwater ecosystem types. In turn, such research would support the typology of the wetland ecosystem map, which is currently being iteratively revised, and the classification and mapping of subterranean aquatic ecosystem types. Notwithstanding, some freshwater features are certainly coastal. Therefore, an initial set of three freshwater features—coastal lakes, swamp forests (freshwater forested wetlands), and dune slacks—are discussed here as they are planned for inclusion in the updated EDCZ, with more ecosystem types likely to be added in future.

Coastal lakes

Parts of the EDCZ with higher rainfall support many scattered shallow lakes. Some contain fresh water, while others are brackish. Several of these lakes support peat soils and are typically vegetated with papyrus *Cyperus papyrus*, among other species. Three lakes with a depth of >2 m occur within the EDCZ, namely: De Hoop and Groenvlei along the south coast (Figure 2k), and Lake Sibaya in northern KwaZulu-Natal Province (KZN) (van Deventer et al. 2020). It is considered likely that all three originated as estuarine lagoons, and still host marine relics in their faunal assemblages even though they no longer have evidence of marine connectivity to the sea (Noble and Hemens 1978; Whitfield et al. 2017). Lake Futululu in KZN may also be considered coastal, although it is not limnetic in nature (i.e. does not have an open body of water) (Grenfell et al. 2010).

Swamp forests (freshwater forested wetlands)

Swamp forests (Figure 2j) are subtropical forested wetlands with influence from the land and sea that reach their southernmost distribution limit along the African coast in the Eastern Cape Province (Mucina and Rutherford 2006; van Deventer et al. 2021). Within KZN, these wetlands occur mostly along slow-flowing streams, where they are protected from fire, and where water from additional lateral groundwater discharge from adjacent dunes assures near-constant soil saturation and frequent flooding (Walters et al. 2019). The primary aquifer on the Maputaland Coastal Plain is the most important source of water for wetlands in the region (Grundling et al. 2013; Kelbe et al. 2016). In the Eastern Cape, swamp forests are associated with continuous subsurface water flows from fractured sandstone geology. They extend up to 10 km inland, occurring in small patches. Generally, the drivers of swamp forest community composition, overall ecology, and the autecology of the most important swamp forest species are not well understood (Walters et al. 2019). Swamp forests also co-occur with some of the deepest, oldest and highest volumes of peatlands of South Africa (Grundling et al. 2021). More research is needed on functional ranges of organic material, salinity and flow rates to distinguish different types of forested wetlands (e.g. floodplain and riverine wetlands) and determine which might be considered coastal.

Dune slacks

Coastal dune slack (or inter-dune) wetlands occur in the troughs between dunes where the sand intersects or comes close to intersecting the water table. A range of potential conditions are supported by these wetlands, from brackish to fresh, and seasonal to permanently wet, being split broadly into stable and dynamic systems. Stable dune slacks are vegetated, seasonal or semi-permanent depressional wetlands, whereas dynamic dune slacks are sparsely vegetated or unvegetated, and shrink, expand or move together with shifting sand dunes, even periodically becoming infilled. Dune slack wetlands are particularly prevalent in large, transgressive dunefields, such as at Alexandria (Figure 2c) and in barrier dunes, such as at Cape St Francis. In addition to those that intersect the groundwater table, dune slack wetlands may form following ‘perching’ or ponding of water above layers of calcrete or aeolianite. The more stable, seasonal and permanent dune slack wetlands may also commonly form above an impermeable clay lens, and some may accumulate high organic content soils (e.g. along the south coast) or even peat (e.g. in KZN).

Dune slack wetlands support important diversity, including a variety of invertebrates, such as the isopod *Tylos capensis*, the amphipod *Capeorchestia capensis*, and insects, as well as vertebrates, such as mammals (e.g. the gerbil *Gerbillurus paeba exilis*, antelope, mongooses and jackals), amphibians, reptiles and birds (Van Teylingen et al. 1993; McLachlan et al. 1996). Typical plant species associated with dune slack wetlands include salt-tolerant pioneer species, such as *Sporobolus virginicus* and *Cladoraphis cyperoides*, as well as *Ficinia nodosa*, *Juncus krausii*, *Plecostachys serpyllifolia*, *Typha capensis*, *Elegia tectorum*, *Arctotheca populifolia* and *Gazania rigens* (Avis and Lubke 1996; McLachlan et al. 1996; Mucina et al. 2006).

Groundwater, aquifers, seeps and springs

Subterranean freshwater features play an important role in coastal habitats (e.g. microbialites: Rishworth et al. 2020), in supporting surf-diatom accumulations in the surf zone (Campbell and Bate 1996) and as important cues that help guide sea turtle nest site selection in iSimangaliso (Hughes 1973). Areas of subterranean water are currently not classified or mapped as separate ecosystem types in South Africa (Dayaram et al. 2021). However, the IUCN Global Ecosystem Typology (https://global-ecosystems.org; Keith et al. 2020) recognises Subterranean Freshwater as a realm, with Underground Streams and Pools (SF1.1) and Groundwater Ecosystems (SF1.2) listed as two functional groups in the Subterranean Freshwaters Biome (SF1). If mapped as ecosystem types in the future, it is likely that at least some of them will be included in the EDCZ. For example, there are several ‘blind’ rivers between the Cape Peninsula and the Eastern Cape that disperse into the inland face of dunes, feeding local aquifers. There are also numerous springs and coastal seep wetlands within the EDCZ that discharge along beaches and rocky outcrops into the ocean. These freshwater features are currently under-mapped owing to their typically small size, and are generally very poorly known. In KZN, many have peatlands as substrates, offering unique and high-organic habitats (Grundling et al. 2021). More research is required to fully understand, classify and map groundwater flows, coastal aquifers, seeps and springs.

