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ECOLOGY OF PSAMMOPHILY IN THE NAMIB DUNES

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Abstract

Across the hyperarid Namib Desert, winds have shaped sand into dunes and sandsheets, regulated moisture and temperature levels, and transported organic material, engendering the evolution of psammophilous (sand-living) plants, animals and microbes. Namib dunes stretch from the Buffelsrivier in the Namaqualand Sandveld, South Africa, across the Tsau||Khaeb National Park and the Namib Sand Sea in Namibia, resuming in the Iona Skeleton Coast Transfrontier Park, up to the Rio Curoca in Angola. In their width, the Namib dunefields and sandsheets straddle the coastal fog belt and desert grasslands near the base of the escarpment, while in their length, they span opposite gradients of winter and summer rainfall. Geophysical characteristics vary between seven biotopes and their different configurations in different dune types: interdunes, dune bases, dune plinths, slipfaces, dune crests, sandsheets and nebkha dunes. For over 15 Ma, winds have driven dunes from south to north, transporting evolving psammophilic xerophiles (desert-adapted). Subterranean dynamics in dunes enable psammophiles to obtain water from moisture-retaining sand. Equally important is the above-ground availability of fog due to elevated dunes intercepting advective fog and trapping radiative fog that recycles moisture. Multiple abilities to harvest fog water with benefits that trickle through the biotic communities make fog a key ecosystem driver in most Namib dunes. Many dune plants cope with mobile sand by outgrowing sand deposition or building nebkhas. To cope with sandblasting, psammophorous plants fix a protective layer of sand grains to leaves and roots while other psammophilous plants shield themselves with a thick epidermis and bark or hairs and nested structures or by temporarily or seasonally withdrawing into the sand. Psammophilous animals have developed specialised methods to move through and on the sand, construct stable burrows, and apply sand attributes such as communication via microseismic vibrations. The biotic communities and the special traits of their constituents differ between biotopes. The Namib dune ecosystems' structures, processes and functioning fundamentally depend on only a few keystone species of plants. Threats to psammophile communities include off-road driving, infrastructure developments, and climate change effects on the wind regimes that alter the most important characteristics of dune dynamics for psammophiles. Ecological restoration of impacts on dune communities is challenging and requires more research. The existing knowledge of Namib dunes was primarily built up in the Namib Sand Sea. However, increased accessibility of other Namib dunefields offers opportunities to broaden research while continuing to increase knowledge of well-studied systems to shrink vital gaps, such as an improved understanding of the subsurface dynamics of moisture and above-ground dynamics of keystone plants.

1. Introduction

Desert dunes shape their plant and animal communities, which, in turn, modify dunes. Organisms living in dunes need to cope with and make optimal use of the physical characteristics of sand at the scales of grains, dunes, dunefields and sandsheets. Primary features concern how sand affects the availability of moisture to organisms living in and on the sand and how this is affected by wind.

In this chapter, we depict the characteristics and processes relating to the biota and ecology of plants and animals and their communities across the dunefields of the Namib Desert, the most wind-erosion-prone strip of southern Africa (Kestel et al., 2023). We take into account previous overviews of the ecology of the Namib dunefields (Seely, 1978b; Robinson and Seely, 1980; Seely, 1984, 1991; Pallett, 1995; Jürgens et al., 1997; Burke, 2004, 2006; Robertson et al., 2012; Mendelsohn and Mendelsohn, 2018; Burke, 2020; Wassenaar et al., 2021; Huntley, 2023). We give examples, largely based on the linear dunes of the Namib Sand Sea, where most of the research has taken place, of the traits of plants, animals, and their communities and how they relate to the physical properties and dynamics of various dune biotopes. Nevertheless, it was possible to widen the scope for plants across the Namib and biotopes in the winter rainfall region. Next, we examine the vulnerability of dune biota to anthropogenic impacts and climate change, as well as conservation and restoration approaches. We end by suggesting future research questions.

2. Geophysical context

The Namib dunefields demonstrate the interplay of biota with moisture, wind and substrate characteristics at sand grain to landscape levels (Seely, 1991). Important geophysical characteristics include sand being more or less unconsolidated and penetrable, with subsurface aerated humid pore spaces, good thermal conductance and sonic transmission, and primarily bare surfaces (Robinson and Seely, 1980). Water-related characteristics of dune sand include rapid infiltration, limited water retention, and slow capillary transport of moisture (Li et al., 2016; Jürgens et al., 2023). Wind transports sand, shapes dunes and sorts grains (Lancaster, 1989; Livingstone, 2013), sandblasts, exposes or buries organisms and organic material through erosion or deposition (Robinson and Seely, 1980; Jürgens, 1996), and enhances above-ground convective heat exchange (Heinrich, 1993). In turn, vegetation cover affects the transport of sand by wind (Lancaster and Baas, 1998). Of all geophysical factors, wind is considered to be the most important for controlling dune morphology, influencing the amount of advective fog and rain that reaches dunes, distributing and concentrating plant detritus and seeds, and affecting the temperature conditions experienced on dune surfaces (Seely, 1984).

These factors vary across the latitudinal extent of the extensive sandsheets and small dunefields in the Namaqualand Sandveld (28.6-29.7 °S), several dunefields and expansive sandsheets in the Tsau||Khaeb National Park (Sperrgebiet) (28.6-27.4°S), the Namib Sand Sea in the Namib-Naukluft Park (27.1-22.7°S), and the Skeleton Coast and Iona Dunefields in the Iona Skeleton Coast Transfrontier Park (15.7-20.4°S) (Lancaster, 2014) (Fig. 1). Beyond these large dunefields, there are numerous smaller dunefields, sandsheets and topographic dunes in the 1600 km stretch between and beyond the Buffelsrivier in South Africa (29.7°S) and Rio Curoca in Angola (15.7°S) (Lancaster, 1989; Pallett, 1995; Jürgens, 2006; Mucina et al., 2006; Livingstone, 2013; Mendelsohn and Mendelsohn, 2018; Mendelsohn et al., 2022) (Fig. 1).

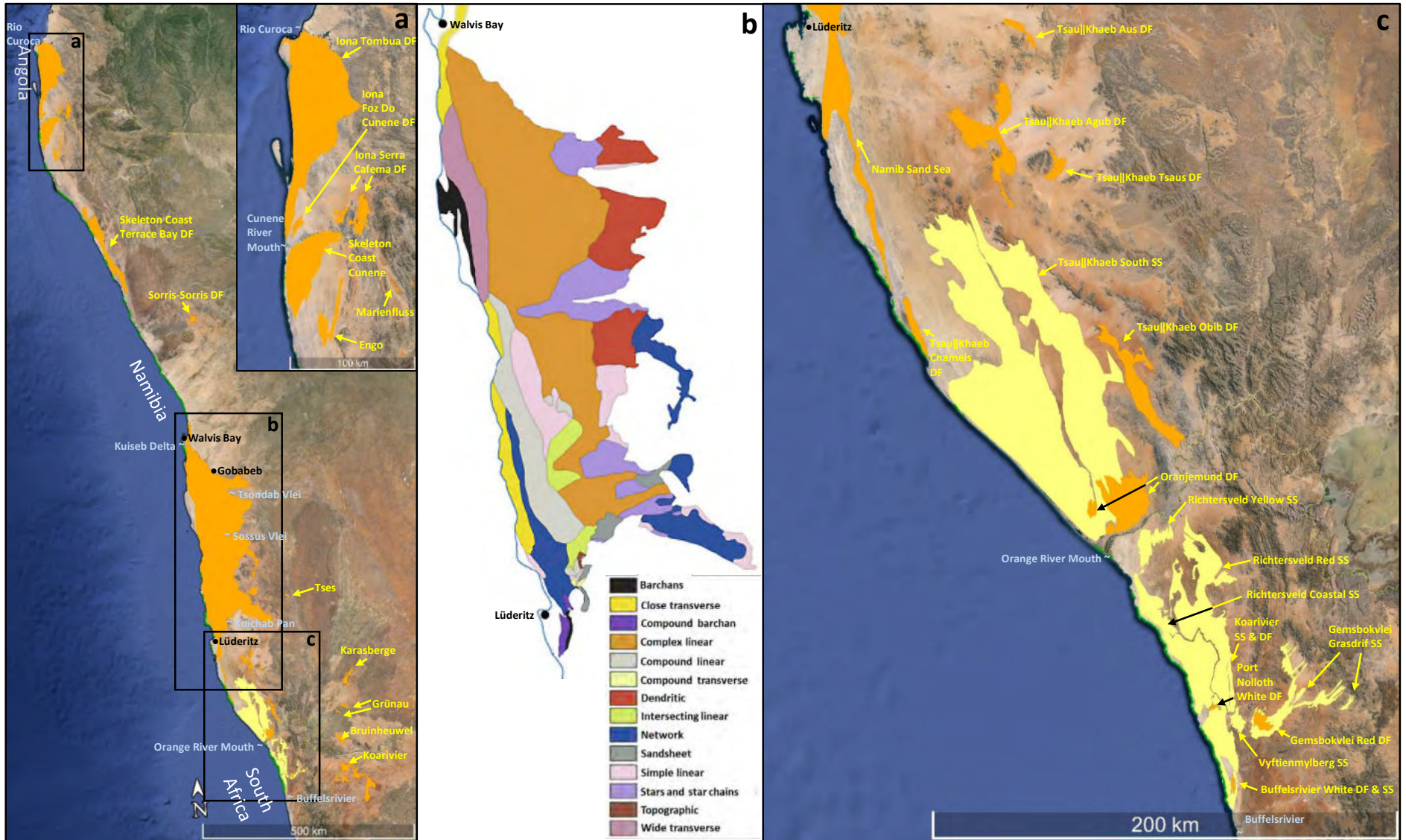


Figure 1: Map of the dunefields (orange), sandsheets (yellow) and coastal nebkhas (green) of the Namib Desert (MAP < 100 mm plus buffer zone) between Buffelsrivier in South Africa and Rio Curoca in Angola. The left panel shows an overview of all Namib dunes, with inset (a) showing details of the Cunene-Iona dunes and also showing the locations of panel (b) with details of the Namib Sand Sea and panel (c) with details of the Tsau||Khaeb and Namaqualand dunefields and sandsheets. DF=dunefield, SS=sandsheet. (Left and Right panels were compiled from Google Earth, as mapped by Norbert Jürgens; middle panel was adapted from Fig.2d of Livingstone, 2013)

The northern dunefields fall into a predominantly summer rainfall region, with increasing importance of winter rainfall in the southern dunefields (Tyson and Preston-Whyte, 2001). Another gradient is oriented west to east from the coastal nebkhas and adjacent transverse and barchan dunes, giving way in the Namib Sand Sea to several kinds of linear dunes, then star dunes further inland, and network dunes along the eastern margins situated up to 150 km from the coast (Lancaster, 1989; Livingstone, 2013) (Fig. 1). The Namib dunefields cross several climatic zones (Walter, 1936; Jürgens, 1991; Jürgens et al., 1997; Hachfeld and Jürgens, 2000; Loris et al., 2001; Jürgens et al., 2013). Within 60 km of the coast, where the mean annual precipitation from rain is low (MAP = 10 mm), the primary sources of moisture are high humidity and advective fog during 37-87 nights per annum (Lancaster et al., 1984; Mitchell et al., 2020). Further inland, the hot, dry atmosphere is interspersed by sporadic rainfalls amounting to MAP of 20-30 mm in the middle zone and up to MAP of 100 mm in the eastern zone (Lancaster et al., 1984; Eckardt et al., 2013). At least once per year, the latter zone experiences effective rainfall events, defined as >11 mm a week, sufficient to trigger ephemeral grasses to germinate and complete a lifecycle (Seely, 1978a; Henschel et al., 2005). The dunefields are devoid of surface water except temporarily where dunes cross ephemeral rivers and dam floodwaters or where a few isolated freshwater springs near the coast are fed from groundwater (Hellwig, 1988; Christelis and Struckmeier, 2001). Shallow groundwater underlying dunefields slowly seeps through buried palaeochannels from adjacent rivers or terminal vleis (Schmidt and Plöthner, 1999; Krapf, 2003; Klaus et al., 2008; Stone and Thomas, 2013; Paillou et al., 2020) and is tapped by phreatophytes (Robinson, 1976; Jürgens et al., 1997; Soderberg, 2010).

Each dune represents a composite of several biotopes. In simplified terms, there are seven distinct biotopes, not always present on all dune types (Table 1) (Fig. 2): a slipface below the dune crest, flanked by windward and lee-side plinths ending at level dune bases, separated by interdune plains that sometimes contain nebkha dunes and may extend into sandsheets. Patterns of wind, temperature, moisture, slope aspect, grain size composition, sand compaction, substrate stability, sand erosion and deposition, detritus dispersion, mineral composition, and other factors affecting biota differ across these biotopes (Robinson and Seely, 1980; Lancaster, 1989; Ronca et al., 2015). Furthermore, dune-living organisms are influenced by constantly changing vertical gradients of temperature, moisture, and vapour pressure above and below dune surfaces (Seely and Mitchell, 1987; Seely et al., 1990; Roberts, 1991; Seely, 1991; Mitchell et al., 2020).

The southern Namib dunes are ancient, although not quite as old as the onset of aridity at the end of the Cretaceous (Ward et al., 1983). The first dunes near the Orange River date back to 43 Ma, developing into dunefields with intensifying aridification during 15-8 Ma and fossilising into Tsondeb Sandstone during a subsequent slightly wetter phase (Ward, 1987). The current dunes of the Namib Sand Sea were initiated 5 Ma ago and have a minimum residence period of 1 Ma (Vermeesch et al., 2010), overlying and incorporating sand from the Tsondeb sandstone (Ward and Corbett, 1990; Garzanti et al., 2012). The Skeleton Coast and Iona dunefields, a mix of local river sands and longshore transport of Orange River sands, date back to the Pleistocene sea level changes (Krapf, 2003; Garzanti et al., 2014; Miller et al., 2021).

