A Brief Introduction to Hot Desert Environments: Climate, Geomorphology, Habitats, and Soils

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Abstract

This chapter provides a broad introduction to dryland environments with a focus on desert climate, geomorphology, habitats, and soils that collectively provide opportunities and limitations for microbial life. Desert precipitation is governed by global circulation patterns, which determine the distribution of drylands and associated rainfall gradients. Desert margins especially are subject to pronounced inter-annual variability, and good years may be replaced by a negative departure from mean rainfall, resulting in drought. The depth of drought for any location can be examined using the widely accessible Standardised Precipitation-Evapotranspiration Index (SPEI) and Normalised Difference Vegetation Index (NDVI). The topography of desert surfaces and habitats can be characterised by rocky run-off from uplands and fluvial run-on in channels and fan settings. Other settings may be dominated by mobile sediments such as dunes or shallow groundwater, which promotes evaporation and build-up of salts. Gravel plains, on the other hand, may provide stable surfaces. Desert soils and associated surfaces, the so-called pedoderm, require stability to form and prevail. The abiotic properties of unconsolidated porous media moderate the physical and chemical subsurface environment. Crusts in particular, play a role in regulating fluxes, including water, carbon, and nitrogen, which collectively determine the microbial subsurface environment. Moisture regimes vary in space and time along with geomorphic conditions, the distribution of habitats, and the state of the pedoderm.

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Keywords

Dryland precipitation · Geomorphology · Habitat · Soil · Pedoderm

The chapter wishes to introduce hot, arid regions, also referred to as drylands or desert environments. These are defined by a lack of moisture, the result of low precipitation and high evapotranspiration rates (Thornthwaite 1948), and which cover close to half of the earth's surface. Meteorological deserts extend into the polar region and cover large parts of the world's ocean also. For the purpose of this book, we shall focus on hot deserts in terrestrial subtropics. This chapter serves as a broad and general introduction to dryland environments, determined by climate, geomorphology, habitats, and soil conditions. These provide both limitations and opportunities for microbial life at various scales: first globally, in terms of climate, then regionally, due to landscapes and landforms, and subsequently locally, due to habitats and soil processes.

1.1 Desert Climatology

1.1.1 Desert Precipitation

While a number of climatic factors influence microbial activity in deserts, this chapter focuses on precipitation as the dominant limiting resource and driver of desert ecosystems. Hot deserts in terrestrial subtropics are largely determined by the positioning of dry, descending air, associated with high-pressure systems that form part of the global Hadley Cell circulation patterns with quasi-stationary positions over north and south Africa, Australia, Asia, and the west of North and South America (Figs. 1.1 and 1.2). The positions of these high-pressure systems are subject to a seasonal latitudinal shift, giving way to tropical, convective summer rain, especially the Intertropical Convergence Zone towards the equator and frontal, winter rain in Mediterranean latitudes. These pressure constellations generate rainfall gradients that extend from the equatorial regions, with high rainfall regimes, into semi-arid drylands, deserts, and hyper-arid desert cores. For an introduction to desert climatology, refer to Nicholson (2011).

Additional factors play a role in further limiting rain, such as distance from oceans, which are the primary source of moisture, the blocking of moisture bearing, westward flowing air by topographic barriers, and the suppression of convective cloud formation over cool waters, especially ocean upwelling systems along subtropical west coasts. The results are the major arid regions of the world, to be found to the west of North and South America, Southern Africa, the Sahara of North Africa, Arabia, and much of the Middle East, as well as Central Asia and most of Australia. Due to the movement of pressure systems, the core of drylands tends to be hyper-arid, while desert margins are considered semi-arid. The resulting gradients can be steep over short distances, as seen in Fig. 1.3.

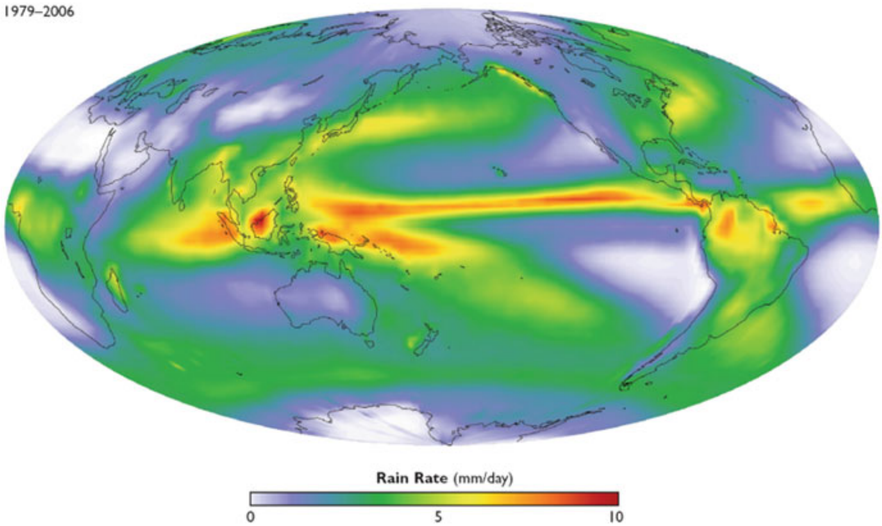


Fig. 1.1 Global long-term rainfall patterns. Note the lack of rain in the subtropics over land and sea (King 2007)