River–estuary transition zones

River–estuary transition zones are defined as river reaches that are subject to only riverine abiotic processes during any time of their hydroperiod, but host both riverine and estuarine biota (van Niekerk et al. 2019; van Deventer et al. 2020). These zones are not influenced by tidal action or back-flooding, and at no stage experience an increase in salinity as a result of tidal penetration. They exist immediately upstream of the estuary for a length of 0.5–30 km, but do not include the river–estuary interface (Bate et al. 2002), which is the area in an estuary within which salinity ranges from 0–10 under the influence of the upstream limits of back-flooding or tidal intrusion. These areas support a mixture of typically estuarine species, species equally adept at completing their entire lifecycle in both rivers and estuaries, freshwater species that may have an estuarine phase of their life-history, and catadromous crabs and anguillid eels that are either resident or passing through (Whitfield 1998).

River–estuary transition zones can serve as refugia from adverse conditions in estuaries, such as hypersalinity, eutrophication, hypoxia and temperature extremes (van Niekerk et al. 2019; van Deventer et al. 2020). They can also be used to shed attached pathogens and parasites from the estuarine or marine environment through osmotic stress. Although closely associated with the coast, the river–estuary transition zone is not included in the EDCZ because these areas are currently considered part of the river. However, they are mentioned here because further research is needed to determine whether they constitute a separate ecosystem type, which may then be included in future versions of the EDCZ.

Estuarine ecosystem types

South Africa has 290 estuaries (e.g. Figure 2m,n) and 42 micro-estuaries that have been respectively classified into 22 estuarine ecosystem types and 3 micro-estuary types, the diversity of which is driven by climatic, oceanographic and geological features (van Niekerk et al. 2020). Given their essential role as the primary aquatic conduits between land and sea, all of the estuary and micro-estuary ecosystem types are included in the EDCZ (Figure 1; Supplementary Table S2). In addition to delivering flows of fresh water, nutrients and sediments to the marine environment, estuaries also provide important spawning and nursery areas for coastal invertebrates and fish, including some marine species of commercial importance. Although extending beyond the recognised estuarine functional zone, river–estuary transition zones and estuarine fans and plumes are also important estuarine-associated features that play a key role in coastal biodiversity and ecology.

Estuaries and micro-estuaries

The contrast from arid to mesic conditions between the west and east coasts, respectively, has a strong influence on the distribution of watercourses across the country. Most of South Africa's estuaries are located on the east coast, where the relatively close proximity of the escarpment and higher rainfall results in many coastal outlets. The differences in rainfall patterns around South Africa also affect catchment size, which varies significantly, ranging from very small (<1 km^2) to very large (>10 000 km^2), with catchments in the arid cool-temperate region tending to be the largest (Jezewski et al. 1984; Reddering and Rust 1990).

Overall, the annual runoff is highly variable and unpredictable, fluctuating between floods and extremely low to no freshwater inflow to estuaries. Periods of low freshwater inflow often result in limited inlet stability because strong sea wave action, coupled with high sediment availability, forms a sandbar across the estuary mouth (Whitfield 1992; van Niekerk et al. 2020). More than 90% of estuaries in South Africa have restricted inlets, and more than 75% of systems close for varying periods of time. Thus, the estuary classification in South Africa recognises that these systems may not necessarily have a 'free connection with the sea' but are 'either permanently or periodically open to the sea' (Day 1980; van Niekerk et al. 2020). Although most systems rely on surface flows, some South African estuaries are groundwater-dependant (e.g. Langebaan, uMgobezeleni and Kosi).

Estuarine habitats

Habitats within estuaries vary by ecoregion. Overall, reeds and sedges are the most dominant habitat type, followed by intertidal and supratidal salt marsh, swamp forest, submerged macrophytes (seagrass beds) and mangroves (van Niekerk et al. 2019). Reeds, sedges and rushes are important in the freshwater and brackish zones of estuaries. Typical dominant species are the common reed *Phragmites australis* and the sedges *Schoenoplectus scirpoides* and *Bolboschoenus maritimus*. Salt marsh habitat consists of halophytic herbs, grasses and shrubs and is dominant in estuaries along the west and south coast, extending from the low-water intertidal to supratidal salt marsh (between 1.5 and 2.5 m above mean sea level). Extensive intertidal salt marsh areas are found in the Berg, Langebaan and Knysna estuaries (Adams 2020).

Most of the submerged macrophyte habitat in estuaries comprises the Endangered seagrass *Zostera capensis* (Watson et al. In press), which occurs in 37 estuaries, from the Olifants on the west coast to Kosi on the east coast. It occurs in the intertidal zone of permanently open estuaries, but can also be found in closed estuaries when conditions are saline. The largest area of *Z. capensis* is found in the Knysna Estuary, followed by in the Langebaan and Berg estuaries. Seagrass provides necessary shelter and food for a variety of invertebrate and fish species (Adams 2016).

Mangrove trees (Figure 2o) from five species form intertidal forests that support important biodiversity and critical ecological processes, and provide substantial benefits to people. Mangroves occur in South Africa at one of their most southern distribution limits globally (van Niekerk et al. 2019; Raw et al. 2023), with the high-energy and wave-dominated conditions of the South African coast restricting their presence to only 29 sheltered estuaries. This restricted distribution is driven by the geomorphology of the estuary (floodplain size and accommodation space), stability of the inlet (because mangrove trees cannot survive prolonged inundation) and flow regime of the estuary (as a control on deposition or erosion). In other words, their distribution limit in South Africa is controlled more by coastal geomorphology and estuarine dynamics than by temperature minima (Raw et al. 2019). Understanding these environmental drivers is important for making predictions about how mangrove distribution, and the concomitant benefits mangroves provide, will be influenced by climate change (Adams and Rajkaran 2020; Raw et al. 2023).