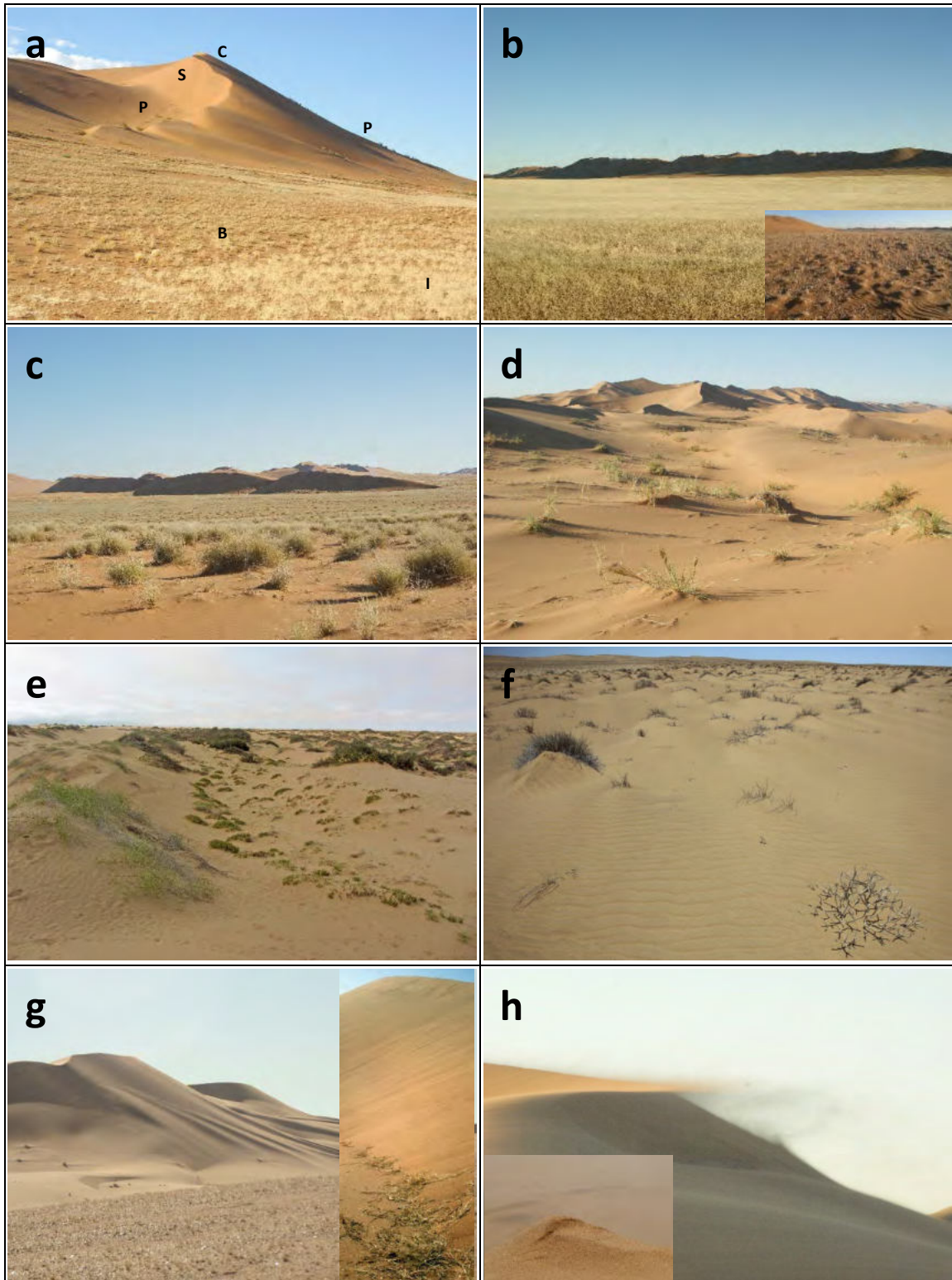


Figure 2: Namib dune biotopes: a) Examples of relative locations of interdune (I), dune base (B), plinth (P), slipface (S) and crest (C); b) Interdune plain with *Stipagrostis gonatostachys*, inset: sand remnants around withered grass as interdune gets bare; c) Dune base (foreground) with *S. lutescens*; d) Plinth (foreground) with *S. sabulicola*; e) Nebkha dune with *Acanthosicyos horridus*, *Trianthema hereroensis* and *Capparis hereroensis*; f) Sandsheet with *Cladoraphis cyperoides*; g) Slipface, inset: detritus at avalanche base; h) Dune crest with wind-mobilised sand, inset: the crest is the wettest location on dunes during advective fog. (Photos: Joh Henschel, except Fig.2f: Norbert Jürgens)

Table 1: Occurrence of Biotopes on different types of dunes. T=typical, S=sometimes.

Dune Type	Dune Biotope						
	Interdune	Base	Nebkha Dune	Plinth	Slipface	Crest	Sandsheet
Barchan	T			T	T	T	
Transverse	S	S	S	T	T	T	
Linear	T	T	S	T	T	T	
Star	T	T	S	T	T	T	
Network	T	T	S	T	S	T	
Sandsheet	S	S	T				T
Whaleback	T		S	T			T
Coastal Nebkhas	S		T				S
Topographic	T	T	S	T	S		
Wind Streak	T		S	T	S	T	

3. Psammophily

Many desert organisms are substrate specialists (Danin, 1991; Prendini, 2001). The biotic constituents of the Namib dunes have had a long time to adapt to the arid to hyperarid conditions and sandy substrates in the context of the above-mentioned geophysical characteristics and processes, especially the interplay of wind, sand and moisture (Robinson and Seely, 1980; Seely, 1991) (Table 2). These properties include grain size composition, bulk density, substrate stability, sand erosion and deposition, and sandblasting. The sand grain size on slipfaces is the smallest, on average, and its composition is least variable, getting progressively larger and more variable down the plinths, coarsest at the dune base, and most variable on the interdune (Lancaster, 1989). Compaction and substrate stability are lowest on the slipface, intermediate on dune plinths and bases, and highest on interdunes. Psammophilous plants, animals and microbes specialise living in these conditions and are distributed across dune biotopes according to these sand grain characteristics, though several other chemical, microclimatic, and community factors also come into play (Robinson and Seely, 1980; Ronca et al., 2015) (Table 2).

The total above-ground biomass (plants, animals, detritus) in the Namib dunes is extremely low, around 2.7 g.m⁻² in dry years and 26.1 g.m⁻² in wet years (Seely and Louw, 1980), less than the dry-to-wet range in other deserts, 13-924 g.m⁻² (Hadley and Szarek, 1981; Fei et al., 2022).

3.1. Psammophilous plants

The biodiversity of plants in the Namib dunes is lower than in adjacent gravel plains, mountains or river valleys (Jürgens, 1996; Craven, 2009; Robertson et al., 2012; Seely, 2012; Burke and Loots, 2020). Plant endemism is exceptionally high in the sandsheets and dunefields of the Tsau||Khaeb and Richtersveld, reflecting the high degrees of habitat specialisation and the biogeographical history of the northernmost Succulent Karoo. By comparison, the levels of plant endemism are moderate and at a larger geographic scale in the dunefields elsewhere.

Psammophilous plants of the Namib sandy habitats developed many, but not all, adaptations to aridity found in xerophilic plants in other habitats. Survival strategies include improving water uptake, reducing evapotranspirational water loss, and forming succulent water-storing organs or tissues. They also include biochemical and genetic mechanisms that enhance the ability to survive water losses at the tissue and cell level so that dehydrating poikilohydric plants maintain the potential to rehydrate. Furthermore, geophytes, hemicryptophytes and stem-reducing chamaephytes shed some organs and

resprout, while annuals and ephemerals die and re-establish from seed. The Namib dune plants use one or combine several of the above adaptation strategies to fit the different geophysical environments.

In regions within reach of fog, a principal feature of some Namib psammophytes, such as the Namib Dune Bushman Grass *Stipagrostis sabulicola*, the succulent Muisvygie *Trianthea hereroensis*, and the cucurbit !Nara *Acanthosicyos horridus*, is their ability to harvest fog with their canopies (Robinson, 1976; Seely et al., 1977; Ebner et al., 2011; Kool et al., 2021) and employ extensive lateral shallow roots to access sand moisture at fog-penetration levels (Louw and Seely, 1980; Nott and Savage, 1985b) (Fig. 3). Besides watering plants, fog washes mineral-rich dust from plant leaves and stems, providing nutrients to plants in the fog zone (Gottlieb et al., 2019). In addition to the adaptation to fog, phreatophytes like !Nara, which also occur outside the fog zone, have deep roots and very wide xylem vessels, allowing accelerated water transport to tap groundwater (Robinson, 1976; Kutschera et al., 1997; Müller, 2000; Soderberg, 2010).

Numerous species show morphological adaptations interpreted as ways to reduce water losses. In extreme cases, leaves are lacking altogether, and photosynthesis and carboxylation occur in the chloroplast carrying primary cortex tissue of stems, as found in !Nara, and in many stem succulent *Euphorbia*. However, the latter rarely occur in dunes, with *Euphorbia virosa* in the Iona Dunefields being a rare example. Small leaves with a reduced surface area are found in most grasses, many *Calobota* species, and some *Hermannia* species, e.g., *H. minimifolia*. Various types of hairs reduce transpiration in most *Hermannia* species. Some plants shed their leaves, twigs or branches, while geophytes shed their entire above-ground shoot system during drought.

The overwhelming success of grasses in the dunes of the Namib summer rainfall region (*Stipagrostis sabulicola*, *S. lutescens*, *S. seelyae*, *S. ciliata*, *S. obtusa*, *S. subacaulis*, *S. gonatostachys*, *S. giessii*, *S. prodigiosa*, *S. brevifolia*, *Cladoraphis spinosa*, *C. cyperoides*) and the Kalahari (*Stipagrostis amabilis*, *Schmidtia kalahariensis*) is interpreted as the combined effects of reduced leaf surface area and protection of buds and parts of the stems by leaf sheaths. In the Namib winter rainfall region, *Cladoraphis cyperoides*, *S. ciliata*, and *S. subacaulis* sometimes reach high cover as pioneers after disturbance, while *S. geminifolia*, *S. dregeana*, *S. obtusa* and *C. spinosa* remain sparse. Especially *S. ciliata* and, to a lesser extent, *S. obtusa* and *S. giessii*, rapidly germinate and develop efficient root systems following effective rainfalls and produce the dominant biomass over vast areas, with mass flowering producing long-lived seedbanks. Other plant annuals, ephemerals and geophytes sometimes also undergo impressive mass germination and flowering, especially in the sandsheets of the winter rainfall region, when most of the competing perennial plants have died, as in Tsau||Khaeb after the long drought of 2012 to 2023.

Water storage in succulent organs and tissues is a widespread adaptation, more frequently observed closer to the Atlantic coast and very well developed in the winter rainfall ecosystems of the Succulent Karoo. Some leaf succulent Aizoaceae grow on sandsheets in the Tsau||Khaeb and more so in the Richtersveld. These are primarily woody dwarf shrubs of the genera *Brownanthus*, *Amphibolia*, *Cheiridopsis*, *Eberlanzia*, *Lampranthus*, and *Stoebertia*, but also annual or ephemeral life forms of the genera *Mesembryanthemum* and *Galenia*. Many leaf succulent dune chamaephytes shed smaller roots during drought to avoid water losses by root transpiration into the dry sand. Regarding desiccation-tolerant plants, it is notable that no poikilohydric vascular plant exists in the Namib dunes. However, many plants shed their leaves, twigs or branches during drought.

Table 2. Effects of physical and biotic features of Namib dune sand on each other, where ● indicates a direct impact of a feature (column) on another (row), and ○ indicates an indirect impact (adapted and expanded from Robinson and Seely (1980))

← Independent	↓ Dependent	Wind	Dune morphology	Rain	Fog deposition	Sand temperature	Sand moisture	Grain size	Air temperature (1-5 cm)	Air humidity (1-5 cm)	Sand aeration	Seismic vibrations	Dune driving	Plant growth	Microbial communities	Detritus	Fog drinking	Detritus feeding	Sand burrowing	Sand swimming	Subsurface activity	Surface activity
Wind		-	●	-	●	●	●	-	●	●	●	●	-	●	●	●	●	●	-	-	○	●
Dune morphology		●	-	-	●	●	●	-	○	○	○	○	●	●	●	●	○	○	○	○	-	○
Rain		-	○	-	-	○	●	-	●	●	●	●	○	●	●	-	○	-	○	○	-	○
Fog deposition		-	-	-	-	●	●	-	●	●	●	○	○	●	●	-	●	○	-	-	●	●
Sand temperature		-	-	-	-	-	●	-	●	●	-	○	○	●	●	-	-	○	●	●	●	●
Sand moisture		○	-	-	-	●	-	-	-	-	●	○	-	●	●	-	●	-	●	●	-	○
Grain size		○	-	-	-	●	●	-	-	-	●	●	○	○	●	-	●	-	●	●	-	-
Air temperature (1-5 cm)		-	-	-	○	●	●	-	-	●	-	-	○	●	-	-	-	○	-	-	-	●
Air humidity (1-5 cm)		-	-	-	●	○	●	-	●	-	-	-	-	●	-	-	○	-	-	-	-	○
Sand aeration		-	-	-	-	●	●	-	-	-	-	●	-	●	●	-	-	-	●	●	●	-
Seismic vibrations		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●	●	●	●	●
Dune driving		-	○	-	○	○	○	○	○	○	●	-	-	●	●	○	-	-	○	-	-	●
Plant growth		-	●	-	●	●	●	-	●	●	○	●	○	●	●	●	●	○	○	○	○	●
Microbial communities		-	-	-	-	-	-	-	-	-	○	-	-	●	●	●	●	●	○	-	-	-
Detritus		-	-	-	●	●	-	-	-	-	○	●	-	○	-	-	○	●	-	-	●	●
Fog drinking		-	-	-	○	-	●	-	-	-	-	-	-	-	-	-	-	○	-	-	●	●
Detritus feeding		-	-	-	-	-	-	-	-	-	-	-	-	-	●	●	-	-	-	-	●	●
Sand burrowing		-	-	-	-	○	○	-	-	-	●	●	-	-	-	-	-	-	-	-	-	-
Sand swimming		-	-	-	-	○	○	-	-	-	●	●	-	-	-	-	-	-	-	-	-	-
Subsurface activity		-	-	-	-	-	-	-	-	-	●	●	-	-	-	-	○	●	-	-	-	-
Surface activity		-	-	-	-	-	-	-	-	-	-	●	-	-	-	-	●	●	-	-	-	-