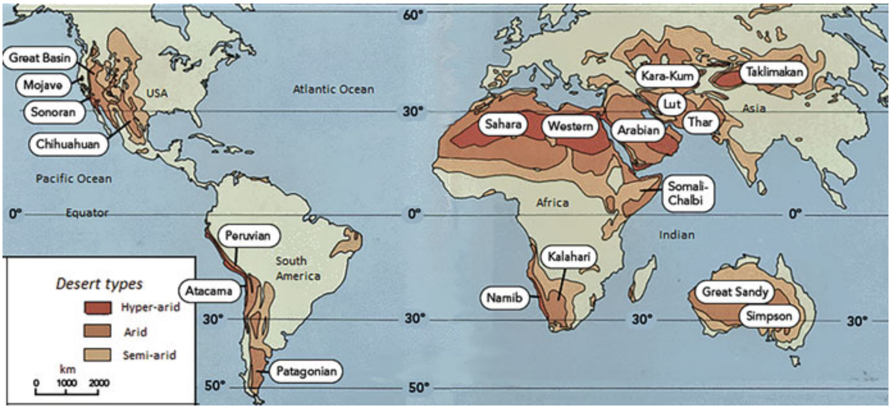


Fig. 1.2 Map of global deserts (Provided by A.S. Goudie)

Opportunities for rain are seasonal but diminish significantly towards the quasi-stationary centres of continental high-pressure systems. This results in rainfall gradients, some of which may be relatively short and dramatic, especially in areas with pronounced topography (Zipser et al. 2006). Since convective rain in the subtropics is also mostly associated with stationary rising air, this often produces localised rain events, making rainfall patterns both patchy and unpredictable in nature. Rains in drylands can be described as infrequent but also often intense, given that the annual total might be associated with a few major events.

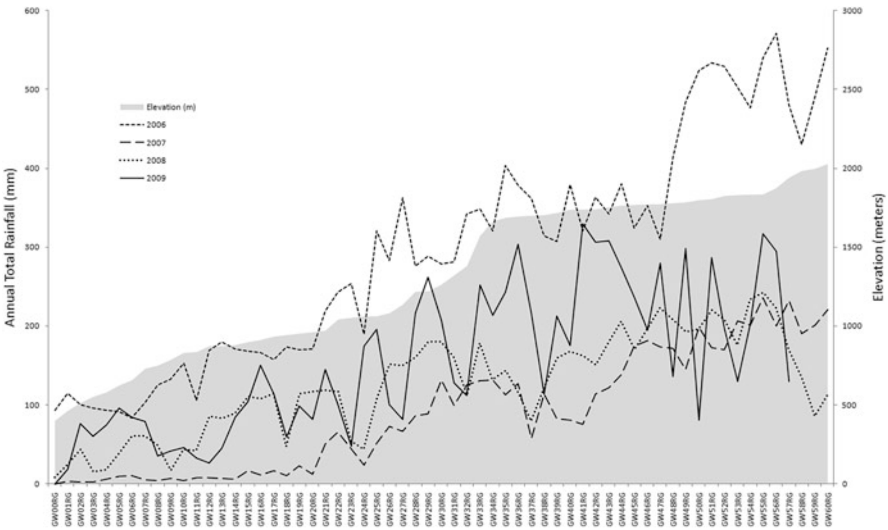


Fig. 1.3 Rainfall gradient in Namibia over a few hundred kilometres from the interior to the coast, between 2006 and 2009. Note the diminishing rainfall towards the hyper-arid coast and the inter-annual variability of rainfall (*y*-axis on the left). The grey depicts elevation from the interior at 2000 m towards the coasts at 500 m (*y*-axis on the right) (Eckardt et al. 2013)

1.1.2 Drought

The uncertainty of rainfall is also temporal in nature, given that individual rainy seasons may differ considerably from year to year, which may cause both drought and wet years. The so-called inter-annual variability is largely determined by global sea surface temperature anomalies and oscillations in the equatorial Pacific (El Niño–Southern Oscillation) and beyond. Firstly, cooler oceans tend to suppress rainfall and warmer oceans tend to promote it, and secondly, these associated shifts in rising and descending air masses also determine the positioning and persistence of high-pressure cells. As a result, it is not uncommon for seasonal rainfall yields to be either above or below average, with the average rainfall seldom being met. The mean rainfall, however, establishes a baseline against which to compare individual months and years. It is, furthermore, not uncommon for rainfall patterns at any location to vary in a cyclic manner with several above average years followed by several below average years.

While deserts can be classified according to their average rainfall and evaporation, it is also useful to quantify drought conditions. A meteorological drought would be associated with an anomalously dry month. Several months with a persistent absence of rain would result in below average soil moisture and reduced plant growth, also referred to as agricultural drought. A number of below average dry years would result in a decline of surface waters and drop in groundwater tables, which can be described as a hydrological drought (Fig. 1.4). This cyclic nature is common in all arid regions.