Coastal marine ecosystem types

Marine ecosystem types that are considered coastal are all those that are influenced directly by land, which includes ecosystem types from the shore to the inner shelf, because the seaward boundary of the latter is the fair-weather wave base—the point at which waves begin to interact with the seabed (Harris et al. 2019). All river-influenced ecosystem types have also been classified as coastal because of how dependent they are on flows of fresh water, nutrients and especially terrigenous sediments (Harris et al. 2019). No changes have been made to the marine component of the EDCZ since the NBA 2018, although future updates to the Marine Ecosystem Map are needed so as to include new and revised coastal ecosystem types. Therefore, currently, there are 85 coastal marine ecosystem types, nearly half of which are shore types (n = 37, excluding estuarine shores) (Figure 1; Supplementary Table S2); however, this number is expected to change in the near future.

Shores

Shores comprise the area between the dune base and the back of the surf zone (Harris et al. 2019). South Africa has a wide variety of shore ecosystem types, and each has unique biological communities. The geological setting is the first-order determinant of shore ecosystem types because it provides the underlying framework of shoreline orientation, gradient, structure and hardness (Short 2010; Harris et al. 2013). The distribution of estuaries influences the relative amount of fresh water, sediment and nutrients delivered to the coast, which contributes to the relative prevalence of different shore types around South Africa (Tinley 1985; Harris et al. 2011).

Tides and waves also play key roles in determining the shore types and their associated biota. South Africa is microtidal (tide range of 1.5 m on average, rarely exceeding 2.2 m), with regular, semi-diurnal tides (Rautenbach et al. 2019; South African National Hydrographer 2024). Most of the shoreline is exposed and subject to strong wave action, except inside bays and in the wave-shadow of rocky headlands and promontories that provide isolated areas of relative calm. Significant wave heights are mostly between 2 and 3 m, yet maximum recorded wave heights along the south coast can exceed 10 m, diminishing to ~6.5 m up the west and east coasts (Joubert and van Niekerk 2013). The wave period is largely similar around the country, averaging about 12 s (Rossouw et al. 1982; Rautenbach et al. 2019). Wave power is strongest in the region of Cape Point (~20 to >35 kW m^{-1}), diminishing up the west and east coasts, with maximum wave power in winter and least wave power in summer (Joubert and van Niekerk 2013). The wave climate along the South African coast is largely a result of the prevailing swell direction being driven from the southwest by storm-generated waves originating south of the mainland from cold fronts, with other cyclones and oscillations also contributing (Rossouw et al. 1982; Veitch et al. 2019; Oliver et al. 2022). In South Africa, rocky (including boulder), mixed and sandy shores are represented in approximately equal proportions overall, but the relative proportions vary regionally (Harris et al. 2011).

Sandy beaches

Beach morphodynamics and biogeography are the two biggest drivers of sandy-beach communities (Harris 2012), where the former describes the continuum of beach types that result from the interaction of tides, waves and sand (Short and Wright 1983; McLachlan and Defeo 2018). South Africa has wave-dominated beaches that range between reflective and dissipative states. Reflective beaches (e.g. Lala Nek: Figure 2r) comprise coarse sand, have steep and narrow intertidal zones, and narrow surf zones, with wave energy reflecting off the beach face. Dissipative beaches (e.g. Melkbos: Figure 2p) have fine sand, flat and wide intertidal zones, wide surf zones, and wave energy that dissipates on the beach face. They tend to be very long beaches, and often form where there is a source of fine sand available, which can be wind-blown (aeolian). Various intermediate types of beaches comprising medium-grained sand are also present, evident by cusps (undulating hills of sand orientated across-shore) on the beach, and rip currents and sand bars in the surf (Figure 2q).

Importantly, because conditions on beaches are generally so harsh, the abiotic environment is more important in structuring beach communities than are biological interactions, *sensu* the autecological hypothesis (Noy-Meir 1979; McLachlan et al. 1993). As grain size gets finer, swash period gets slower and wave climate gets less harsh from reflective to dissipative beaches, so conditions become easier for macrofauna to burrow into the sediment between swashes and avoid being washed away *sensu* the swash-exclusion hypothesis (McLachlan et al. 1993; Nel et al. 2001). This means that reflective beaches tend to support generalist species that are fast-burrowing, robust or agile, like ghost crabs *Ocypode* spp. and the mole crab *Emerita austroafricana*.

Through the beach morphodynamics continuum to dissipative beaches, more intermediate species (e.g. beach clams *Donax* and *Latona*) and delicate, specialist species (e.g. polychaetes) can survive. In turn, both species richness and abundance increase from reflective to dissipative sandy shores (McLachlan et al. 1993; Defeo and McLachlan 2005). As for most other biota, beach species live within their thermal limits, and the strong temperature gradient along the South African shoreline drives three biogeographic regions for beaches (McLachlan et al. 1981). Beaches largely rely on allochthonous inputs, particularly marine wrack and carrion. However, microphytobenthos and surf diatom accumulations are important primary producers, with the latter contributing significantly to productivity on sandy shores (Campbell and Bate 1988; Odebrecht et al. 2014). Many vertebrates are also associated with beaches for foraging and breeding, including a variety of shorebirds and nesting sea turtles (Harris et al. 2014). The latter provide sandy beaches with important nutrient subsidies via eggs and hatchlings (e.g. Le Gouvello et al. 2017).