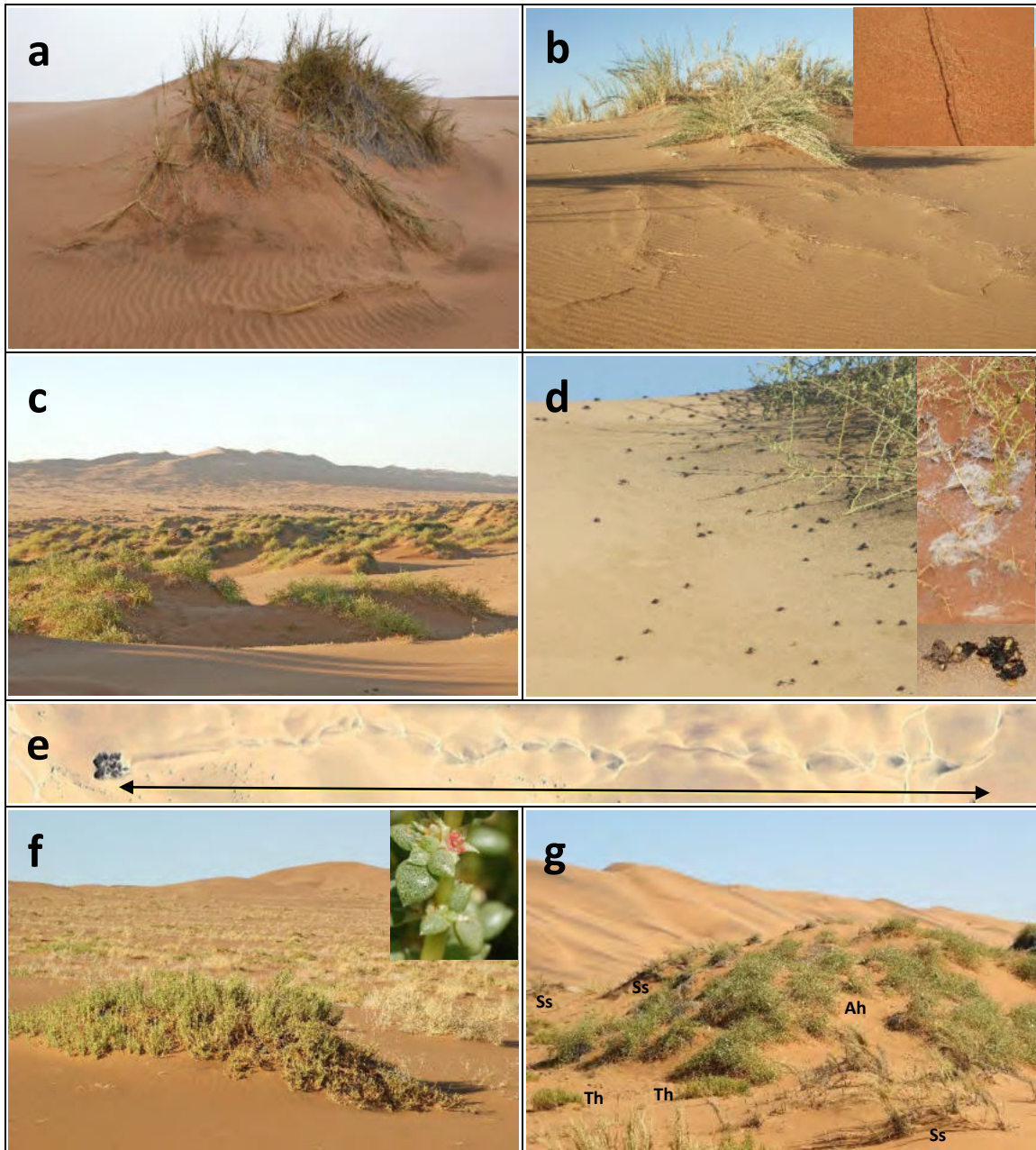


Figure 3: Three of the keystone plant species that harvest fog and grow large nebkhas are: a) *Stipagrostis sabulicola* nebkha; b) *S. sabulicola* with wind-exposed shallow roots, root detail (inset); c) *Acanthosicyos horridus* (!Nara) nebkhas; d) !Nara is rich with satellite fauna, some associated with accumulated detritus (top inset), frugivorous jackals disperse viable !Nara seeds in nutrient-rich dung (bottom inset); e) !Nara nebkhas can form very long wind streaks (scale = 893 m); f) *Trianthema hereroensis* nebkha, flowers year-round (inset); g) Part of a Nebkha Dune biotope showing Nara (Ah), *S. sabulicola* (Ss) and *T. hereroensis* (Th). (Photos: Joh Henschel, except Fig.3e: Google Earth)

A specialised adaptation of dune plants is their ability to cope with mobile sand transported by wind by growing faster than the sand deposition, thereby creating phytogenic micro-dunes, also known as nebkhas or hummocks (Robinson, 1976) (Fig. 3). Growth of *Stipagrostis sabulicola* and !Nara can even outpace small crescentic dunes that briefly move over them (Mitchell et al., 1987; Yeaton, 1990). In addition to simple nebkhas, !Nara can generate kilometre-long dune wind streaks in their wake (Fig. 3e). These psammophytes are ecosystem engineers, as their nebkhas can merge and grow new dunes or diminish when they release the sand during extreme droughts (Southgate et al., 1996; Aushiku et al., 2015). The plants cope with wind erosion by having thick rhizosheaths that withstand occasional root exposure and sand blasting (Jürgens, 1996; Marasco et al., 2018). Other psammophytes that cannot tolerate the extremes of dune sand dynamics, such as plant communities dominated by *Stipagrostis gonatostachys* and *S. lutescens*, are confined to more stable dune bases and interdune plains, where sand deposition and erosion are not so severe (Robinson, 1976).

Globally unique adaptations evolved in the southern Namib, which experiences the highest wind speeds. Such adaptations are mainly found in plants located between the Orange River Mouth and the Uri Hauchab Mountains (Jürgens, 1996; Burke et al., 1998), with the highest wind speeds between Chameisbaai and Lüderitz (Corbett, 2018). These plants avoid proper dunes but occur in sandsheets and on shallow sand layers. Here, Jürgens (1996) observed peculiar plant structures interpreted as adaptations to the mechanical impact of sandblasting (Fig. 4). Some species disappear with all their organs below the sand surface by shrinking their succulent tissues during the dry summer months, followed by re-emergence upon water uptake following effective rainfall (e.g., *Fenestraria rhopalophylla*, *Psammophora nissenii*, *Euphorbia caput-medusae*). Others shield their stems from sandblasting with thick bark or wax layers (e.g., *Pelargonium*, Bushman's Candle *Monsonia*). Leaf surfaces are protected by thickened outer cell walls and hairs and by nested arrangements of (partly dead) leaves (e.g., *Brownanthus ciliatus*, *Anacampseros*, *Crassula muscosa*). Some species orient their leaves horizontally with strengthened leaf edges, facilitating leaf vibrations to shake sand off the leaf surface (e.g., *Monsonia ignorata*). Many psammophorous species actively fix sand grains as a protective layer on their leaf surfaces, made possible by structures of epidermal cells or trichomes. These sometimes involve significant changes in the anatomy of the epidermis (Jürgens, 1996) (Fig. 4).

3.2. Psammophilous animals

A unique set of psammophilous animals has evolved in the Namib dunes (Koch, 1962b; Seely, 1989; Crawford, 1991), with sand moisture being the most critical driver (Wharton and Seely, 1982; Seely, 1991). Psammophiles have developed the ability to sand-swim or sand-dive (Coineau et al., 1982; Seymour et al., 1998; Edwards et al., 2016) (Fig. 5), walk on sand (Griffin, 1990; Bauer and Russell, 1991; Prendini, 2001) (Fig. 6), side-wind across it (Robinson and Hughes, 1978), bind sand grains together to build burrow walls (Peters, 1992; Jürgens, 2013) (Fig. 7), respire in the sand (Louw et al., 1986; Seymour and Seely, 1996), and sequester moisture from it (Watson and Irish, 1988; Grube and Rudolph, 1995). They can detect microseismic vibrations transmitted by walking or sand-swimming animals (Fielden et al., 1990; Brownell and van Hemmen, 2001; Lewis et al., 2006) or by falling wind-blown detritus (Crawford and Seely, 1993; Hanrahan and Kirchner, 1994, 1997). Easy penetration into sand facilitates oviposition and progeny development in subsurface shelters protected from the desert's microclimatic extremes and surface predators (Seely and Mitchell, 1987; Prendini, 2001). Much of the surface area of dune plinths and slipfaces is bare and relatively smooth, allowing locomotion by wheeling in spiders (Henschel, 1990b) and unfettered sprinting by beetles for convective cooling in the boundary layer above dune surfaces (Nicolson et al., 1984; Roberts, 1991; Roberts et al., 1991) (Fig. 6).

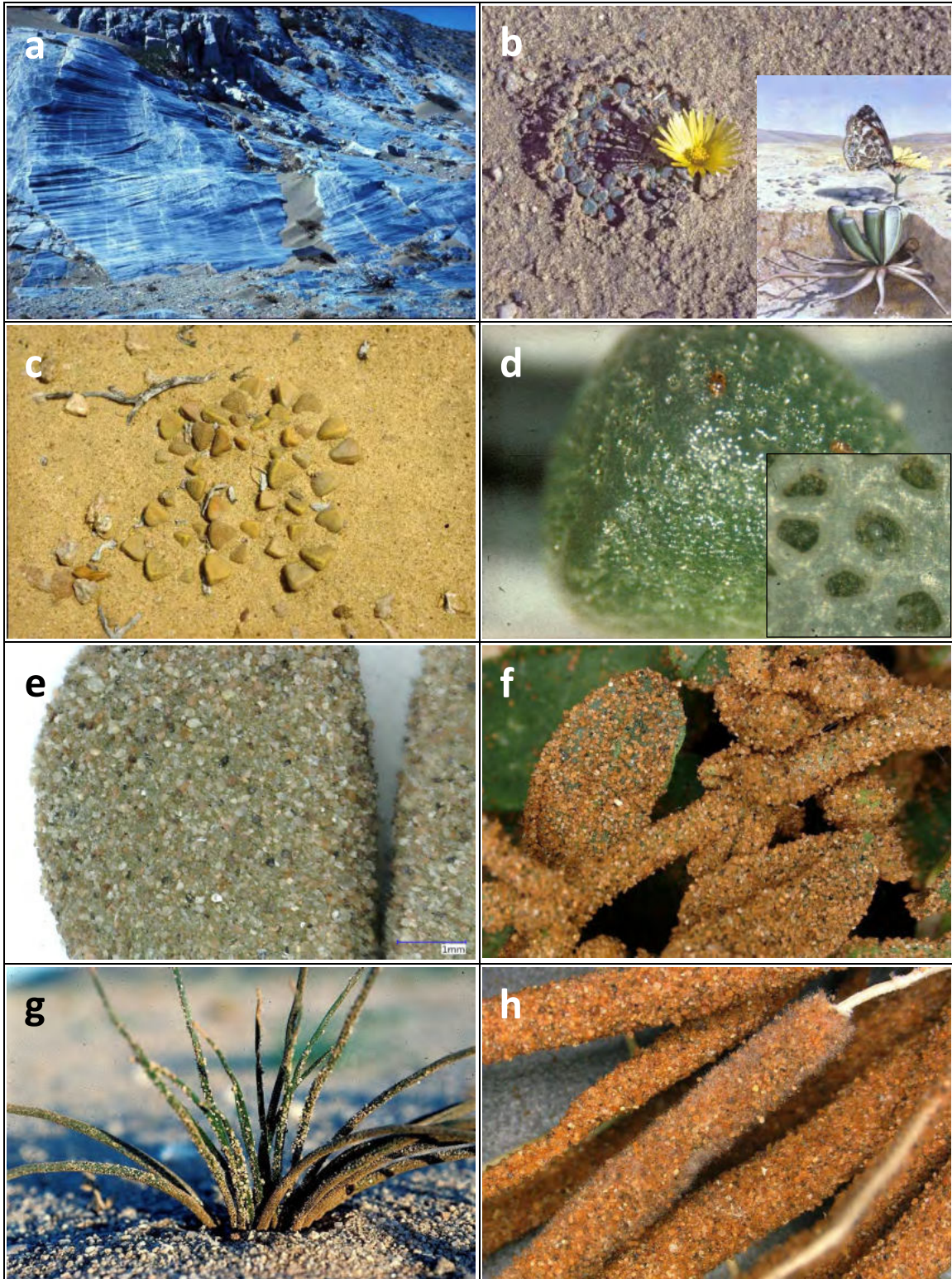


Figure 4: Psammophorous plants use an adhesive layer of sand to protect themselves from sandblasting: a) The abrasive power of aeolian sand transport is demonstrated by an eroded dolomite yardang in the Grillental barchan street south of Lüderitz in the Tsau||Khaeb; b) *Fenestraria rhopalophylla* (Aizoaceae) re-emerging from the sand after uptake of water following winter rain; inset: its sunken growth with an abbreviated shoot at a depth of several centimetres and numerous succulent leaves with translucent windows at the leaf tips allows entry of light and photosynthesis at depth; c) In addition to having a sunken growth form, *Psammophora nissenii* (Aizoaceae) has a thick layer of sand fixed to the leaf surface (psammophory); d) The young leaf of a greenhouse *Psammophora nissenii* produces a sticky substance on the leaf surface, which later turns into a

solid cement that fixes sand grains (see inset) that protect the leaf against mechanical abrasion of wind-blown sand; e) Psammophorous leaf of *Psammophora modesta*; f) and of *Limeum viscosum*; g) and *Chlorophytum viscosum*; h) The rhizosheaths of *Stipagrostis* grass protect the roots when exposed by wind erosion. (Photos: Norbert Jürgens, except Fig.4b inset: adapted from Marloth, 1913)

Elevated dunes intercept more advective fog than low-lying interdune plains, enabling a few highly specialised tenebrionid beetles to capture water by fog-basking on top of dunes (Hamilton and Seely, 1976; Seely, 1979; Ward and Seely, 1996) or drink from wet dune surfaces (Seely and Hamilton, 1976; Seely et al., 1983; Seely et al., 2005; Mitchell et al., 2020) (Fig. 8). Linear dunes can trap radiation fog and dew in interdune valleys (Kaseke et al., 2017; Adhikari and Wang, 2020), where various animals, ranging from beetles to ostrich and springbok, imbibe the condensation (Louw, 1972; Polis and Seely, 1990; Henschel and Seely, 2008; Lovegrove, 2020) (Fig. 8). Fog wets the top centimetre of sand and increases humidity to depths of 5 cm (Besler and Gut, 1997) to the benefit of chthonic animals (Mitchell et al., 2020).