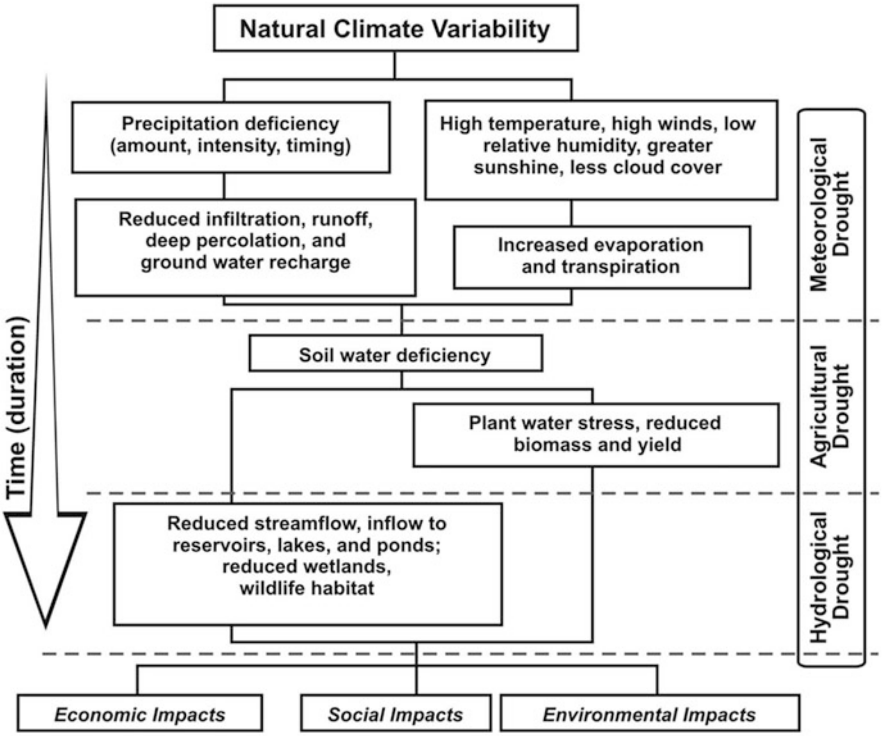


Fig. 1.4 Drought and progression with time, from short-lived meteorological to long-term hydrological drought (source: National Drought Mitigation Centre, University of Nebraska)

Two readily available indices can be used to quantify drought at any location on the globe, namely the Standardised Precipitation-Evapotranspiration Index (SPEI) and Normalised Difference Vegetation Index (NDVI). The unitless SPEI index is available in half degree tiles at a monthly resolution and on a range of timescales from 1 to 48 months. The index makes use of the Thornthwaite (1948) equation and draws on a number of global datasets (Beguería et al. 2014). By resorting to smoothed time series, the different types of drought are identifiable (Fig. 1.5). The resulting 1-month (SPEI-01) product emphasises meteorological drought cycles. The SPEI-03 (3 months) accentuates seasonal short- and medium-term trends, such as soil moisture, and is suitable for the study of agricultural drought. SPEI-12 (1 year) examines annual moisture cycles that would flag hydrological drought conditions. SPEI-48 (4 years) is the coarsest SPEI product and depicts accumulative long-term decadal drought cycles. The SPEI dataset has now been extended to 1901 and provides near real-time results for any location on the earth surface, which is ideally suited for drought monitoring and early-warning purposes. The graphic interface is easy to negotiate, and raw data can be obtained as well.

The satellite-based Moderate Resolution Imaging Spectroradiometer (MODIS) produces a global NDVI (Normalised Difference Vegetation Index) time series. This

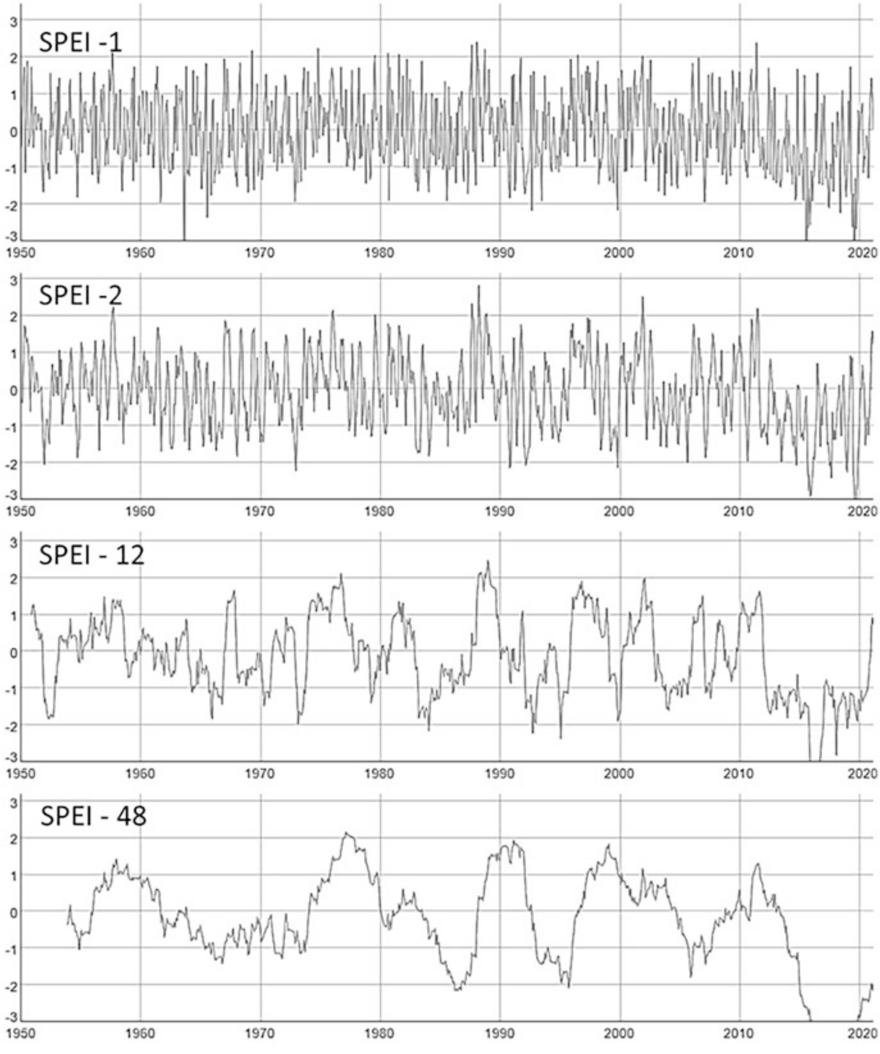


Fig. 1.5 The unitless Standardised Precipitation-Evapotranspiration Index (SPEI) for Bloemfontein South Africa (1954–2020) (source: SPEI online portal https://spei.csic.es/database.html). From top to bottom: SPEI 01 meteorological drought, SPEI-03 agricultural drought, SPEI-12 hydrological drought, SPEI-48 decadal drought. Positive values indicate wetter conditions and negative values indicate the opposite. The recent deep drought is evident in the time series and the result of numerous dry months and years

monitors the state of vegetation, measuring reflected infrared radiation and red absorption as an indicator of plant growth (Tucker 1979). The results can be interrogated through the Global Agriculture Monitoring (GLAM) project portal (Becker-Reshef et al. 2010), which depicts vegetation in 8-day timesteps and