Shingle shores and boulder shores

The diversity of shingle shores (Figure 2s,t) and boulder shores (Figure 2u) has only recently been investigated in South Africa. Although information regarding these ecosystems is limited, the biological communities associated with shingles and boulders are sufficiently different to be classified as separate ecosystem types (Tucker et al. 2017; Robbins et al. 2022). In the southwestern Cape, for example, boulder shores support more species (n = 175) than rocky shores (n = 124), with 92 species unique to boulder shores, 23 species unique to rocky shores, and the remaining 99 species shared between them (Tucker et al. 2017). These results confirm that boulder shores support a rich and distinct faunal community and are a separate ecosystem type to rocky shores. Similarly, shingle shores, comprising granules, pebbles and cobbles, are also distinct from boulder, rocky and sandy shores (Robbins et al. 2022). Cobble shores do not have distinct communities *per se*, and rather serve as a transition between shingle and boulder shores (Robbins et al. 2022). This likely reflects the transition between a mobile unconsolidated sediment (shingle shores) that can move under wave and tidal action, posing a risk of crushing to some species, to a more stable environment (boulder shores) for biota as the grain size and weight increase.

The types of invertebrates associated with shingle shores are all motile, unlike the fossorial sandy shore species, and largely sessile rocky and boulder shore species (Robbins and Griffiths 2023). Furthermore, the harsh environment associated with shingle shores means that the faunal communities concentrate at the high shore and migrate tidally to readily available food in the form of beach-cast kelp wrack (Robbins and Griffiths 2023). Currently, boulder shores are represented as a single ecosystem type per ecoregion, and once shingle shores are mapped they will likely be represented in the same way. More research is needed at a national scale to determine whether this classification is appropriate or whether there is more than one ecosystem type per ecoregion.

Mixed shores

Mixed shores (Figure 2v,w,x) have been defined and mapped where at least one of the across-shore zones of sandy beaches is taken up by rocks for a length of shore that is longer than the shore is wide (Harris et al. 2019). There are four mixed-shore ecosystem types in South Africa (Harris et al. 2019), one per ecoregion, with their communities comprising species from both rocky and sandy shores that are tolerant of sand inundation and rock presence, respectively (Smith 1999; Garner 2013). Consequently, mixed-shore communities can be more, less, or equally diverse as the communities on adjacent rocky or sandy shores. There is limited information on mixed shores in South Africa, particularly in comparison with the substantial amount of research on rocky and sandy shores. Mixed shores were first recognised in the country by Bally et al. (1984), with the first quantitative work comparing mixed, rocky and sandy shores conducted 25 years ago (Smith 1999), and only a few, subsequent studies undertaken since (e.g. Garner 2013). Given the limited work on the ecology of these ecosystems, there is still no ecologically based classification for mixed shores, even though they comprise a third of the shoreline length (Harris et al. 2011). Mixed shores are also poorly recognised as ecosystem types globally, with the current IUCN Global Ecosystem Typology not including a mixed-shore type (Keith et al. 2020). More research is needed to better understand these coastal ecosystems. It is likely that the four currently recognised mixed-shore ecosystem types in South Africa need to be split further—at the very least into a sand-dominated and rock-dominated type per ecoregion.

Rocky shores

The biodiversity of South African rocky shores exhibits distinct spatial structure both along and across the shore. As nutrients decline along the coast from west to east, biomass on rocky shores also decreases by about two-thirds (Bustamante and Branch 1996), with species richness increasing by an order of magnitude as a result of enhanced competition for more-limited resources (Branch and Branch 2018). Distinct rocky shore communities are thus associated with the northwest (Namaqua: Figure 2y), southwest (Cape), south (Agulhas: Figure 2z), east (Natal: Figure 2aa) and northeast (Delagoa) coasts (Sink et al. 2023). Within these five regions, biotic communities on rocky shores are shaped by tides, wave exposure, shoreline configuration, and rock type. Rocky shore biodiversity at a given site is additionally shaped by a complex interplay of physical and biological factors, such as sand inundation and scour, competition and predation (Menge and Branch 2001).

Organisms that are adapted to specific physical conditions occupy different horizontal bands on the shore, forming characteristic intertidal zonation patterns (Branch and Branch 2018; Pfaff and Nel 2019). Species richness and biomass increase from the higher to lower parts of the shore, as conditions become wetter, and food and larval supply are more continuous (Bustamante et al. 1997). Zonation occurs consistently along the shore, but is significantly modulated by wave action (Menge and Branch 2001). For example, wave-beaten rocky headlands are ideal habitats for filter-feeding organisms that depend on the delivery of suspended food particles, but are harsh environments for maintaining attachment. Therefore, species that can firmly attach to the rocks, like mussels (e.g. *Perna perna*, *Aulacomya atra*), barnacles (e.g. *Chthamalus dentatus*, *Tetraclita* spp.) and their predators (e.g. *Nucella* spp.), are dominant in such places. However, in sheltered bays, where wave force and delivery of particulate food are reduced, seaweeds (e.g. *Gelidium* spp., *Dictyota* spp., *Plocamium* spp.) and mobile grazers, such as limpets (e.g. *Scutellastra* spp., *Cymbula* spp.) and periwinkles (e.g. *Oxystele* spp.), flourish but filter-feeders are less abundant. Rocky shore ecosystems are therefore generally classified according to wave exposure, as very exposed, exposed, semi-exposed or sheltered.

Most species found on rocky shores have planktonic larvae. Topographic features along the shore, such as major headlands and bays, alter the coastal currents that deliver larvae and particulate food to the shore and thus generate patterns in community structure and function at mesoscales (10–100 km), with rocky shores inside bays tending to serve as source populations (Nicastro et al. 2008). In bays, where larvae accumulate, recruitment of rocky shore species is up to an order of magnitude greater than at headlands, where larvae are advected offshore (Pfaff et al. 2011, 2015). Such pronounced differences in recruitment and food supply have far-reaching effects on adult community composition, reproductive output and community resilience, and are therefore important considerations in the spatial management of marine resources (Kritzer and Sale 2004; Gaines et al. 2010) on which many small-scale, subsistence fishers depend.