Given the extremely low overall primary productivity of the hyperarid Namib (Seely and Louw, 1980), exacerbated by low nutrient availability and lack of stable soil in the dunes, many omnivorous psammophiles feed primarily on detritus, comprising mostly dead plant and animal matter (Crawford, 1991). Detritus is constantly being buried and re-exposed and, therefore, forms the most stable source of energy underlying Namib dune food webs (Holm and Scholtz, 1980; Robinson and Seely, 1980; Seely and Louw, 1980; Louw and Seely, 1982). The highest concentrations of surface detritus can be found at the avalanche bases of leefaces, where detritivores congregate. By contrast, dune plinths, dune bases and nebkha dunes have perennial sources of detritus comprising flowers, seeds, and other litter dropping off dispersed perennial plants. In these biotopes, many detritivores commute between resource patches (Seely and Louw, 1980).

Due to the substrate specialisation and climatic conditions, the levels of endemism in the Namib dunefields are very high (>50%) for beetles, zygentomans, arachnids, and reptiles (Holm and Scholtz, 1980; Barnard, 1998; Simmons et al., 1998; Craven and Vorster, 2006; Robertson et al., 2012; Seely, 2012; Burke and Loots, 2020; Wassenaar et al., 2021). Three dune-endemic birds are the Dune Lark *Calendulauda erythrochlamys* in the Namib Sand Sea, Barlow's Lark *C. barlowi* in Tsau||Khaeb and the Richtersveld, and the Red Lark *C. burra* in the Koarivier and Aggenys dunefields and northern Bushmanland dunes (Dean et al., 1991; Hockey et al., 2005; Ryan and Bloomer, 2010). Also endemic are the Hairy-footed Gerbil *Gerbillurus tytonis* (Downs and Perrin, 1989) and the Desert Rain Frog *Breviceps macrops* (Du Preez and Carruthers, 2009). However, the biodiversity of animals in the Namib dunefields is lower than in adjacent, more mesic inland areas to the east (Mendelsohn et al., 2022), with notable exceptions for tenebrionid beetles (Koch, 1962a; Henschel and Wassenaar, 2022) and solifugids (Wharton, 1981; Bird in Mendelsohn et al., 2022).

The high alpha diversity of tenebrionids appears to be due to their multiple demographic responses to highly variable rainfall and drought over space and time (Henschel, 2021), conditions that promote the coexistence of competing species (Chesson and Warner, 1981). On the hyperarid gravel plains of the Central Namib, Henschel (2021) found that populations of tenebrionids showed at least six different response patterns to shifting hydrological states. Diversity patterns changed continuously as different species dominated successive time niches of advancing dehydration over time since episodic rainfall events. A succession of ever more tenacious tenebrionid species that could not compete with dominant species during moister times increased their abundance when dominant species declined with advancing drought. Furthermore, in the Namib dunes, biotope heterogeneity (interdune, base, nebkhas, plinth, slipface) promotes high beta diversity (Holm and Scholtz, 1980; Robinson and Seely, 1980; Henschel, in prep.).

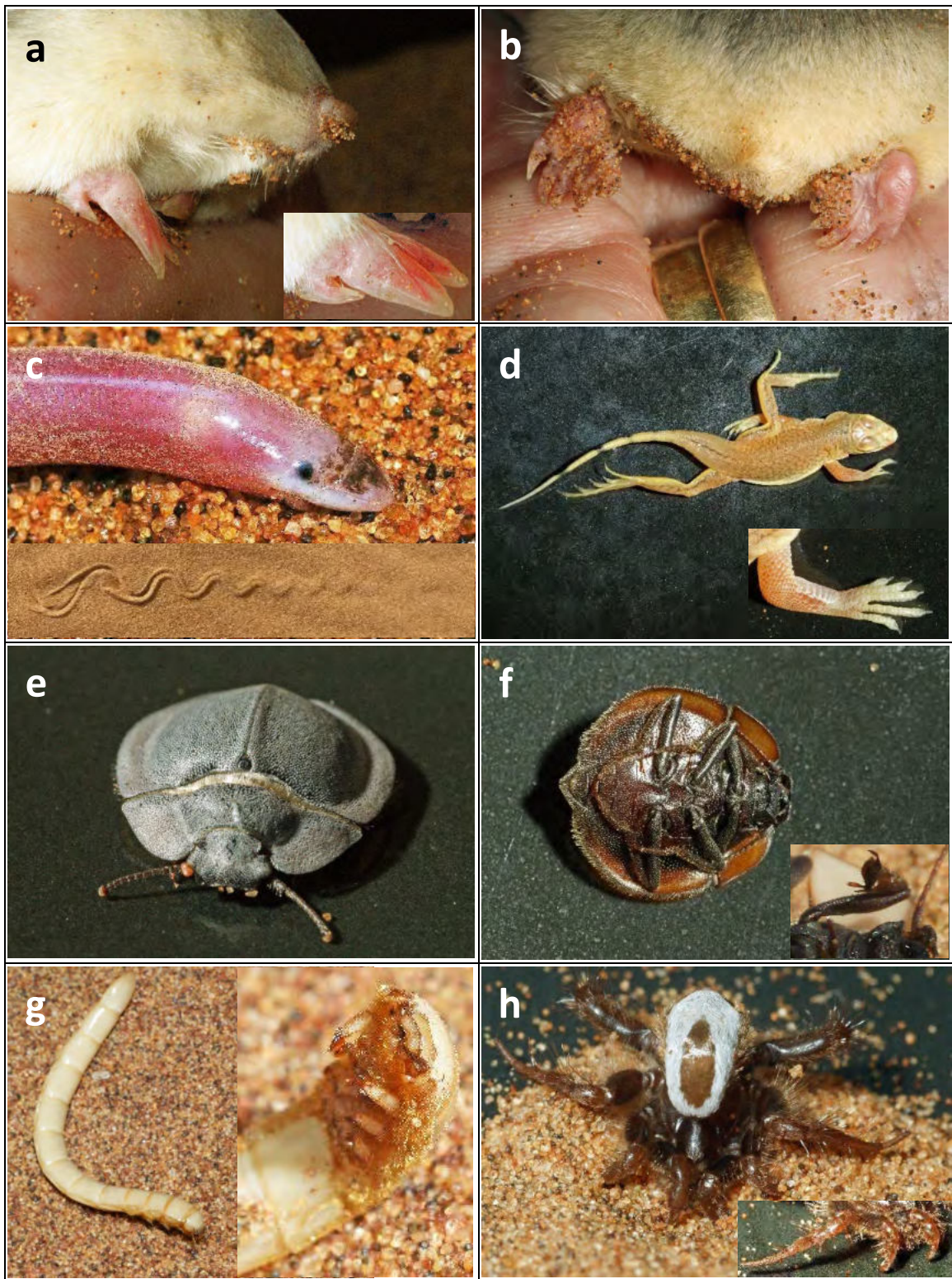


Figure 5: Examples of structures enabling animals to penetrate and propel themselves when sand-swimming (insets with details): a & b) *Eremitalpa granti*: spatulate front claws and broad hind feet; c) *Typhlosaurus braini*: wedged head shield and serpentine locomotion; d) *Meroles anchietae*: wedged snout, spatulate scales on toes; e & f) *Lepidochora discoidalis*: discoid body, sand-mobilising legs; g) *Onymacris plana* larva: setose legs, spatulate claws; h) *Psammoduon deserticola*: stocky, dextrous, setose pointed front legs to mobilise sand and long hind legs to clear sand. (Photos: Joh Henschel)

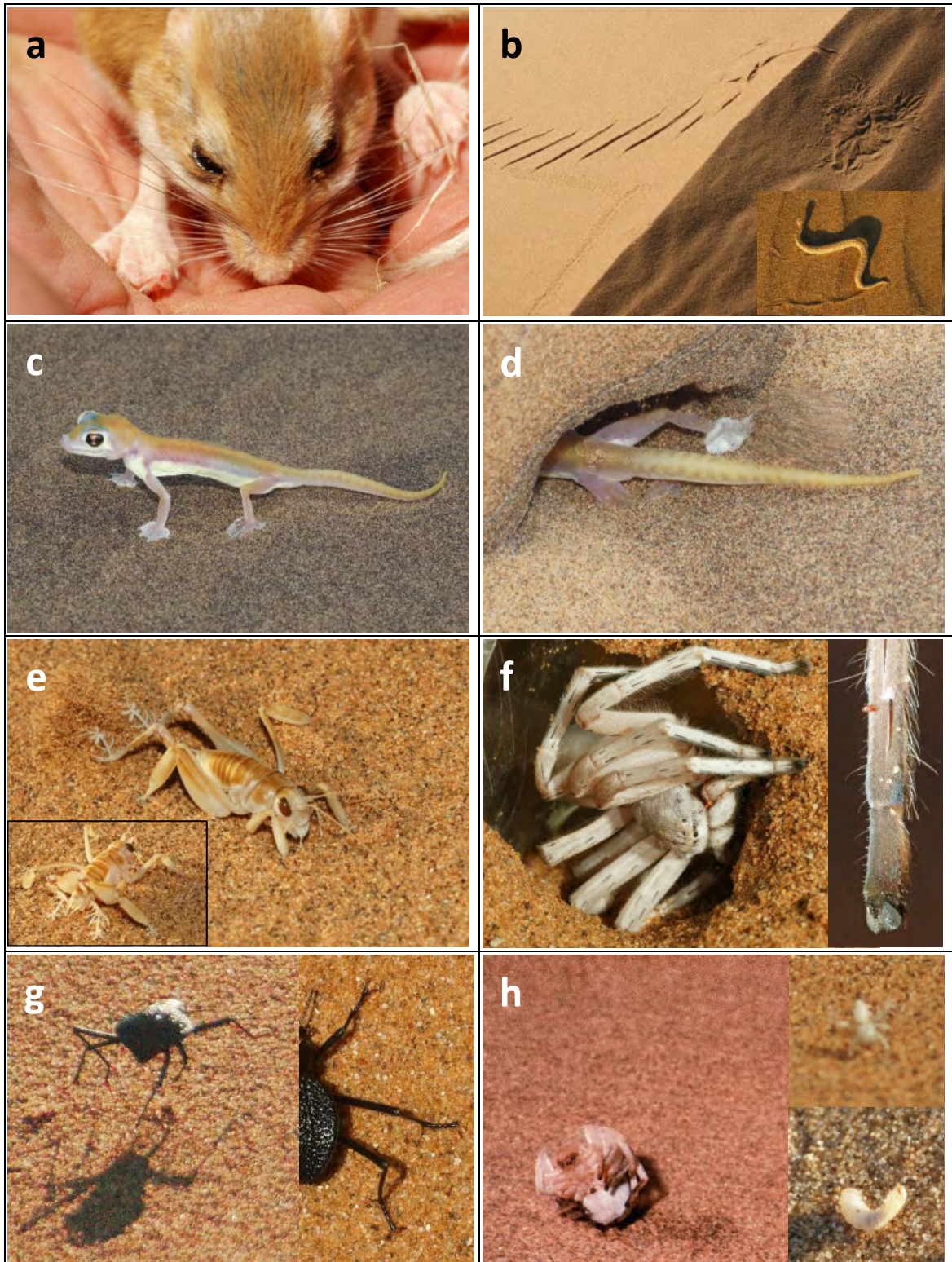


Figure 6: Mechanisms to assist walking and digging in sand include: a) *Gerbillurus tytonis*: broad hairy feet; b) *Bitis peringueyi*: side-winding and wriggling below surface sand to ambush prey; c & d) *Pachydactylus rangei*: webbed feet; e) *Comicus calcaris*: elongated tibial spurs; f) *Leucorchestris arenicola*: thick brushes of tarsal and metatarsal scopula hairs; g) *Onymacris plana*: long tarsal spurs; h) *Carparachne aureoflava*: wheeling down smooth dune slope, top inset: wind-blown wheeling salticid spider, bottom inset: wind-blown helical rolling of the larva of *Zophosis fairmaerei*. (Photos: Joh Henschel)