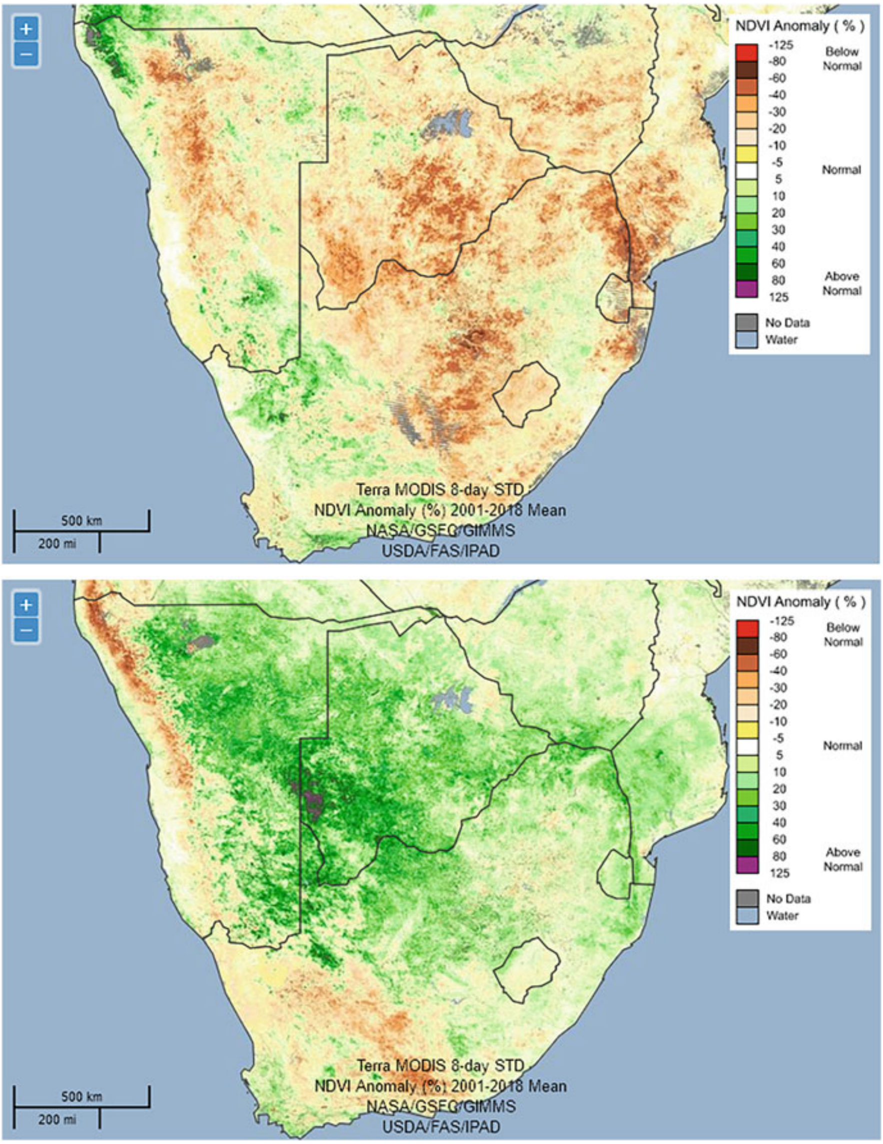


Fig. 1.6 Significant inter-annual variation in chlorophyl response to rainfall for southern Africa, captured by the Normalised Difference Vegetation (NDVI) Anomaly for February 10–17, 2016 (a severe drought year) at the top and March 30–April 06, 2021 (a very wet year) at the bottom (source: Global Agriculture Monitoring (GLAM) Project (https://pekko.geog.umd.edu/usda/test/)

determines the NDVI anomaly at a 250 m resolution since February 2000 for any part of the earth surface (Fig. 1.6). Anomalies for any 8-day time period can be generated.

1.2 Desert Geomorphology

1.2.1 Desert Landscapes and Sediments

While hot deserts are subject to more-or-less similar climatic conditions, surface processes differ considerably, given a host of varied and distinct landscapes and associated environments (Goudie 2002). The following section will focus on five contrasting geomorphic units commonly found around the world (Table 1.1 and Fig. 1.7), such as uplands, drainage systems, saline basins, sand dunes, and gravel plains, all with distinct substrate and abiotic conditions, but also habitats for fauna (including microorganisms; Chap. 4) and flora and soil conditions.

There are several recent textbooks on dryland geomorphology available (e.g. Cooke et al. 1993; Parsons and Abrahams 2009). These have been through multiple editions, drawing on key researchers in the field, and provide a synergy on such topics as landscapes, weathering, fluvial, and aeolian processes. We will be referring mostly to some most recent edited chapters by Thomas (2011).