Microbialites

Microbialites (Figure 2ab) are biologically deposited structures formed by microbial mats as a calcium carbonate by-product of cyanobacterial metabolism or through the binding and trapping of sediment by microalgae (Rishworth et al. 2020). Although they are the Earth's earliest forms of fossilised life, modern microbialites are scarce owing to several factors, including grazing and burrowing pressures from metazoans, shifts in water chemistry and limited nutrient availability (Rishworth et al. 2016). In South Africa, however, there is an extensive network of actively accreting microbialites, including both layered stromatolites and clotted thrombolites that have been discovered since the 2000s, spanning from Richards Bay on the east coast to Port Nolloth on the west coast, with highest abundance along the south coast (Rishworth et al. 2020).

Supratidal microbialites form at the interface of groundwater seepage and regular marine input during high tides and storm overtopping events (Rishworth et al. 2017), relying on the unique groundwater characteristics to flourish (Dodd et al. 2018). A persistent microalgal assemblage of predominantly cyanobacteria and diatoms construct the microbialite biofilm, which also supports a diverse array of metazoans (Rishworth et al. 2020). The associated biodiversity includes some unique species that have only recently been discovered, such as the tanaid *Sinelobus stromatoliticus* (Rishworth et al. 2019). The dynamic physical forces operating within the microbialite pools create a unique habitat that functions as an environmental refuge for some estuarine invertebrates and juvenile fishes (Grundlingh et al. 2023; Rishworth et al. 2024). Microbialites are currently considered habitats within some of the rocky and mixed-shore ecosystem types (Harris et al. 2019; Sink et al. 2023), but more research is needed to determine whether this is the best ecosystem classification for these coastal features.

Islands

There are two island ecosystem types in South Africa: Agulhas Island (Figure 2ac) and Cape Island, with at least 30 rocky coastal islands distributed along the mainland's west to south coasts. They range in size from approximately 500 ha (Robben Island) down to small islets of <0.5 ha, with considerable variation in geology, distance from the mainland, and local climatic and oceanographic conditions among islands (Williams et al. 2000). Most islands are dominated by colonies of Cape fur seals *Arctocephalus pusillus pusillus*, or one or more species of seabird, including the Critically Endangered African penguin *Spheniscus demersus*, Endangered bank cormorant *Phalacrocorax neglectus*, Cape cormorant *P. capensis* and Cape gannet *Morus capensis* (e.g. Kemper et al. 2007; Kirkman et al. 2013). The islands therefore provide critical habitat for these focal species to complete their life-history stages. High densities of these animals on islands cause trampling impacts, as well as high nutrient concentrations from their waste products (e.g. guano and feathers of seabirds; faeces, urine and fur of seals) and the decomposition of dead animals. These, together with wave action and restricted precipitation, cause islands to have depauperate terrestrial plant and invertebrate communities (Williams et al. 2000).

Intertidal and subtidal communities around the islands differ from those adjoining nearby mainland areas as a result of the high nutrient inputs and local depletion of seal and seabird prey species (Bosman and Hockey 1986). These nearshore communities of the islands have generally been less exploited than those of the mainland and may therefore provide reservoirs of biodiversity (Williams et al. 2000). Nevertheless, human interference, including historical removal of guano deposits, the building of structures and seal hunting, has severely modified many of the islands and resulted in considerable faunal changes (Shaughnessy 1984). Most notably, seals have been extirpated at several of the larger islands, and seabirds have been replaced by seals at some of the smaller ones (Rand 1963, 1972).

Reefs

Coastal reef ecosystem types in South Africa include coral communities (Kosi, Leadsman and Sodwana), reef complexes (Durnford, KZN Bight, Aliwal, Trafalgar and Agulhas), and reef mosaics (uThukela, Kei and Orange Cone) (Harris et al. 2019; Sink et al. 2023). The three coral community ecosystem types (e.g. Figure 2af) are the southern limit of coral reefs in the western Indian Ocean, and are all protected in iSimangaliso Wetland Park. They comprise algae and zooxanthellate corals, particularly soft corals (Porter et al. 2013; Schleyer and Porter 2018). Because the corals are at the edge of their distribution, the reefs are non-accretive but are nevertheless diverse (Porter and Schleyer 2017), supporting rich communities of sharks, rays, teleosts, cetaceans, sea turtles, and a plethora of invertebrates. Consequently, they play a critical role in ecotourism in the area (Walters and Samways 2001) and provide other important ecosystem services as well (Laing et al. 2020). The temperate reefs (Figure 2ae) and reef mosaics farther south and west are rocky, and some are associated with kelp forests.

In contrast to the well-studied coral reefs on the northeast coast, rocky reefs on the west coast are hardly known, with information increasing for rocky reefs along the south coast and east coasts (Sink et al. 2019). Rocky reefs support diverse communities of algae and marine invertebrates (Celliers et al. 2007; Porter et al. 2013), and, like their coral counterparts, are important sites for ecotourism (du Preez et al. 2012). They also play a key role as essential habitat for shellfish (e.g. oysters, abalone, alikreukel), rock lobsters and fish, including many linefish species that support food, livelihoods and cultural identity.

Kelp forests

Three kelp forest ecosystem types (e.g. Figure 2ad) are recognised in South Africa: Agulhas, Cape and Namaqua (Sink et al. 2023). They include three of the four species of large brown macroalgae, with the two common west coast species, sea bamboo *Ecklonia maxima* and split-fan kelp *Laminaria pallida*, being the species of economic significance in South Africa (Blamey and Bolton 2018). *Ecklonia maxima* is the dominant canopy-forming kelp that grows in the shallows to depths of ~30 m. Its distribution extends from the Orange River on the west coast to De Hoop on the south coast (Dunga 2020), with its eastern range limit expanding along the southwest coast (Bolton et al. 2012). *Laminaria pallida* is confined to the west coast, where it is a subcanopy species to *E. maxima* up to depths of ~30 m. However, in the northwest, *L. pallida* develops a hollow stipe and replaces *E. maxima* in the shallows (Rothman et al. 2017). It is found from Danger Point on the southwest coast of South Africa to Rocky Point in northern Namibia, where it is the only kelp species present (Dunga 2020). Much less is known about the giant kelp *Macrocystis pyrifera* in South Africa. It is present in forests dominated by other kelp species, and has been found at only eight localities west of Cape Point, along ~200 km of the coast (Fleischman et al. 2020).