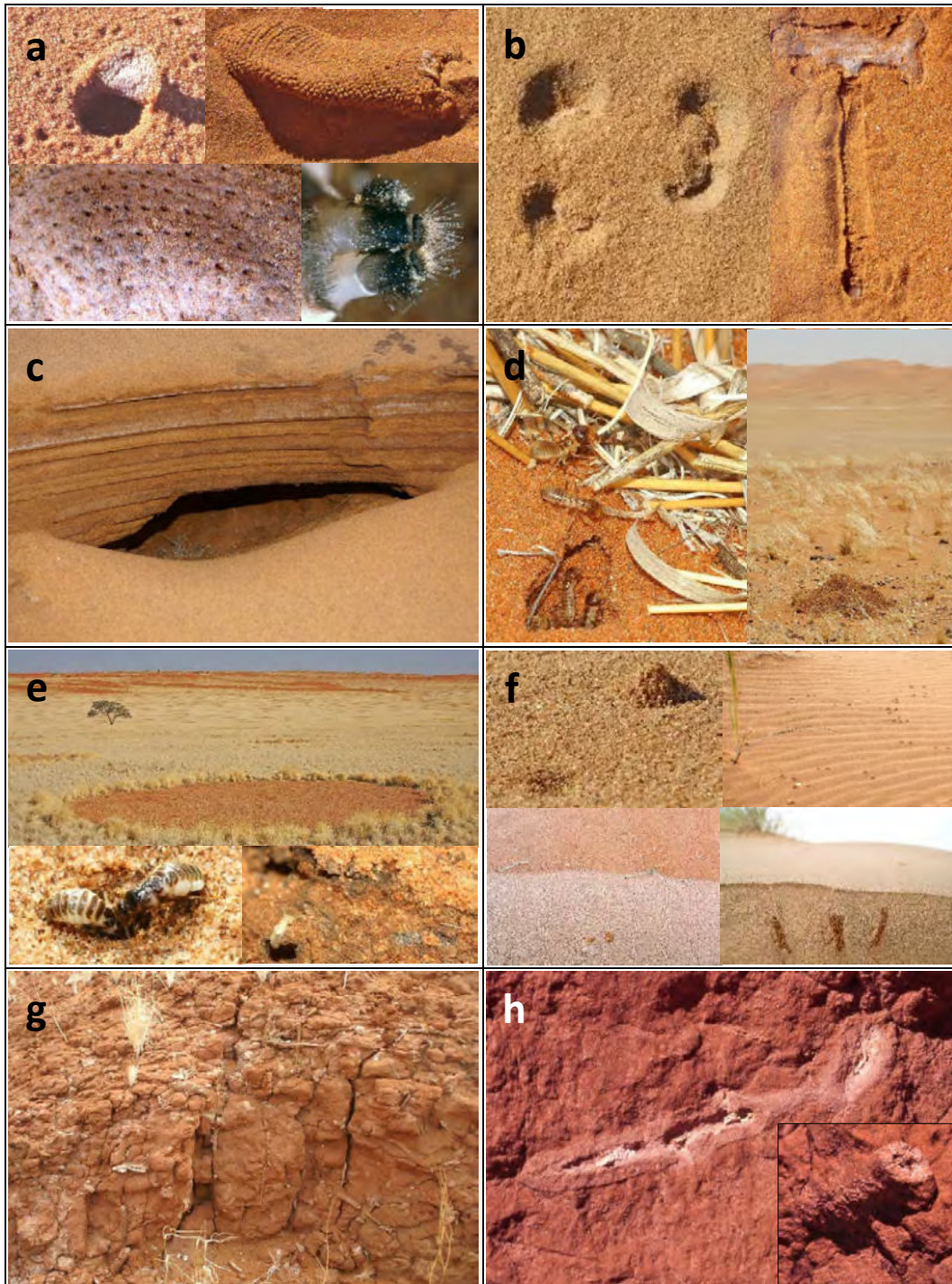


Figure 7: Stable burrows in sand: a) *Leucorchestris arenicola* spiders cover entrances of 19-29° sloping burrows with trapdoors, fix burrow walls by spinning rows of sand nodules (shown from outside and inside) using numerous long filamentous spigots at the end of spinnerets; b) *Seothyra henscheli* spiders construct capture webs on sand surfaces, and wait at the relatively cool bottoms of vertical burrows for prey to be entangled in the hot web's cribellar silk; c) Cape fox *Vulpes chama* burrowed a den into consolidated moist sand at the bottom of a deflation hollow; d) *Hodotermes mossambicus* cement their foraging portals (left) and ejecta portals (right) to transport material down to and up from their nest; e) *Psammotermes allocerus* termitaria establish bare patches (fairy circles) below which are numerous burrows initiated by a reproductive pair and later expanded by workers; f) *P. allocerus* also nest below *S. sabulicola* and adjacent to avalanche bases of slipfaces, where they push up small mounds of ejecta; g) Termite and spider burrows ichnofossilise over time, as seen in Tsondab sandstone; h) Ichnofossil burrows typical in structure and texture for sparassid spiders. (Photos: Joh Henschel)

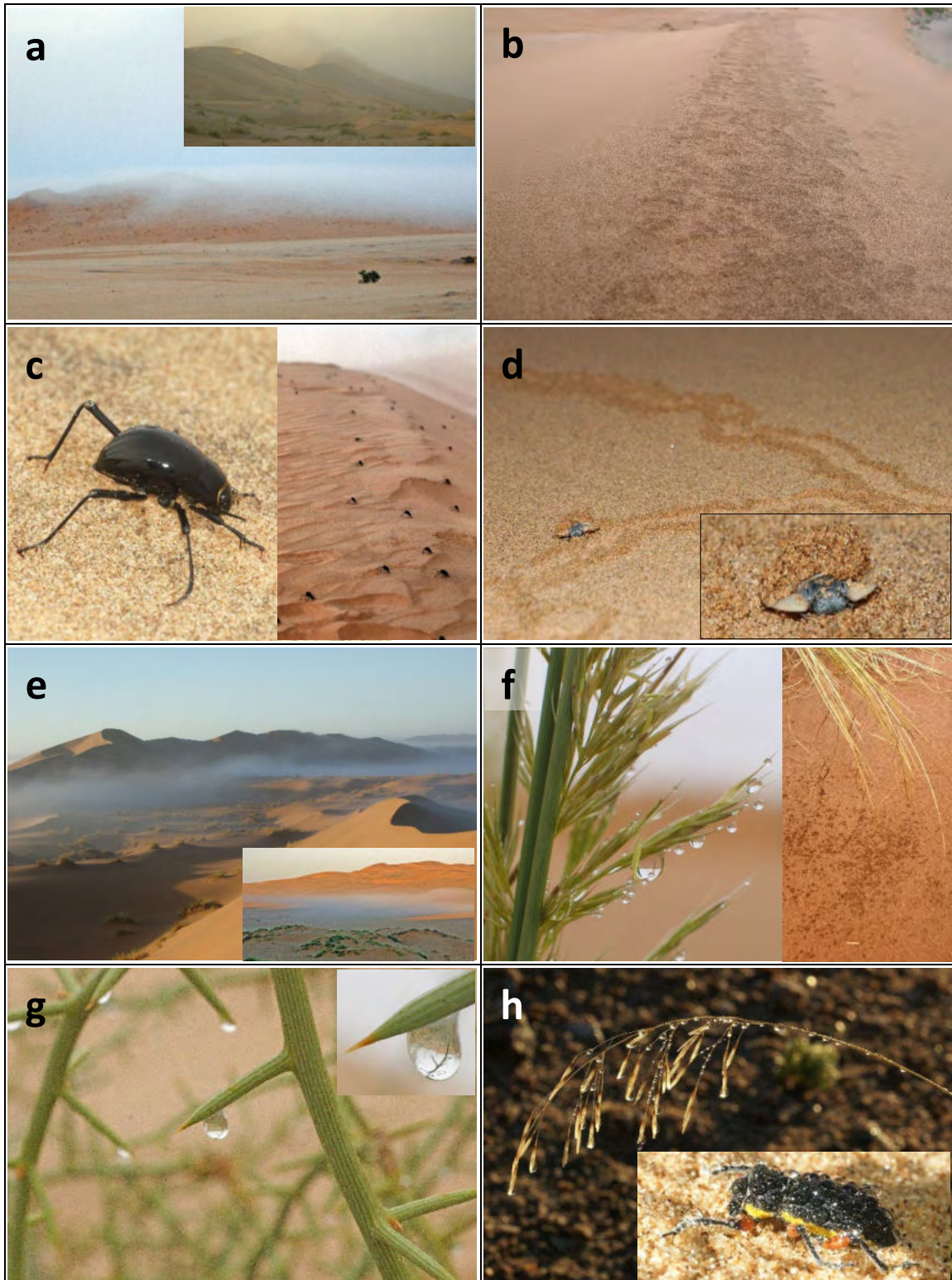


Figure 8: Fog provides water to the Namib dunes: a) Wind blows advective fog across the top of dunes; b) wetting the dune crests; c) where fog-basking beetles *Onymacris unguicularis* fog-bask; d) and trench-building *Lepidochora kahani* drink from wet sand. e) Radiation fog arises in dune valleys on calm mornings; f) condensing on *Stipagrostis sabulicola*, which collects fallen drops with shallow roots; g) likewise with Nara; h) and condensing on interdune grass to be imbibed by animals, some, such as *Leptostethus marginatus*, collecting such condensate on their bodies. (Photos: Joh Henschel, except Fig. 8c right: Ron Tilson, and Fig. 8f left: Norbert Jürgens)

3.3. Psammophilous microbes

In a study of Namib dune bacterial communities across a transect encompassing two dune crests, plinths, dune bases and one interdune, Ronca et al. (2015) recorded 30 phyla, dominated by Proteobacteria, Actinobacteria, and Bacteroidetes. Bacterial assemblages differed strongly between biotopes, and only 2-15% of the taxonomic units occurred across all sites. Among 15 edaphic factors, sand particle size was most important in influencing niche partitioning between biotopes, with different concentrations of nutrients (potassium and nitrogen), salts (sodium and potassium), and metals (iron, manganese, aluminium) also serving as habitat filters (Ronca et al., 2015). Surprisingly, aeolian transport and cellular dispersal of bacteria were insignificant. The interdune, dune bases and plinths had well-defined communities with different dominant genera, while on slipfaces, the communities were more variable. The highest levels of bacterial activity were detected on the interdune, which dropped to intermediate and variable at the dune bases and declined up the plinths, lowest at dune tops. Ronca et al. (2015) did not examine bacteria in detritus pads at slipface avalanche bases or within dune nebkhas, where Ascomycete communities proliferate and metabolise lignin thereby initiating the decomposition of detritus (Jacobson and Jacobson, 1998; Jacobson et al., 2015; Logan et al., 2021).

4. Dune biotopes

The Namib has many different dune types (Lancaster, 1989, 2014), including dome dunes; simple or compound barchans; close or wide transverse dunes (crescentic); simple, compound, complex or intersecting linear dunes; star dunes; dendritic and network dunes (reticulate); coastal nebkhas; topographic dunes; and sandsheets (Livingstone, 2013). These different dune types can be dissected into different biotopes, namely interdunes, dune bases, dune plinths, and slipfaces below dune crests, though not all dune types have all biotopes (Table 1) (Fig. 2). Our descriptions are based on the classification by Robinson and Seely (1980) for the north-central Namib Sand Sea. We treat the dune crest separately for its distinctive characteristics. We added nebkha dunes that sometimes occur as isolated patches on interdunes or between dune bases and plinths and are also common along the coast (Table 1). We treated sandsheets as a separate biotope due to their ecological significance and aeolian sand transport characteristics, which affect downwind dunefields.

4.1. Interdunes

Interdunes are sandy plains (narrow or wide, short or long, sandy or gravelly) forming valleys between elevated dunes of any type (Table 1). They cover about 50% of the dunefields and have highly variable, patchy and complex sand grain and gravel composition (Lancaster and Teller, 1988; Lancaster, 1989; Baddock et al., 2007). Their biotic communities are distinct from the other dune biotopes (Robinson and Seely, 1980). Over long periods between effective rainfalls, the interdune plains are almost devoid of vegetation and detritus (Seely and Louw, 1980), with only a few patches of perennial grasses and isolated shrubs (Robinson and Seely, 1980).

They are pulsed environments, responding more quickly and briefly to episodic rainfalls than the other dune biotopes (Seely and Louw, 1980; Aushiku et al., 2015). Following effective rainfalls, many interdunes are covered with ephemeral grasses such as *Stipagrostis gonatostachys* (southern dunefields), *S. ciliata* (eastern zone of southern dunefields), *S. obtusa* (on calcareous soil), *Stipagrostis giessi* or *S. hirtigluma*, and sometimes *Brachiaria glomeratae* (northern dunefields). These grasses facilitate the deposition of a 5 cm layer of wind-blown fine sand with a relatively high field capacity (moisture retention), prolonging grass survival (Seely and Louw, 1980). However, when these grasses eventually die and decompose, the layer of fine sand disappears with wind erosion, leaving remnants

of shallow soil (Baddock et al., 2007) (Fig. 2). These dynamics of sand layers on the interdunes lead to high variability of sand grain composition, which differentiates the geophysical conditions for ground-living biota, including hypolithic microbes, from those prevailing on neighbouring gravel plains (Wharton and Seely, 1982; Henschel et al., 2005; Ramond et al., 2018; Henschel, 2021). At high densities, !Nara and other shrubs can turn the interdune biotope into a nebkha dune biotope (see below).