Most of the world deserts are mountainous and include the active tectonic plate boundaries of several continents, including North Africa (Atlas), Arabia and the Middle East (Sinai, Zagros), Asia (Thar and Takla Makan), as well as the western Americas (Mojave, Sonoran, Atacama) (Rendell 2011). Rocky surfaces are also associated with denudated plate interiors (Karoo and Australia), volcanic highlands (Sahara), and escarpments in Africa. Bedrock outcrops in drylands are subject to limited shade and large diurnal temperature cycles, which may impose stresses and volumetric changes on rock surfaces and result in the gradual separation of grains and rock structures. Weathering in rocky deserts is primarily physical in character, resulting in a fragmentation of rocks, with little or no chemical alteration (Viles 2011). Given the lack of chemical alteration, clay formation is also not widespread in deserts. Weathering may be slow, but the removal of loose material is efficient. In general, fluvial processes and associated landforms are remarkably widespread in drylands, even if they are not active for long periods of time (Wainwright and Bracken 2011). Low-frequency, high-magnitude floods have the ability to carry very high sediment loads in an environment that is largely devoid of vegetation. In addition, thin soils do not favour infiltration but promote run-off. In areas with soft and unconsolidated sediments, the resulting drainage networks can be very dense, which produces so-called Badlands (Howard and Kerby 1983), common in a number of drylands including those of southern Europe. Despite long periods of drought and significant dry seasons, the imprint of fluvial processes in arid landscapes is both pronounced and widespread and often dramatic.

Upland regions and associated fluvial processes tend to generate coarse angular colluvium on slopes. Should flow become unconstrained at the base of slopes, diverging alluvial fans develop, which results in finer and rounder sediment along the toe of fans (Harvey 2011). If flow remains constrained, valley sides or flood plains accumulate terraces through successive episodes of fluvial cutting and filling. Accumulations of fine alluvial sediments may line the valley sides and extend towards river endpoints, including inland basins. It is here where finer material can

Table 1.1 Major desert environmental characteristics

Geomorphology	Substrate	Hydrology	Radiation	Surface Temperature (max, min, and range)	Vegetation (Main source soil organic matter)	Macrofauna	Nutrient dynamics	Substrate processes
Rock outcrops, inselbergs, uplands	Very stable, bare rock, gravel, colluvial or accretion fans/ slopes	Limited surface water retention, rapid infiltration and storage in cracks, aspect, and size/ orogenic effects	Variable (affected considerably by aspect, slope, and surface roughness)	Variable (dependent on colour, aspect, slope, surface roughness, altitude, wind exposure)	Diverse (cremnophilous, refugial, cryptic and specialist species), expect higher diversity and aspect differences	Petrophilous, refugial and herbivorous specialists, niche specialisation, high species to area diversity ratios	Weathering, organic trapping	Weathering, colluvium, accretion, limited pedogenesis
Mixed plains	Stable, desert armour, gravel, sometimes calcrete, gypsum	Rapid surface desiccation, shallow storage of available moisture	High (affected by degree of vegetation cover, surface colour)	High (ameliorated by pebble size, lighter colours, vegetation cover)	Mainly grasses, sparse dwarf shrubs, annuals, geophytes, and succulents	Fossorial, cryptic, vagile and dormant species common, low species to area diversity ratios	Trap dust and nutrients	Aggregation, accretion, pedogenic cementation
Sandy plains, sand sheets, dunes	Unstable to very dynamic sand, Aeolian surface saltation and abrasion	Rapid surface desiccation, porous, store water at depth, water vapour absorption near surface	High (affected by degree of vegetation cover, aspect, sand colour)	Very high due to small grain size (ameliorated by lighter colours, vegetation cover, aspect)	Mainly grass and geophytes, occasional specially adapted succulents or shrubs	Psammophiles, fossorial species, high incidence of omnivores and generalist scavengers, very low species to area diversity ratios	Poor in nutrients and soil organic carbon	Accretion

(continued)

Table 1.1 (continued)

Geomorphology	Substrate	Hydrology	Radiation	Surface Temperature (max, min, and range)	Vegetation (Main source soil organic matter)	Macrofauna	Nutrient dynamics	Substrate processes
Playas, river end points, saline basins	Very stable, sandy, and silty	Porous, moisture often salty and close to the surface/ shallow surface water	Very high, reflective, no shade	High (ameliorated by reflection and evaporative cooling)	Halophytes, specially adapted species	Habitat/Niche specialist (halophiles) and transient spp.	Very poor, high Na Mg content	Aggregation, evaporites
Drainage systems	Mostly stable, sandy, and silty alluvium, downstream changes depending on gradient and frequency and magnitude of discharge	Porous, may hold and retain water at depth (fossil water becomes salty), infrequent and potentially high magnitude floods/ discharge	Variable (high in open channel, ameliorated by vegetation, width to depth ratio of channel, slope, and direction of banks)	Variable (ameliorated by substrate grain/pebble size, substrate colour, vegetation, width to depth ratio of channel, bearing)	Phreatophytes, shrubs and other perennial species, herbaceous opportunists	Linear oasis providing refuge to local, adventive and transient spp., high diversity of poorly adapted spp.	Traps organic materials and other nutrients, higher autochthonous organic deposition	Alluvium, accretion, aggregation, erosion

Fig. 1.7 Examples of desert landscapes and landforms. Significant variation in topography, substrate, habitats, and soils is evident. Depicted are (**a**) rocky uplands and a dry river, Oman, (**b**) sand dune on buried fluvial sediments, Namibia, (**c**) saline pan crusts, USA, (**d**) gravel plain, desert pavement, and vegetation polygons, Namibia, (**e**) incised fluvial sediments in badlands, Spain, (**f**) loess silt deposit, China (credit: F. Eckardt)

be preferentially sorted and deflated by aeolian processes, resulting in the accumulation of coarser material, such as sand, and the loss of fine material such as silt, which provides atmospheric dust. Drainage endpoints also have the tendency to accumulate sand, prone to saltation and creep, which may form a range of dune types, depending on a variety of wind regimes and the amount of sediment supplied (Lancaster 2002). Large sand deposits and active sand seas tend to occupy low-lying continental basins but may also be found along coastal margins close to river mouths, where the distinction between coastal and inland dunes becomes blurred. Large sand seas are particularly prevalent in the Sahara, Southern Africa, Asia, and Australia and to a lesser extent in the Americas (McKee 1979). The associated dust generated from saltating sand and abrasion processes may undergo transport over a variety of distances, accompanied by the dispersion of silt, along with bioavailable nutrients and salts. The deposition of vast quantities of fine-grained silt-sized dust results in the accumulation of loess, which is globally widespread, often covered by vegetation, but also exposed on desert margins and interiors (Pye 1995). Loess found in desert margins is fertile, but easily eroded by wind and water.