The spiny kelp *Ecklonia radiata* is present along the south and east coasts, and is the only species not yet mapped and included in the kelp ecosystem types. This is because of limited local studies on its spatial distribution as it forms a subtidal fringe in sheltered habitats and occurs in poorly known, deeper subtidal populations (e.g. on the Agulhas Bank and Alphard Bank, at Sodwana Bay, and in Mozambique: Wernberg et al. 2019), where it may fall outside of the EDCZ. Kelp species are important formers of habitats that, in turn, support diverse communities of fish, crustaceans and molluscs, and serve as important nursery areas for a variety of species. They link coastal ecosystems through exports of nutrients, such as by providing sandy-beach invertebrates with valuable allochthonous inputs when washed up as kelp wrack (Koop et al. 1982).

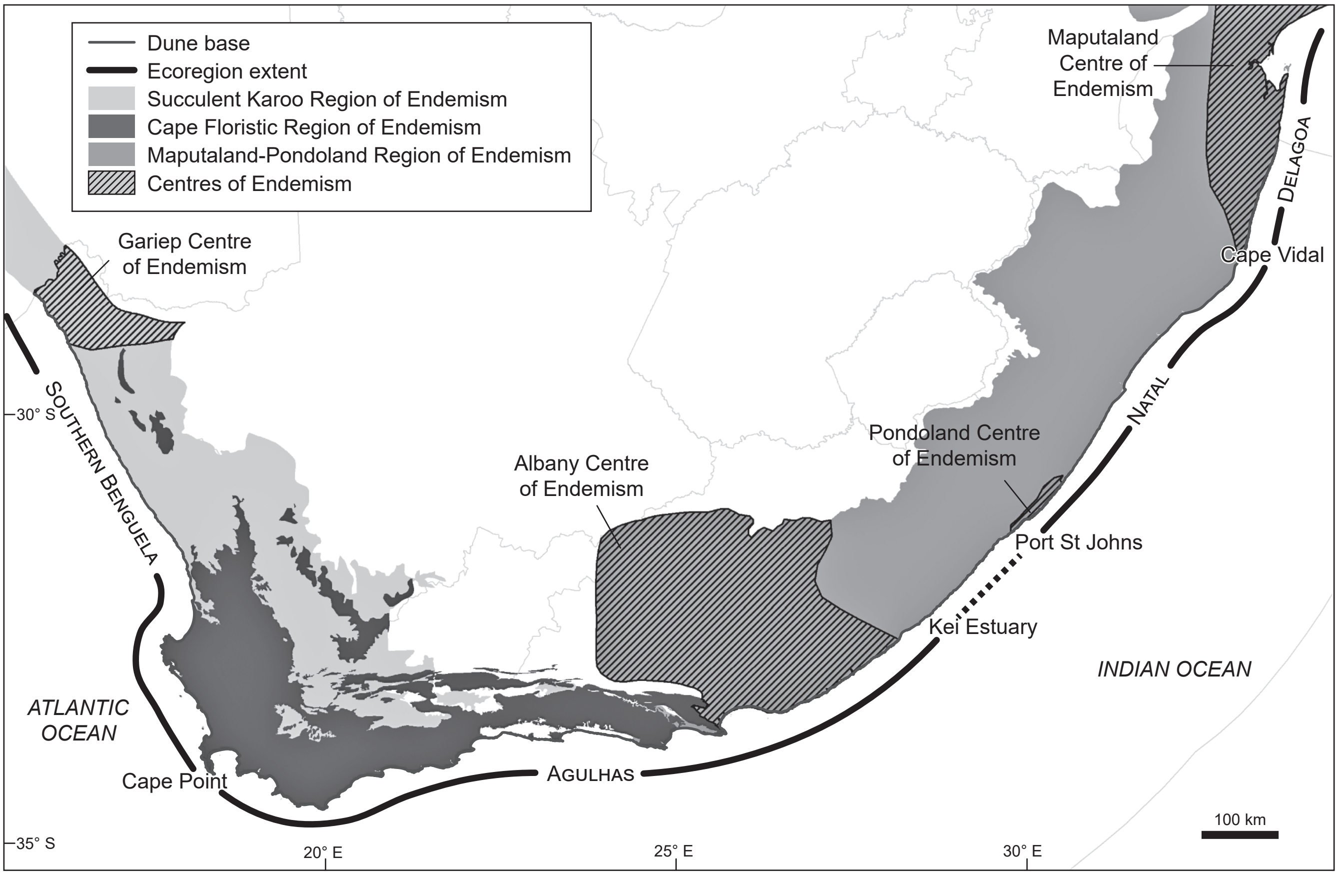

Figure 3: The four South African ecoregions, with place names indicating the biogeographic breaks; the area between Kei Estuary and Port St Johns is a transition zone between the Natal and Agulhas ecoregions. The three Regions of Endemism and four of the Centres of Endemism that are part of the coast are also shown. Data sources: van Wyk and Smith (2001); ESRI (2024)

Kelp forests also provide a myriad of important ecosystem services to people, ranging from commercial to recreational values (Blamey and Bolton 2018; Wernberg et al. 2019).