The diversity of animals in the interdune is comparable to the dune plinth, although the species composition is distinctive and their abundance lower (Holm and Scholtz, 1980; Robinson and Seely, 1980; Henschel et al., 2003a; pers. obs.). Many interdune residents seldom frequent adjacent dunes. In the Namib Sand Sea, examples are tractrac chats *Cercomela tractrac*, barking geckos *Ptenopus garrulus* and *P. kochi*, huntsman spiders *Orchestrella longipes*, scorpions *Protophthalmus holmi* and *Parabuthus laevifrons*, solifugids *Metasolpuga picta* and *Lawrencegea minuta*, zygentomans *Hyperlepisma australis*, harvester termites *Hodotermes mossambicus*, and tenebrionid beetles *Eustolopus octoseriatus* and *Zophosis moralesi*. Typical avian and mammalian predators include Ludwig's Bustards *Neotis ludwigii* and Cape Foxes *Vulpes chama*. Populations of gemsbok *Oryx gazella*, springbok *Antidorcas marsupialis*, and ostrich *Struthio camelus* track the boom-and-bust patterns of productivity of the eastern interdunes (Berry and Siegfried, 1991), although their ability to disperse when the grass withers is confined by the eastern boundary fence of the Namib Naukluft Park (Kilian, 1995).

Along the eastern borders of the Namib dunefields, fairy circles, which are bare sand patches with relatively high subsurface moisture, fringed with perennial grasses or succulent dwarf shrubs, dot the sandy plains, which are dominated by ephemeral grasses (Jürgens, 2013, 2022). Numerous organisms associate with these patches for their resources, mainly sand moisture, plant material or shelter of the perennial belt, or to feed on the causative sand termites *Psammotermes allocerus* nesting below fairy circles (Jürgens, 2022; Jürgens et al., 2023). Even larger fairy circles, occupied by *Microhodotermes*-like termites, occur on sandy terrain north of the Iona dunefields (Jürgens et al., 2021). Large heuweltjies (broad, low termitaria mounds) are formed by *Microhodotermes viator* colonies in older interdunes of the western Richtersveld, while younger interdunes and dune bases are covered by fairy circles with *Psammotermes colonies*.

4.2. Dune Bases

The valleys beyond the elevated dunes are gently sloping sand sheets, distinguishable from interdunes by the lack of gravel and at least 10 cm of sand (Robinson and Seely, 1980; Baddock et al., 2007). We interpret wide sand sheets not associated with elevated dunes as equivalent to dune base biotopes. Typical plants are the grasses *Stipagrostis lutescens*, *S. sabulicola*, *Cladoraphis spinosa*, and *Centropodia glauca*, the Geraniaceae *Monsonia ignorata*, the succulent *Trianthema hereroensis*, and the !Nara.

Numerous arthropods occur on dune bases, some typical species being the tenebrionids *Onymacris plana* and *Stips stali*, the ants *Camponotus detritus*, *Tetramorium rufescens*, and *T. sericeiventre*, zygentomans *Ctenolepisma terebrans* and *Nebkhalepisma australis*, solifugids *Blossia sabulosa*, *Prosolpuga schultzei* and *Eberlanzia flava*, spiders *Leucorchestris arenicola* and *Seothyra henscheli*, and scorpions *Opisthophthalmus flavescens* and *Protophthalmus holmi*. Typical reptiles include lizards *Meroles cuneirostris*, chameleons *Chamaeleo namaquensis*, geckos *Pachydactylus rangei*, and snakes *Psammophis namibensis* and *Bitis peringueyi*.

The substrate is sufficiently stable in many locations for some animals, ranging from gerbils to scorpions and geckos, to burrow into the sand without needing to reinforce the walls (Fig. 6d). They

block entrances with loose sand or trapdoors. Sand stability for burrow construction can also be facilitated by gemsbok urine that consolidates sand when dry (Seely, 1977). Termites cement their burrow walls, and spiders stabilise them with silk, spinning discrete nodules into the burrow walls with exceptionally long spigots (Peters, 1992) (Fig. 7a,b). However, stabilising sand with silk requires a considerable investment of energy and material (Henschel and Lubin, 1992; Henschel, 1997; Haddad et al., 2023), limiting spiders' dispersal and rendering their populations vulnerable to dune dynamics and disturbances (Henschel and Lubin, 1997; Birkhofer et al., 2012). Male Whitelady spiders that walk far from their burrows (30-314 m) avoid rebuilding costs by navigating back to their burrows (Henschel, 2002; Norgaard, 2005; Norgaard et al., 2007).

These silken or cemented structures endure ichnofossilisation, indicating that similar termites and spiders have existed in the Namib dunefields since the Miocene (Seely and Mitchell, 1986; Pickford, 2000; Pickford and Senut, 2002). Also among the fossils are snails *Trigonephrus* sp. (Pickford and Senut, 2002). *Trigonephrus* populations are extant in the winter-rainfall Tsau||Khaeb and Richtersveld Dunefields, where they bury in the sand between nebkhas, becoming active during moist winter conditions (Dallas et al., 1991). Insects shelter in the shells of these snails when they have died (Gess and Gess, 2008), representing one of many dunefield examples of inter-species facilitation.

4.3. Dune Plinths

Sand becomes more mobile with increasing elevation up the flanks of dunes. In the Namib Sand Sea, *Stipagrostis sabulicola* communities and their satellite fauna dominate dune plinths, with densities decreasing from lower to mid-dune heights and disappearing on the upper dunes (Yeaton, 1988). Many animals, fungi, and bacteria are associated with the roots, stems, leaves, flowers, seeds and shelter provided by nebkhas of fog- or dew-harvesting *Stipagrostis sabulicola* (Koch, 1961; Louw and Seely, 1980; Boyer, 1988; Curtis, 1990; Fielden et al., 1990; Marasco et al., 2018; Wenndt et al., 2021; Gan et al., 2023) with many trophic interactions among these associated organisms. Weevils, *Leptostethus marginatus*, gain elevated positions by clinging to the leaves of the grass, where they collect fog or dew on their cuticles (Lovegrove, 2020) (Fig. 8h). The Dune Lark nests in the shelter provided by large *S. sabulicola* (Boyer, 1988; Hockey et al., 2005), and the distribution ranges of bird and grass coincide (Hockey et al., 2005; Fish et al., 2015).

Similarly, numerous species are associated with phreatophytic, fog-harvesting and water-recycling !Nara (Robinson, 1976; Pietruszka et al., 1986; Klopatek and Stock, 1994; Henschel et al., 2004; Kaseke et al., 2017; Sherman et al., 2019; Unc et al., 2019; Kool et al., 2021) (Fig. 3). !Naras have keystone properties as nodes of enriched nutrients sourced from mineral-rich groundwater via taproots (Bethune, 2008; Soderberg, 2010) in an otherwise nutrient-poor dune environment (Jacobson, 1997), attracting many consumers and fertilising the dunes with its decaying litter (Klopatek and Stock, 1994). !Nara seeds are mainly dispersed by frugivorous jackals who lack chewing molars that would destroy seeds and deposit intact seeds in their nutrient-rich dung (Stuart, 1976a; Müller, 2006; Goldenberg et al., 2010; Shikesho et al., 2024). The fruit is also eaten by spotted hyaenas who regurgitate intact seeds (Stuart, 1976b; Tilson et al., 1980) and probably also by brown hyaenas near the Namib coast, as this species is known to eat other cucurbit melons and defecate intact seeds in the Kalahari (Mills, 1990).

Trianthema hereroensis also has a bevy of satellite fauna (Seely et al., 1977; Nott and Savage, 1985a); for example, pompilid spider-hunting wasps *Schistonyx aterrimus* rely on the nectar of its perennial flowers as an energy source (Fig. 3f) (Henschel, 1990b). Gemsbok browse heavily on *T. hereroensis*, which stimulates vigorous regrowth and viability of this succulent shrub in the dunefields as long as the browsing continues (Nott and Savage, 1985a). Many animals also frequent other plants not known

to collect fog, such as the annual succulent *Zygophyllum simplex*, which has over a hundred associated arthropod species (Wharton, 1980).

In the Skeleton Coast Terrace Bay Dunefield, dune plinths are mostly bare of vegetation, except in the easternmost reaches where *S. giessii* is sometimes found. These dune plinth plants constantly generate and trap detritus, thus representing reliable resource nodes. Many animal species that frequent dune bases can also be found on the plinth, although the species assemblages differ. Notably, on dune plinths, Sand Termites *Psammotermes allocerus* are among the satellite fauna associated with *S. sabulicola* nebkhas, where Namib Golden Moles *Eremitalpa granti namibensis* hunt for them (Fielden et al., 1990), as do Brain's Blind Legless Skinks *Typhlosaurus braini* (Holm and Scholtz, 1980).

The Namib Sprinter *Onymacris plana* (Tenebrionidae) runs at speeds of about 1 m.s⁻¹ – the fastest of any dune arthropod – to generate sufficient headwind for convection to cool it down while crossing bare stretches of sand between distant dune nebkhas during hot hours (Roberts, 1991) (Fig. 6g). A salticid spider (Salticinae) crosses between nebkhas by somersaulting with legs outstretched and lets the wind drive it onward until it encounters the next nebkha (Henschel, 1990b) (Fig. 6h) akin to the Sahara Flickflack Spider (Rast et al., 2015). Namib Sand Adders *Bitis peringueyi* minimise contact with hot sand surfaces when side-winding by alternating the body parts in contact with sand (Fig. 6b). Many other animals minimise exposure by sand-swimming between resource patches, with tenebrionid larvae, golden moles, legless skinks, and thread snakes leaving conspicuous subsurface trails (Fig. 5c). Traits that overcome the difficulties of walking on and digging into loose sand include the broadening of feet, as seen with Hairy-footed Gerbils *Gerbillurus tytonis* (Downs and Perrin, 1989; Griffin, 1990) and web-footed Palmatogeckos *Pachydactylus rangei* (Bauer and Russell, 1991; Lamb and Bauer, 2006); the elongated tibial spurs of Dune Crickets *Comicus calcaris* (Irish, 1986, 1995); and thick brushes of tarsal and metatarsal scopula hairs of Whitelady Spiders *Leucorchestris arenicola* and Golden Wheel Spiders *Carparachne aureoflava* (Lawrence, 1962, 1966) (Fig. 6f).

Stretches of bare sand enable communication and orientation via microseismic vibrations transmitted through the sand. Compressional and Rayleigh waves travel more slowly through unconsolidated sand than other substrates, enabling sensory organs to resolve their direction from the time delays of detection by at least two sensors. The ability to detect these directional vibrations was first discovered in scorpions (Brownell, 1977). In the Namib, it has been best studied in Golden Moles. The massively hypertrophied ear mallei – which led to this species' discovery in owl pellets (Haacke, 1963) – and its behaviour of periodically thrusting its head into the sand when foraging at night enable it to detect subsurface prey from its movements (Lewis et al., 2006; Narins and Willi, 2011). The territorial Whitelady Spider also detects prey and communicates with conspecifics through vibrations (Henschel, 1990a, 2002; Norgaard et al., 2006). A further example is the ability of male *Onymacris plana* beetles to detect the location of buried females or mating pairs and dig them out to attempt mating or challenge an ongoing mating process (Enders et al., 1998). The utility of sand vibrations may be more common among Namib psammophiles than currently known. For example, snakes (Hartline, 1971) and chameleons (Denny et al., 2023) emit and detect microseismic vibrations, but this has not been examined in dune-living species.

4.4. Slipfaces

Slipfaces are the least stable biotope, continuously reshaped by the dominant winds – in summer, southwesterlies, and in winter, northeasterlies – flipping slipfaces between east-facing and west-facing. In summer, slipfaces usually face eastwards in their elevated position just below the crests and warm up rapidly in the mornings, giving ectotherms a headstart to their day's activities. In the later afternoons, the 32° steeply sloping slipfaces facing away from the sun are the first to cool down from

the daily thermally prohibitive heat levels around noon, enabling more extended activity periods (Robinson and Seely, 1980). Ectotherms can thermoregulate by shuttling between the windy crest and the less windy slipface, although this is not entirely wind-still due to turbulent eddies (Joubert et al., 2012). These above-surface thermal properties are used to good effect by lizards which shuttle between the two biotopes (Louw and Holm, 1972; Seely et al., 1990).

Slipfaces lack vegetation (Fig. 2) except when a wandering dune crosses a plant. Following rain, seeds may germinate at the avalanche base but are buried when the slipface advances. This biotope is a local hotspot for an abundance of detritivores and their predators, particularly at the avalanche base, where wind-blown detritus and seeds accumulate (Muller, 2010) (Fig. 2), soon to be buried, energising a slipface-associated food web (Crawford and Seely, 1993). The most conspicuous detritivores are tenebrionids such as *Lepidochora discoidalis* (Louw and Hamilton, 1972; Crawford and Seely, 1993), which become active when wind deposits fresh material, which is detected by the beetles within the sand from vibrations generated by dropping sand grains and detritus (Hanrahan and Kirchner, 1997). Other typical slipface tenebrionids are *Zophosis fairmairei*, *Onymacris laeviceps* and *O. unguicularis* (Hamilton and Seely, 1976) and zygantomans *Mormisma wygodzinskyi*, *Sabulepisma multiformis* and *Swalepisma mirabilis* (Watson and Irish, 1988; Irish, 2018). At the avalanche bases, dominant detritivores include Sand Termites (Crawford and Seely, 1994), whose occurrence in virtually all dune biotopes from dune bases to slipface is evident from ichnofossils of termite chambers and burrows (Pickford and Senut, 2002; Pickford, 2006) (Fig. 7g,h).

The unconsolidated nature of slipfaces allows sand grains to transition to a fluid-like state with vibrations (Zuniga et al., 2022). This transition enables the lizards *Meroles anchietae* and *Gerrhosaurus skoogi* to sand-dive, plunging into the sand to escape danger (Robinson and Barrows, 2013; Edwards et al., 2016; Evans et al., 2017) (Fig. 5d). Unusually for lizards, both are insectivorous as well as herbivorous (Mitchell et al., 1987; Murray and Schramm, 1987; Robinson, 1987; Nagy and Shemanski, 2009). Many other animals sand-swim through the slipface to shelter or move between buried resources (Fig. 5). The Backflip Spider *Psammoduon deserticola* sand-swims to hunt sand-swimming tenebrionid larvae (Rössl and Henschel, 1999) (Fig. 5h).