Rocky surfaces provide very limited opportunities for retaining water; hence, highland catchments are very quick at converting intense convective rain into flash floods. Upland regions have a limited ability to retain water; however, deep sedimentary valley fills are able to sustain groundwater into the dry season and beyond. Lowland areas, especially, accumulate sediments, but may even store shallow groundwater and occasional surface water. Here, salts may accumulate at discharge points and seeps, around inland basins and playas (Shaw and Bryant 2011), given the high evaporation rates of shallow groundwater tables. Coastal salt pans, or sabkhas as they are also known, are widespread in the Persian Gulf coast and beyond and, despite their proximity to the ocean, often accumulate evaporation products derived from inland subsurface run-off, rather than seawater evaporation (Wood et al. 2002). Salts are only sustained at the surface in the driest of deserts, as any rain quickly results in a solution of most evaporation products. Dry saline surfaces at inland playas and coastal sabkhas are prevalent in the broad valleys of the Americas and Asia or shallow basins of Africa and Australia, as well as associated coastlines. The remaining desert surfaces may be quite unremarkable and include vegetation-covered sand deposits and dunes, or deflated lag gravel deposits. However, here stability may not only result in the accumulation of sediments but also the formation of soils. These varied environments provide a wide range of opportunities for creating habitats and may locally be subject to run-off and run-off which may hinder or facilitate patches of soil formation.

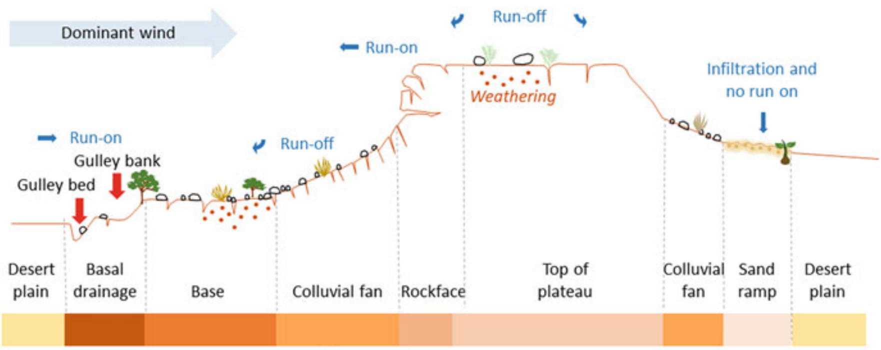
1.3 Desert Habitats

1.3.1 Introduction

The desert landscapes described in the previous section may appear to be barren and devoid of life. However, they provide a range of habitats that are largely determined by the abiotic environment, e.g. climate, topography, and soil properties (Gibson 1996) and support a host of organisms. Desert biota are adapted to survive a scarcity of resources like water and nutrients, of which the spatial and temporal concentration and availability is particularly pronounced in deserts (Shmida et al. 1986), and to exploit brief periods of abundant resources (Seely and Louw 1980). The most defining variable for biodiversity is low, erratic, and unpredictable precipitation that determines water relations and nutrient mobilisation. Understanding the spatial patterns of the biotic environment, and how these change over time, is a key element for characterising nutrient pools in deserts. Biogeochemical cycling is an important driver of both the evolution and persistence of highly adapted, unique, and diverse assemblages of macro- and microorganisms able to flourish in such extreme arid conditions. Habitats are both a result and a feature of landscapes. However, the geomorphic processes introduced in the previous section are the primary mechanism shaping desert habitats. Table 1.1 depicts the relationship between geomorphic units and habitat descriptions listed here.

1.3.2 Uplands, Inselbergs, and Rocky Outcrops

Desert mountain and hill profiles often transition abruptly from the gentle slopes of desert plains (Fig. 1.8). Although sparsely vegetated, these mountainous landforms nevertheless support a much more diverse and abundant biota than the surrounding plains, due to a greater range of microhabitats associated with hydrologic and geohydrologic moisture regimes. Desert mountains host high levels of biodiversity and endemism (Barthlott and Porembski 2000) due to their microhabitat diversity and insularity. Other important influences of mountains on the fauna and flora include size, elevation, topography, orientation, degree of isolation, climatic effects, as well as lithology (Kruckeberg 2002). Spatial complexity of mountainous habitats is particularly noticeable in deserts, primarily due to the influence of microtopographic heterogeneity on moisture regimes. Generally, there is a decrease



Basal drainage	*Pheatophytes, perennial shrubs, sedges and grasses (ecotone)*
Base	*Desert plains species, pheatophytes (ecotone)*
Colluvial fan	*Phreatophytes, petrophiles, desert plains species, inselberg endemics, cryptic, endogenic and hypolithic species, poikilohydric cryptogams*
Rockface	*Cremnophytes, chasmophytes, petrophiles, refugial species*
Top of plateau	*Chasmophytes, petrophiles, refugial species, inselberg endemics*
Sand ramp	*Psammophiles, geophytes*

Fig. 1.8 Habitats associated with uplands, inselbergs, and rocky outcrops (modified from Shmida et al. 1986)

in the numbers of species of organisms with increasing altitude, although vegetation zonation on desert mountains is not always distinct. Flat mountain tops serve as a sump for moisture, as well as weathered substrate material. As a result, they offer unique habitats for specialised and endemic organisms and are often refugia for relict taxa (Rahbek et al. 2019).