Bays

There are several major embayments between St Helena Bay and Algoa Bay (Figure 2ah). These are retentive and relatively sheltered coastal environments, important for ecological processes (Pfaff et al. 2022). Bays provide natural shelter from high wave energy, storms and swell, and serve as refugia for species that seek calm conditions, either permanently or during certain parts of their life cycle. The circulation in bays traps and retains seawater, causing longer residence time in bays than on the open coast (Pfaff et al. 2022). Bays in temperate regions are therefore areas of relative warmth (Smit et al. 2013) and thermal stratification, fostering enhanced phytoplankton abundance and primary production (Broitman and Kinlan 2006; Largier 2020). This productivity boosts the entire food web (Kudela et al. 2008), such that higher trophic levels, like zooplankton, fish, birds and megafauna, aggregate in bays to feed or reproduce. Bays have therefore also become hotspots for many human activities, leading to increased threats on bay ecosystem types through overexploitation, shipping, invasive species, pollution and harmful algal blooms (Pfaff et al. 2022).

Hard and soft inner shelf, and river-influenced ecosystem types

Marine ecosystem types beyond the surf zone are considered coastal if they have a strong, direct influence from land (Harris et al. 2019)—for example, the interaction between the swell and sea floor, and dependence on flows of fresh water and terrigenous sediments through estuaries (Porter et al. 2014). Hence, they include ecosystem types on the inner shelf (rocky, sandy, muddy and mosaics), bays, as well as those muddy (Figure 2ag) and sandy ecosystem types influenced by rivers (Harris et al. 2019), primarily the Orange, Olifants, Groot Berg, Mzimvubu and uThukela rivers. Freshwater flow can be relatively low and dissipate quickly on the coast, except during flood events, where millions of tonnes of fresh water and silt can be transported onto the entire shelf region. Work on estuarine fans and plumes is still emerging in South Africa, with some progress in mapping these coastal features (Mtetandaba 2022), some of which are recognised as ecosystem types (e.g. Kei Fluvial Fan: Sink et al. 2023). Ecosystem types influenced by the Orange River on the west coast (e.g. Orange Cone Muddy Mid Shelf) mark the farthest offshore extent of the EDCZ. In the KZN Bight on the east coast, the continental shelf is narrow, and the terrigenous supply of water, nutrients and sediment from the uThukela River (Figure 2m) is so substantial (Scharler and Ayers 2019) that it influences ecosystems slightly beyond the shelf edge, which is the only location in South Africa where this is the case (Harris et al. 2019).

Coastal biodiversity patterns

South African coastal biodiversity is broadly arranged in four ecoregions (Figure 3): cool-temperate west coast (Southern Benguela); warm-temperate south coast (Agulhas); subtropical east coast (Natal); and tropical northeast coast (Delagoa) (Teske et al. 2011; van Niekerk et al. 2020; Sink et al. 2023). The breaks between these ecoregions are broadly similar across realms, and often form transition zones rather than sharp boundaries, with species likely responding to similar physical gradients (e.g. temperature, rainfall) and various barriers and corridors to connectivity (Teske et al. 2011; Lett et al. 2023). Many coastal species are present in only one or two of these ecoregions, such that the coast has particularly high levels of endemism (Kier et al. 2009; Teske et al. 2011; Scott et al. 2012; Harris et al. 2014).

On land, all three broad regions of high plant diversity and endemism in the country occur along the coast: Succulent Karoo, Cape Floristic, and Maputaland–Pondoland regions (van Wyk and Smith 2001; Raimondo 2015) (Figure 3). This includes four centres of plant endemism: Gariep, Albany, Pondoland and Maputaland (van Wyk and Smith 2001) (Figure 3). The EDCZ also overlaps slightly with the Knersvlakte and Little Karoo centres of endemism, but the overlap in both cases is so small that they are not considered to be coastal. The Cape Floristic Region is particularly exceptional, ranking second globally (out of 90 bioregions) in endemism richness (Kier et al. 2009). Endemism richness in amphibians, reptiles, birds and mammals in South Africa is also high within the EDCZ (Kier et al. 2009; Lewin et al. 2016). The number of coastal freshwater endemic species is limited, with examples including the giant palm *Raphia australis* from Maputaland (Mucina et al. 2006), Pickersgill's reed frog *Hyperolius pickersgilli* (Kotze et al. 2019), and blue river crab *Potamonautes lividus* found primarily in Indian Ocean Coastal Belt forests and swamp forests (Daniels et al. 2020).

Approximately one-third of the 150 estuarine-associated fish species that regularly occur in South African estuaries are southern African endemics. Twenty of these species are found exclusively in South African waters, with some species confined to only a few systems, for instance the Knysna seahorse *Hippocampus capensis*, Bot River klipfish *Clinus spatulatus*, and estuarine pipefish *Syngnathus watermeyeri* (van Niekerk et al. 2019). Even important 'bait' invertebrate species are endemic to South Africa (e.g. freshwater sand-shrimp *Palaemon capensis*) or to southern Africa (e.g. sandprawn *Kraussillichirus kraussi*; mudprawns *Upogebia africana* and *Macrobrachium petersii*). Although 35 bird species are considered dependent on estuaries as more than 15% of their regional populations have been found in coastal lagoons and estuaries (Hockey et al. 2005; Turpie et al. 2012), there are no entirely estuary-dependent bird species.

In the sea, marine species richness is also high, with a current estimate of >13 000 species reported from South Africa's mainland maritime domain (Sink et al. 2019), which includes some species beyond the coastal zone. Estimates of marine species endemism range between 26% and 33% (e.g. Awad et al. 2002; Griffiths et al. 2010; Griffiths and Robinson 2016), with South Africa reported as having the third-highest marine endemism after New Zealand (51%) and Antarctica (45%) (Costello et al. 2010). As before, these statistics include non-coastal marine species, but the pattern is also expected to hold for the coast specifically. There are more than 2 000 coastal marine invertebrate species, almost a third of which have alongshore ranges of <500 km, with hotspots of range-restricted endemic species at False Bay, Gqeberha, Durban and St Lucia (Scott et al. 2012). Notably, all the colonial seabird species that nest in the South African coastal zone (Crawford et al. 2015) and more than half the chiton, prosobranch gastropod and beach macrofauna species are endemic (Awad et al. 2002; Harris et al. 2014). About 18% of coastal fishes are also endemic species (227 of the 1 239 species included in Turpie et al. [2000]), primarily from the families Clinidae, Sparidae and Gobiidae (Turpie et al. 2000).