Wheel Spiders are the only animals able to construct and maintain 51 cm deep burrows (maximum 122 cm) into the slipface (Henschel, 1997), with walls affixed with silk (Peters, 1992). The steeply sloping, smooth surface of the slipface enables these spiders to escape their predators by wheeling rapidly down the slope (Henschel, 1990b).

As fog rolls over the dunes, the density of droplets increases at dune tops. The only beetle species known to fog-bask are slipface-living *Onymacris unguicularis* (Hamilton and Seely, 1976) (Fig. 8c) and *O. bicolor* (Ward and Seely, 1996). Even though these diurnal ectotherms are sluggish when cool, they emerge from the warm sand at night to climb to the top of dunes and head-stand against the direction of cool fog to collect and imbibe water from their elytra. Assertions of fog-basking in warm fog on low-lying terrain by *Stenocara* spp. or other bumpy-backed tenebrionids (Parker and Lawrence, 2001) remain unverified (Hamilton et al., 2003; Mitchell et al., 2020) but have nevertheless misled many hydro-engineering studies while the particular morphological, behavioural and physiological traits of the genuine biomimicry models were ignored. Fog-basking behaviour has also been observed in the Namib Sand Adder (Louw, 1972). Slipface-living tenebrionids, *Lepidochora* spp. and *Zophosis fairmairei*, construct sand ridges that enhance fog deposition, which the beetles drink (Seely and Hamilton, 1976; Seely, 1979) (Fig. 8d). Rehydration of Sand-diving Lizards after fog events indicates that they, too, drink fog water from wet sand or vegetation (Louw, 1972). During fog, Golden Wheel Spiders drink from their soaked trapdoors (Mitchell et al., 2020).

4.5. Dune Crest

The sharp-pointed or rounded crests of Namib dunes are typically bare of vegetation and experience the strongest winds (Livingstone, 1990, 2013) (Fig. 2). This biotope can be regarded as an upward extension of the upper plinth and is frequented by animals from the plinth and slipface. The crest serves as a vantage point for lizards and raptors, while the convergence of gentle updrafts facilitates convective cooling during hot days (Louw and Holm, 1972; Louw, 1984; Mitchell et al., 1987). Strong winds across the dune crest increase the vapour pressure, pushing vapour through the sand towards the slipface, benefiting organisms buried there (Louge et al., 2022).

Rainfall infiltration through the bare crests and upper plinths forms the apex of the dunes' internal water storage and percolation system. With dune sand having a higher infiltration rate than the interdunes and the ground below the dune, an elevated water table develops, spreading out with water gradually flowing laterally towards the dune flanks, as demonstrated for the Chebbi Erg in Morocco (García-Rodríguez et al., 2014), Nizzana dunes (Kutiel et al., 2016) and Kalahari dunes (Stone et al., 2022). We can assume, therefore, that water soaking through the bare crest of Namib dunes contributes to available moisture for plants on the plinth and dune base, where even phreatophytes can tap it (Jürgens, 2022).

4.6. Sandsheets

With increasing southern latitude and winter rainfall, proper dunefields are replaced by sandy plains, termed sandsheets (Chojnacki and Kereszturi, 2014). Because of their unique ecosystem characteristics and the resulting relevance for biodiversity, we consider sandsheets a distinct biotope that is dominant in the Tsau||Khaeb and Richtersveld, covering 4957 and 2160 km², respectively. We mapped these southern sandsheets (Fig. 1) to distinguish them from dunefields and sand transport corridors with barchans (Lancaster 2014).

These sandsheets are formed by shifting sand but are devoid of elevated dunes other than arrays of parallel linear whaleback dunes without slipfaces. Typically, the sandsheets carry sparse vegetation composed of numerous plant species and satellite fauna, which differ from those found on other dune biotopes (Marais, 1993; Burke, 2004; Oguz et al., 2004). However, the temporary depositions do not form dunes besides small nebkhas (Fig. 2f). The sandsheets may include smaller stretches of bare sand and are often interspersed with local mosaics of sand, gravel, calcrete and rock (Oguz et al., 2004). The extreme aeolian sand transport is indicated by sandblasting features on stones and rocks and the occurrence of psammophilous plants (Jürgens, 1996) (Fig. 4).

4.7. Nebkha Dunes

In dune passes where advective fog is particularly dense (Mitchell et al., 2020), or where water within a dune percolates to its base (Jürgens, 2022), or where groundwater is within reach of phreatophytes (Lancaster and Teller, 1988; Sobol, 1996), or where radiation fog recycles evapotranspiration-derived water in interdune valleys (Kaseke et al., 2017), the large perennials, !Nara, *Stipagrostis sabulicola*, and *Trianthema hereroensis*, can form dense clusters of high nebkhas, sometimes with other psammophilous shrubs (Fig. 2, 3, 8e). Dense patches of nebkhas are sometimes associated with different dune types where conditions are suitable (Table 1). These nebkhas provide a patchwork of different micro-climates and resources within this biotope. The troughs offer shelter from strong winds, accumulate detritus generated by the plants on nebkhas, and are foraging grounds for predators of animals commuting between plants (Henschel and Lubin, 1997). Such patches of nebkha dunes support an unusually high density, biomass and diversity of dune biota, making this biotope the richest of all (Seely, 1991).

In western parts of the Tsau||Khaeb and the Richtersveld, the number and density of nebkha-forming smaller plant species increase, turning dune surfaces into a dense peak-and-trough configuration (Fig. 2f). Important nebkha-forming species are succulent dwarf shrubs and perennial grasses, including *Brownanthus arenosus*, *Cladoraphis cyperoides*, *Stoebria beetzii*, *Othonna cylindrica*, and *Salsola zeyheri* (Dreber et al., 2010).

An intermittent belt of coastal nebkhas stretches along the length of the Namib coast (Fig. 1). These are formed by salt-tolerant *Salsola nollothensis*, *Zygophyllum clavatum*, and a few other shrubs (Hesp, 1991; Soboil, 1996; Burke et al., 2011).

5. Dunefield structures

5.1. Gradients

The biotic communities of the Namib dunes and gravel plains vary across a steep gradient in atmospheric moisture from the west (fog zone, rainfall MAP 10 mm) to the east (MAP 100 mm). This gradient is tracked by changing productivity and species composition of plants (Robinson, 1976; Yeaton, 1988; Boyer, 1989; Becker and Jürgens, 2000; Hachfeld and Jürgens, 2000; Jürgens et al., 2013), animals (Coetzee, 1969; Stuart, 1975; Penrith, 1977, 1979; Holm and Scholtz, 1980; Henschel and Wassenaar, 2022), and microbes (Jacobson and Jacobson, 1998; Warren-Rhodes et al., 2013; Scola et al., 2018; Monus et al., 2023). Soil respiration of carbon tracks the rainfall gradient, increasing from the coast inland (Throop et al., 2020). The biotic communities differ between the dunefields, which are winter-rainfall dominated in the south, changing to summer-rainfall dominated in the north (Giess, 1971; Craven, 2009; Burke and Loots, 2020).

5.2. Dunefield connectivity

Ultrasammophilous animals are usually confined to specific dunes, isolated by surrounding interdunes or gravel plains, and their dispersal depends on where the dunes they inhabit travel and how these interconnect with other dunes. Conversely, interdunes are relatively isolated biotopes when surrounded by the different biotopes of elevated dunes. These processes are dynamic, as prevailing winds cause Namib dunes to change configuration and extend or migrate from south to north, connecting or disconnecting with other dunes.

The sands of the southern and northern Namib dunefields come from the Orange River (Lancaster and Ollier, 1983; Garzanti et al., 2014; Lancaster, 2014), with contributions from various inland sources increasing northwards (Garzanti et al., 2012; Garzanti et al., 2014). As the Orange River does not form a clear ecotone boundary, the Richtersveld sandsheets transfer material to the Tsau||Khaeb sandsheets and dunefields (Mucina et al., 2006) (Fig. 1). Psammophiles are transported northwards on trains of barchan dunes near the coasts of Tsau||Khaeb and Skeleton Coast (Penrith, 1979; Endrödy-Younga, 1982), driven by the Benguela Low-Level Coastal Jet (Corbett, 2018; Mendelsohn and Mendelsohn, 2018) (Fig. 1). During periods when lower sea levels exposed the continuous sandy belt along the coast (Bluck et al., 2007), northward-moving barchan dunes may have transported psammophiles from the Namib Sand Sea to the northern dunefields (Penrith, 1979; Endrödy-Younga, 1982). Coastal nebkhas are an extant south-to-north corridor for flora and fauna from South Africa to Angola (Fig. 1) (Zúñiga-Reinoso et al., 2023). Topographic Dunes and Wind Streak Dunes at rocky ridges across the gravel plains (Wilkinson, 1990) are potential metapopulation islands for psammophiles. The overall results of dune interconnections from Namaqualand to Iona are traceable along the phylogenetic relationships of tenebrionids (Koch, 1962a; Penrith, 1975, 1977, 1979; Endrödy-Younga, 1982) and termites (Gunter et al., 2023).

Similarly, isolated westward-moving Kalahari dunes in southern Namibia provide potential connections between Kalahari and Namib dune psammophiles (Penrith, 1977, 1984; Louw, 1986; Poller, 2005; Fish et al., 2015). For example, the Karasberg and Tses Dunefields are covered by a grass layer formed by the Kalahari Dune Bushman Grass *Stipagrostis amabilis*, while the Shortleaf Bushman Grass *Stipagrostis brevifolia* often covers dunes in the East Gariep Centre. Intense easterly stormwinds (Bergwinds) occasionally blow grass seeds, detritus and arthropods from the highland interior westwards into the desert, where some get trapped in the dunes, which are too dry for survival, thus augmenting the resources available to detritivores (Louw and Holm, 1972) and adding nutrients to the dunefields.

The highly productive marine Benguela Upwelling System with primary productivity of 0.14–8.83 g C.m⁻².d⁻¹ (Barlow et al., 2009) and secondary productivity (copepods) of 3.1–226.6 g C.m⁻².a⁻¹ (Verheye et al., 2016) results in the deposit of large amounts of organic matter on the coast in the form of algae (e.g. kelp ~1.7 t.m⁻¹.a⁻¹) (Stenton-Dozey and Griffiths, 1983), seal and bird guano and carrion, and other flotsam. These marine organics generate high productivity of macro- and meiofauna and microbes on beaches (~27 kg.m⁻¹.a⁻¹) (Bally, 1987). From the coast, organic material is transported far into the dunefields by westerly winds (Theobald et al., 2006), and mobile consumers such as arthropods, birds, jackals and brown hyaenas, thus enriching an otherwise low-nutrient habitat (Tarr et al., 1985; Dreyer and Nel, 1990; Kuhn et al., 2008; Jenner et al., 2011). Animal abundances mirror the decline of coast-to-inland subsidies of resources (Polis and Hurd, 1996; Polis et al., 2004; Theobald et al., 2006). For example, we recorded *Lepidochora* tenebrionids on slipfaces near the coast (Sandwich Bay) being eleven times as abundant as their counterparts *Lepidochora* on slipfaces 50 km inland (38.592 vs 3.481 beetles.trap-day⁻¹). Predators of *Lepidochora* tracked this trend, with the density of *Carparachne* spiders on the coastal slipfaces being 6-fold that at inland sites (0.1776 vs 0.0282 spiders.m⁻²).

The steep altitudinal and climatic gradients across the Great Escarpment along the east of the Namib Desert serve as an ecological barrier for many organisms (Barnard, 1998). Mountain zebra and gemsbok regularly move between the Great Escarpment and the dunefields, but their populations declined when park fencing curtailed their movements (Joubert, 1973; Kilian, 1995). For many small animals, the transition from the rocky terrain of the escarpment to the sand terrain of dunes is effectively a barrier. Wind-dispersed seeds that reach the dunes borne on Bergwinds cannot establish viable populations except on Inselbergs, such as the Uri-Hauchab mountain complex surrounded by dunes in the Namib Sand Sea (Burke et al., 1998). Even so, the flora of these Inselbergs largely resembles relic populations isolated at the northern extreme of the Succulent Karoo by advancing dunes. The same applies to some Uri-Hauchab fauna, e.g., several tenebrionid and zygentoman species that have otherwise not been recorded in the dunes (Penrith, 1979; Irish, 2018).

Several ephemeral and two perennial rivers that enter or cross the Namib dunefields from east to west represent oases and conduits for plants and animals (Jacobson and Jacobson, 2013). Some species move between riparian systems and dunefields, e.g., elephants (Leggett et al., 2004), gemsbok (Hamilton et al., 1977; Kok and Nel, 1996) and hyaenas (Tilson and Henschel, 1986). Frequent commutes render animal trampling a primary non-anthropogenic erosive force across interdunes near river beds (Boelhouwers and Scheepers, 2004). During boom times, some riparian arthropods expand their ranges into adjacent terrain without establishing resident populations (Wharton and Seely, 1982; Henschel, 2021). Likewise, seeds of some riparian plants may disperse over short distances into the dunefields, where they germinate but fail to establish dense populations. Satellite fauna that follow the dispersing plants need to cope with different trophic relationships encountered in isolated plants compared to dense stands (Polis, 1993).