Compact rock surfaces or steep rock faces on the windward side, with high rates of run-off, are less favourable for plant growth, and only hardy lithophytes, including lichens, can flourish. Elsewhere, seedlings of chasmophytes establish opportunistically (Hegazy and Lovett-Doust 2016) in soft materials and moisture that accumulate in fissured rock surfaces and crevices found in sheltered pockets and lee slopes. The microbial ecology of endolithic microbial communities, i.e. those colonising and inhabiting rock pores and fissures, from hot deserts is described in Chap. 5. Pendulous, cremnophilous plants can be found clinging to rock faces (Fig. 1.8). Slope and aspect further influence vegetation, as exposure to the sun and other elements could result in distinctive plant communities.

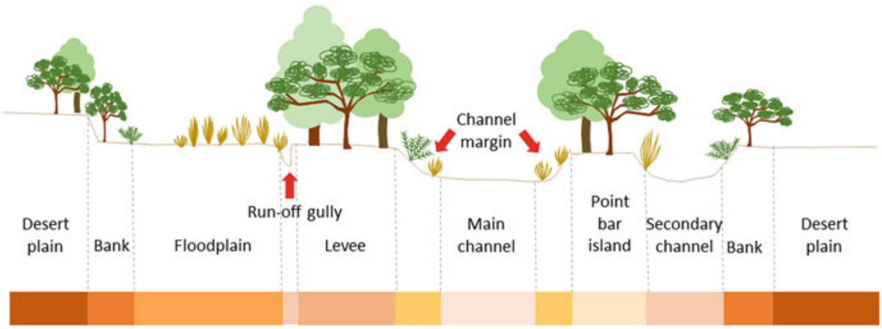
Colluvial fans on lower, less steep slopes typically have loose boulders and rocky lag material, and accumulate water and soil washed down from steeper slopes (Fig. 1.8). This rockiness enhances species diversity as rocks partition the habitat into more microniches. Biota associated with more mesic environments may occur, but these are often miniaturised. Even in extreme arid areas, these slopes support poikilohydric cryptogams and resurrection-type phanerogams that can respond to irregular moisture pulses.

Run-off from desert slopes provides sufficient moisture to maintain vegetation in run-on piedmont areas, particularly in basal drainage systems, where infiltration often results in high spatial patchiness. Infiltration is enhanced by dense root clusters where shrubs support an understory of grasses and herbs. Excessive run-off can cause erosion that strips surface soils, forms desert pavements, and deepens basal washes (Ward 2009), denuding vegetation cover except for deep-rooted phreatophytes. Sand ramps that may develop on either side of the mountain through aeolian action offer a stable substrate to support psammophilous herbs and geophytes, as well as suitable habitat for fossorial animals.

The high incidence of cracks and crevices, as well as deep hollows formed by weathering, provides abundant shelter for endogenic and hypolithic organisms (Chap. 9). The vegetation, complex topography, and habitat heterogeneity result in higher rates of diversity due to species packing, than the surrounding desert plains, particularly in higher vertebrates such as reptiles, birds, and mammals. The greater abundance of resident or seasonal macrobiota contributes additional types of habitat and nutrient supply, such as accumulations of nest materials and excreta.

1.3.3 Drainage Systems

Ephemeral streams and rivers are the dominant fluvial system in desert and quite common. These accommodate run-off from desert precipitation with a high spatial and temporal variability. Even low precipitation events result in run-off from



Bank	*Phreatophytes*
Floodplain	*Halophiles, grasses, sedges*
Levee	*Phreatophytes, perennial woody species, adventives*
Channel margin	*Phreatophytes, grasses, sedges, adventives*
Main channel	*Depauperate*
Point bar island	*Phreatophytes, perennial woody species, adventives*
Secondary channel	*Phreatophytes, psammophiles*

Fig. 1.9 Habitats associated with drainage systems

outcrops, and undulating topography (Fig. 1.9). The main catchments for such ephemeral streams often encompass mountainous or rocky areas, where orographic uplift results in higher precipitation, and steep impervious terrain produces more dynamic hydrological regimes. Rain may also originate in more mesic regions before cutting across or terminating in the desert (Shaw and Cooper 2008). The drainage systems often form linear oases in more inhospitable parts of the desert, providing avenues for migration and dispersal of organisms from adjacent, more mesic areas, or refuges for desert organisms during periods of greater stress.

The hydrological regime typically alternates between wet and dry phases, with short periods of seasonally intermittent surface flows, followed by long periods of inactive streambeds, with some subsurface groundwater flow. The fluvial conditions during wet phases are often characterised by punctuated, high-magnitude flood events, followed by periods of low-flow or no-flow conditions with hysteresis and drying out of associated habitats (Von Schiller et al. 2017). Hysteresis heralds the transition to prolonged dry conditions, dominated by arid terrestrial processes. The surface topography along the course of streams and the intensity of wet phases result in considerable variation in stream types, channel geomorphology, vegetation, and flood impacts (Hooke 2016). These features tend to be spatially discontinuous featuring highly dynamic lateral, vertical, and longitudinal connections with their adjacent ecosystems (Hooke et al. 2005).

The hydrological and sediment transport processes associated with episodic flood events are the drivers of geomorphic, vegetation, habitat, and biochemical variation in ephemeral rivers. The episodic floods trigger a switch from terrestrial conditions to aquatic and semi-aquatic ecosystems, although high spatial and temporal variability of flows, and the state of a system, causes a great deal of uncertainty in how a particular flow will affect the state of an ephemeral river (Hooke 2016). Floods may cause changes in the prevalent geomorphic and vegetation structure and associated ecological and biochemical conditions along its course, governed by the threshold values of those episodic hydraulic conditions; thus, similar sized flows in different years may have different effects.