Across all realms, the highest endemicity is consistently reported for the Agulhas Ecoregion (Figure 3). This ecoregion lies entirely within South Africa's territory, meaning that the country is solely responsible for conserving these unique species. Some taxa show a peak in richness at the biogeographic breaks (e.g. around the southwestern Cape and/or on the Wild Coast) because many species' distributions from each adjacent ecoregion overlap through these transition zones (Awad et al. 2002; Harris et al. 2014). Despite the generally highest endemism along the south coast, some higher taxa increase in species richness from west to east. These are generally the marine taxa that are influenced by the species-rich Indo-Pacific region, or are extensions of the diverse assemblages in the western Indian Ocean, coastal fishes in particular (Turpie et al. 2000). Interestingly, there are similar alongshore patterns in genetic diversity as well (e.g. for rocky shore and reef invertebrates: Wright et al. 2015). The peak in foredune plant species and endemism around the southwestern Cape is largely due to the highly diverse Cape Floristic Region, described above. Although there is no formal assessment of estuarine species richness and endemism nationally, all the South African endemic species listed above are found along the south coast. Consequently, safeguarding the country's unique biota along the south coast is a particular priority given high, cross-realm endemic richness and the contraction of this ecoregion in the face of climate change (Whitfield et al. 2016).

Securing the coast as a national asset and legacy for future generations

South Africa arguably has one of the most diverse and scenic coasts in the world, supporting a wealth of unique biodiversity. The benefits derived from coastal ecosystems and species serve practical needs (e.g. food, medicine, useful materials, jobs), physical needs (e.g. places to play, exercise and recreate), cognitive needs (e.g. places of learning, stimulation and innovation), emotional needs (e.g. enhancing health and wellbeing) and spiritual needs (e.g. sites for connection, cleansing, rituals and worship) (Harris et al. 2021). Consequently, South Africa's coast is a national asset, and a key part of the country's natural heritage. The high number of endemic species highlights the importance of carefully managing this coastal zone for long-term sustainability so that South Africa's globally unique biodiversity can persist to the benefit of current and future generations.

There has been substantial progress in protecting coastal biodiversity in the country (87% of the coastal ecosystem types have some protection), but the amount of degraded habitat (46.9%) and the high proportion of threatened coastal ecosystems (60%) is of concern (Harris et al. 2022). It is especially worrying given that coasts are highly vulnerable to key climate-change vectors (namely, rising sea levels, changing temperatures and ocean currents, increasing intensity and frequency of coastal storms and floods), which are superimposed on intensifying and diversifying coastal pressures. These add both complexity and importance to the management and protection of the coast. The emerging national marine spatial planning process (RSA 2019; DFFE 2021), and targets for restoration and conservation in the Kunming–Montreal Global Biodiversity Framework (Convention on Biological Diversity 2022), provide opportunities and incentives to secure the South African coastal zone as a legacy for future generations. Strategic planning and protection, targeted restoration, and effective coastal management that accounts for the connections and inter-dependencies among ecosystems and with people can safeguard the country's biodiversity and support long-term coastal benefits. It also emphasises the value of standardising and aligning coastal terminology and boundaries so that data and knowledge can flow seamlessly into the assessment, planning, prioritisation and management processes.

Acknowledgements — This review was written as part of the content for the National Biodiversity Assessment 2025. LRH was funded by the South African National Biodiversity Institute. JBA was supported by the National Research Foundation of South Africa through the DSI/NRF Research Chair in Shallow Water Ecosystems (UID 84375). KJS acknowledges the projects of Deep Connections and Agulhas Bank Connections funded by the National Research Foundation (grant nos. 129216 and 129213) through the African Coelacanth Ecosystem Programme. DSI-CSIR Parliamentary Grants supported LVN (Coastal Systems and Earth Observation project) and HVD (DIGITAR project). The MeerWissen project 'CoastWise' also supported LRH during an early phase of the work; MeerWissen is funded by the German Federal Ministry for Economic Cooperation and Development (BMZ) and implemented by the Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) GmbH. All funders are thanked for their support.

ORCID

Janine Adams: https://orcid.org/0000-0001-7204-123X
Anisha Dayaram: https://orcid.org/0000-0003-4160-812X
L.V. Dunga: https://orcid.org/0000-0001-6448-8285
Linda Harris: https://orcid.org/0000-0003-4719-0481
Nancy Job: https://orcid.org/0000-0002-4929-7592
Stephen Kirkman: https://orcid.org/0000-0001-5428-7375
Stephen Lamberth: https://orcid.org/0000-0002-4076-3622
Maya Pfaff: https://orcid.org/0000-0002-9253-0708
Jacqueline Raw: https://orcid.org/0000-0002-5270-032X
Gavin M. Rishworth: https://orcid.org/0000-0003-1148-0081
Amanda Robbins: https://orcid.org/0000-0002-1082-5490
Kerry J. Sink: https://orcid.org/0000-0001-5051-573X
Andrew L. Skowno: https://orcid.org/0000-0002-2726-7886
Heidi van Deventer: https://orcid.org/0000-0002-7854-2155
Lara van Niekerk: https://orcid.org/0000-0001-5761-1337

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Manuscript received November 2024 / revised January 2025 / accepted January 2025