The dynamics of dunefields render many river terminations a mixture of dune and riparian ecosystems with resources that differ from the interior of the dunefields as well as the upstream riverbeds. For example, the potential flow rate of sand across the Kuseb Delta is $440 \text{ t.m}^{-1}.\text{a}^{-1}$ (Lancaster, 1989), with crescentic dunes moving northwards at an average rate of 13 m.a^{-1} (Barnes, 2001). These dunes dam flood waters, thus facilitating periodic recharging of shallow coastal aquifers (Stengel, 1964; Jacobson et al., 1995; Morin et al., 2009) and the deposition of silt, which later erodes in easterly storm winds, generating the most extensive dust plumes in southern Africa (von Holdt and Eckardt, 2017). This dust, in turn, fertilises plankton blooms in the Benguela (Kangueehi, 2021; Dansie et al., 2022), ultimately increasing nutrient transfer from the ocean into the dunefields (Polis et al., 2004). Similar cycles also prevail with silt deposits at other river endings, e.g. Koichab, Tsauchab, Tsondab, Koigab, Uniab, and Hoanib (Teller et al., 1988; Krapf, 2003; Miller et al., 2021). These render the mixture of riparian and dune communities at river terminals exceptionally rich and productive but also highly sensitive to changes in the episodic flooding patterns across the river catchments (Jacobson and Jacobson, 2013). The same applies to the nutrient enrichment of dune ecosystems by !Naras tapping into palaeochannels fed by rivers (Morin et al., 2009).

6. Namib dunefields in the Anthropocene

The Namib dunes and their iconic psammophiles are considered to be aesthetically attractive for ecotourists and nature lovers, recreational playgrounds for 4x4 vehicles and bikes, photographic and film scenes for entertainment, advertising and documentary media, sources of diamonds, minerals, groundwater, and sites for industrial complexes (Robertson et al., 2012). Mines and other infrastructure were established in or across the dunefields despite the high maintenance costs of managing mobile sand (Le Roux, 1974; Slattery, 1990; Schneider, 2008, 2009; Bovin and Jonsson, 2011; Corbett, 2018). Besides this infrastructure, there are few roads or defined tracks through the dunefields. Nevertheless, some Namib dunefields and adjacent sand-blasted corridors, formerly regarded as unsuitable for industrial developments, are currently considered for developing green hydrogen production powered by wind and solar generators, entailing roads, power lines and pipelines. These plans reflect the potential for far more extensive land use changes and accompanying impacts than experienced in the past.

The environmental impacts of the abovementioned land-use changes can be mitigated through ecological restoration (Burke, 2001; Milton, 2001; Burke, 2003; Carrick and Krüger, 2007; Carrick et al., 2022). However, hyperaridity, strong winds, and low levels of plant available nutrients in dunes render ecological restoration challenging, entailing numerous interventions that focus on nurturing individual plants or small patches (Burke, 2003; Carrick et al., 2022; Carrick, 2023). Furthermore, the trajectories of long-term ecosystem recovery are extremely slow, varied and unpredictable, requiring complex assessment criteria of ecosystem integrity and follow-up interventions over many decades (Netshilaphala et al., 2005; Pauw et al., 2018; Steed et al., 2018; Burke, 2024).

Some potential impacts of mining are beyond repair. For example, extracting groundwater from dunefields would be unsustainable (Schmidt and Plöthner, 1999) and degrade ecosystem productivity. In an area near Walvis Bay where river diversion prevented groundwater replenishment over five decades, many !Nara plants died, and their keystone roles disappeared (Ito, 2005). The effects of some other human impacts are unknown, e.g., the application of seismic exploration may deafen inhabitants of the sandy medium where many animals are sensitive to vibrations. Much more research is needed on the impacts and restoration of mining-related and other anthropogenic activities in dune ecosystems.

Most modern human activities entail off-road driving (ORD), which can affect all dunefields in regulated and unregulated areas. Therefore, it is necessary to consider the effects of dune driving and its impacts on the geophysical and biotic components of dunes (Table 2) and ways to mitigate these effects. ORD damages or kills plants and epigeic organisms and changes soil properties that affect ecological processes in and beyond the actual surface tracks (Iverson et al., 1981; Daneel, 1992; Nortjé et al., 2012; Assaeed et al., 2019). ORD threatens vulnerable species such as ground-nesting Damara terns, chameleons and rare plants (Burke and Cloete, 2004; Braby et al., 2010; Tolley, 2013). Tracks from ORD can last for decades to centuries if the capacity for natural recovery is undermined (Seely and Hamilton, 1978; Iverson et al., 1981; Daneel, 1992; Jarrold, 2001).

Small-scale physical factors affected by ORD include the creation of ruts, causing visual impacts, erosion by wind and water, and micro-climatic changes, especially in the interdunes (Seely and Hamilton, 1978). Depending on the soil characteristics, ORD alters soil compaction and stability to depths of one to several decimetres, affecting water runoff, infiltration and retention for weeks, months, or years, even on plinths where visible signs quickly disappear. The damage done by ORD to leaves, branches, and shallow roots imposes significant costs on individual plants and their satellite fauna and can be fatal (Griggs and Walsh, 1981; Nortjé et al., 2016). The first passage of a vehicle causes the most destruction, but the impact compounds with repeated use of the same track (Tuttle and Griggs, 1987; Nortjé et al., 2012). Nevertheless, the reuse of existing tracks limits the spatial extent of the damage and often improves vehicle traction (Lyasko, 2010).

Burke and Cloete (2004) found that raking interdune tracks to reduce compaction and lift depressed pebbles and replanting the most common perennial plants into the tracks from the adjacent plant community reduces fluvial and aeolian erosion and increases water infiltration, with recovery particularly successful on sandy tracks. However, to be effective, rehabilitation requires diligent treatment of each track.

It is recommended to use designated tracks, with routes demarcated to follow even in low visibility (Kalra et al., 2023). Spatial partitioning of Namib dunefields for specific anthropogenic activities and adherence of vehicles to designated areas or routes serves to avoid impacting pristine parts of the dunefields (Braby, 2008, 2009). A decade or more after the spatial partitioning of the Walvis Bay - Swakopmund dunes, the defined impact areas should be examined and compared to similar pristine areas. Likewise, pre- and post-impact studies of permitted concentrated ORD activities elsewhere in the Namib dunes will help understand how to avoid and mitigate the impact and improve rehabilitation.

Despite the many abovementioned local impacts, the ecosystem integrity of the Namib dunes remains relatively intact. However, global climate change and extensive land use changes may cause drastic transformations within the following decades. The most significant environmental parameter, aridity, is projected to increase along with temperature (Engelbrecht et al., 2024). This effect would be enhanced by the weakening of the dominant southerly winds along the Namib coast, weakening the northern Benguela Upwelling System and warming the coastal waters of the Southern Atlantic north of Lüderitz (Brandt et al., 2024). Ocean-to-land subsidies would diminish, and advective fog would disappear along with the prevailing oceanically-driven cool climate across the western Namib Desert (Mitchell et al., 2020). If the occurrence of extreme windstorms were also to increase in the Namib as predicted for the Kalahari, aeolian sand mobility would increase and destabilise the dunefields, rendering them even more barren (Thomas et al., 2005; Baas and Delobel, 2022; Gunn et al., 2022). Adiabatically heated east winds could augment the local effects of global warming and render the Namib intolerably hot for many species, even for the most extreme thermophiles. Psammophiles are finely attuned to specific geophysical characteristics of the dunes, and some species may become

maladapted when these characteristics deviate due to changes in winds, moisture and temperature. Many psammophiles that evolved and existed for several million years in the relatively stable climatic system of the Namib may disappear.

The devastating consequences for the Namib dune ecosystem would likely be as sweeping as the projected near-disappearance of the Succulent Karoo biome by 2080 (Midgley and Thuiller, 2007). An expansion of plant communities of the Desert biome into the Succulent Karoo has already been observed across the Richtersveld due to the prolonged drought of 2012 to 2023 (Jürgens et al., in prep). As a cascading effect, the death of many perennial plants, which formerly anchored nebkhas, mobilized large quantities of sand that buried landscapes further downwind. Similar changes can be expected in the summer rainfall region of the Namib.

Most of the Namib dunefields and associated sandy plains are in designated conservation areas under the responsibilities of the Namibian, South African, and Angolan governments. This responsibility should facilitate coherent conservation and land use plans, regulations and compliance across all dunefields. Furthermore, the Namib Sand Sea is a UNESCO World Heritage site (Seely, 2012). International endorsement by the Transfrontier Conservation Areas (TFCA) programme promoted by the UNEP, IUCN and SADC enhances the management of the Iona-Skeleton Coast and the /Ai/Ais-Richtersveld TFCAs, which could potentially expand into the Three Nations Namib Desert Transfrontier Conservation Area from the Richtersveld to Iona (SADC, 2018).

The ongoing production and revision of a considerable body of textbook knowledge of global relevance is facilitated in the Namib dunes by relatively good accessibility and involvement of several local and international research institutions, with the Gobabeb Namib Research Institute being centrally located (Henschel and Lancaster, 2013; Henschel and Maggs-Kölling, 2022). The Namib dunes continue to be an ideal outdoor laboratory for scientific research.

7. Conclusions

The characteristics of sand in the windy, hyperarid conditions of the Namib dunes engendered a unique group of psammophiles. The specialised traits of psammophiles, in turn, reveal the critical properties of desert sand for harbouring life. Most important are the water infiltration and retention properties of dunes and the ease with which psammophiles can penetrate sand to access subterranean moisture, sustenance, and shelter. However, research on the subterranean dynamics of moisture in dunes and how psammophiles access this has thus far barely breached the surface layer and needs to be deepened, literally and figuratively, as dunefields are becoming multiple-use areas requiring management to avoid, mitigate or redress anthropogenic impacts.

Psammophiles evolved particular abilities to resist, cope with, or utilise the effects of wind to cool, sandblast, inundate or expose organisms and transport detritus and seeds. The ability of some dune vegetation to stabilise wind-driven dunes is a practical tool for protecting industrial and urban infrastructure placed in dune pathways. Further research is required to apply this tool effectively. Winds shape dunes into diverse biotopes at macro- and micro-scales, rendering dunefields more multifaceted and biotically richer than many other desert habitats. The diversity patterns and evolution of psammophiles in the Namib dunefields reflect wind-driven dune movements and connectivity or isolation of dunes.

Remarkably, most of the biomass of the dune vegetation is formed by only a few keystone species of plants whose relevance for dune ecosystems is not yet fully understood. It should be instructive to intensify the exploration of the interaction networks between these keystone plants and their satellite

faunas at ecosystem levels in different Namib dunefields. Such understanding is fundamental for circumventing tipping-point ecosystem degradation if keystones are disturbed.

Phylogenetic research should expand to trace the development of psammophiles and compare them with lithophiles in other Namib habitats much older than the dunefields. For example, knowing the phylogeography of the important *Stipagrostis* grasses would be very instructive. More so, the fundamental influence of the oceanic atmosphere, with its high humidity and fog, as a driver of evolution traceable through phylogeography and resultant biogeography of psammophiles requires further study to understand the risks of climate change on the Benguela.

Many past studies were on the most conspicuous or convenient, unusual, or urgent conservation-related topics, organisms, and ecosystem parameters, while recent research has revealed several previously overlooked features and opened up new avenues. For example, the upcoming publication (Jürgens, in prep.) of a revised vegetation map of Namibia can lead to further research in community ecology. Major paradigm shifts include revisiting the autecological frame concerning the overpowering effects of hyperaridity, high temperatures and wind as driving factors, while many intra- and inter-specific synergies, competition, and trophic relationships are being uncovered. Some intensely studied processes are still inadequately understood, e.g., the subterranean dynamics in dunes of psammophile-accessible moisture.

A looming question is how climate change, as expressed in temperature, moisture, and wind, will affect the Namib dunes and their psammophilous communities. Long-Term Ecological Research (LTER) is a promising tool for building a foundation for tracking changes and elucidating the underlying natural patterns of geophysical and biotic variability (Henschel et al., 2003b; Mirtl et al., 2018). It can also reveal otherwise cryptic properties of psammophile populations of the different dune biotopes and dune types by comparing long-term patterns and drivers of variability among them and with habitats outside the dunes (Henschel, in prep.). While several LTER programmes, coordinated by Gobabeb (Henschel et al., 2000), SASSCAL (Jürgens et al., 2010; Jürgens et al., 2018), SAEON (von Maltitz et al., 2024), CIBIO/ISCED (Huntley, 2023), and others, collect, manage and process long-term data from Namib dunefields, much data awaits analysis and interpretation. Doing this is a priority for evaluating the ultimate usefulness of amassing long-term datasets and planning to collect further needed data.

Most of the publications cited in this chapter were from Gobabeb-based research on the Namib Sand Sea and focused on its most important patterns and principles. However, the southern dunes in the Namaqualand and Tsau||Khaeb and the northern ones in the Skeleton Coast and Iona differ from the Namib Sand Sea in many respects. As public and scientists' access to the Tsau||Khaeb National Park and the Iona-Skeleton-Coast Transfrontier Park improve and plans for industrial and urban developments advance, the urgency for intensifying local ecosystem research in all Namib dunefields increases. Such research will be necessary to advance knowledge, enhance conservation and improve the ability to manage risks and restore degraded ecosystems.

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9. Glossary

Term	Explanation
Namib dunes	specific aeolian sand ridges or mounds tens to hundreds of metres high alternatively, collectively, all or any Namib dunefields and sandsheets
dunefield	interconnected dunes as in an erg or sand sea
sandsheet	featureless, low-relief sand-covered plain without elevated dunes
psammophily	sand-living
xerophilous	desert-adapted
phreatophyte	plant with deep tap roots that reach groundwater
psammophory	fixing a protective layer of sand onto exposed parts of organisms*
nebkha	hummock, phytogenic micro-dune formed from sand accumulating within and on the lee sides of plants
whalebacks	parallel, low, linear, slipfaceless dunes
ORD	off-road driving

* Psammophory, in this sense, was first coined for plants but is also found in some insects. The same term was later also used in a different sense for rows of long hairs on the underside of the head of some ants that are used to carry sand and seeds (Porter and Jorgensen, 1990).

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