A characteristic of dryland streams is the degree of complexity and irregularity in morphology along their course, coupled with abrupt changes in patterns of riparian vegetation (Sandercock et al. 2007). The general effect of vegetation in these channels enhances the processes of sedimentation and increases resistance to erosion, particularly the establishment and stability of embankments and bars. Point bars, which may develop into in-stream islands (Fig. 1.9), and slack water areas are major sediment and nutrient storage environments (Ringrose et al. 2018). Alluvial sediments at bars and islands may vary considerably in grain size, with less coarse sediments along riverbanks and levees and accumulation of fine-grained clay in slackwater deposits, such as floodplains (Sandercock et al. 2007). Such variations in grain size have considerable effects on the hydrological and nutrient dynamics of ephemeral river habitat assemblages (Von Schiller et al. 2017).

The primary producers associated with desert drainage systems are predominantly phreatophytes that commonly share similar traits for coping with rapid changes in water table levels and long periods of desiccation (Sabater et al. 2017). These traits include morphological characteristics such as load-spreading as well as deep root systems to stabilise banks and access moisture and nutrients at different levels. Shrubs and trees closer to the main discharge channel often have distinct traits such as stem flexibility, or a reduced number of stems and low-level branching, to cope with high-intensity dynamic flow (Shaw and Cooper 2008). Vegetation on more infrequently flooded point bar islands or river embankments often have a greater stem and branch cross-sectional area (blockage ratio) closer to the ground (Sabater et al. 2017). Most of these phreatophytes are likely to have adaptations to contend with other physiological stresses such as evapotranspiration, changes in salinity, and high surface temperatures (Sabater et al. 2017). Slackwater habitats, or flood-out areas, are dominated by sedges and grasses, with occasional salt-tolerant phreatophytes. They experience the lowest disturbance, but greatest variation in hydrological and biochemical stress, often with extended periods of either slightly saline, desiccated hardpan playa or desert plain-like conditions, with high diurnal temperature variation, or waterlogged, semi-aquatic wetland conditions.

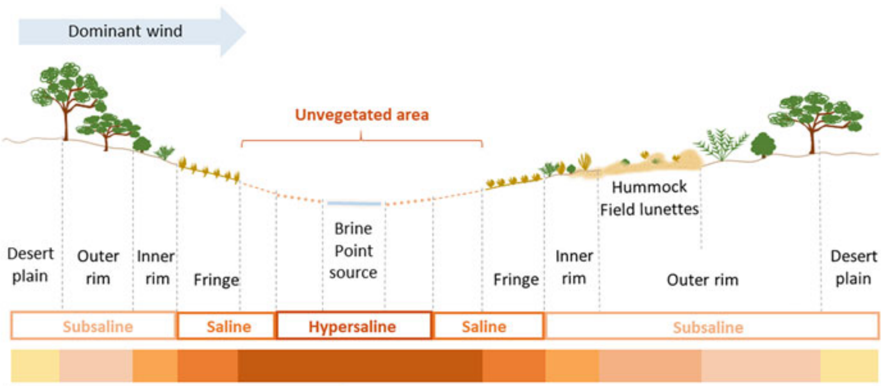
This results in highly heterogeneous systems with spatially complex but consistently predictable patterns in the structure and composition of perennial woody plants along ephemeral stream channels, and grass-dominated communities on flood-out peripheries. The perennial shrub and tree species associated with these habitats contribute consistent primary production, organic matter, nutrient storage, and an abundance of structural diversity and shelter that sustains a diversity of fauna not usually associated with desert ecosystems.

1.3.4 Saline Basins, Playas, and River End Points

Inland saline habitats in deserts typically form within high-evaporation basins and lowlands in proximity to shallow groundwater (Fig. 1.10). The high salinity, extremely toxic to most plants, in combination with high temperatures, exerts a strong influence over the vegetation found in these habitats. Xerohalophytes are specifically adapted to thrive in desert areas with high salt concentrations (Gibson 1996). This is a heterogenous assemblage of plants that have evolved structural, phenological, physiological, and biochemical mechanisms for salt tolerance or salt avoidance (Ward 2009), e.g. some accumulate salt in specific organs and are often succulent, while others excrete salt.

Hypersaline, saline, and subsaline zones can be distinguished (Fig. 1.10). There can be a gradual reduction in salinity away from the point sources, the lowest elevations in the basin, due to increasing depth of subterranean water. Plant diversity and abundance increase away from the point source (Halis et al. 2012), and irregular bands of progressively denser plant growth can be observed. Vegetation is absent where soil salinity is very high, particularly where salt crusts are visible on the surface. The point source is often surrounded by an unvegetated expanse prone to occasional or seasonal run-on flooding and waterlogged conditions. These areas are typically inhabited by salt-tolerant extremophiles and occasionally visited by highly mobile transient visitors attracted by moisture. If the water table is high and close to the surface, the lowest areas will be the most saline, but the same adaptions apply.

The inner edge of vegetation, at the outer margin of flooding, where the salt concentration is lower, is usually composed of rhizomatous grasses with shallow



Brine point source and surrounds	*Unvegetated area, halophile aquatic and subaquatic species*
Fringe	*Halophytic grasses and sedges, grazers*
Inner rim	*Halophytic chamaephytes*
Hummock field lunettes	*Halophytic tussock grasses, psammophiles, endogenic species*
Outer rim	*Halophytic to salt-tolerant tussock grasses, shrubs, succulents, phreatophytes (ecotone)*

Fig. 1.10 Habitats associated with saline basins, playas, and river endpoints

roots that form dense mats and sedges. This distinctive inner fringe of vegetation morphs into the outer zones. Halophytic chamaephytes, represented by various perennial herbs and subshrubs, thrive in the inner subsaline zone. On the outer edge, a denser zone of shrubby vegetation, tussock grasses, and scattered woody phreatophytes is found (Fig. 1.10). Halophytic and non-halophytic species can occur together in this zone.

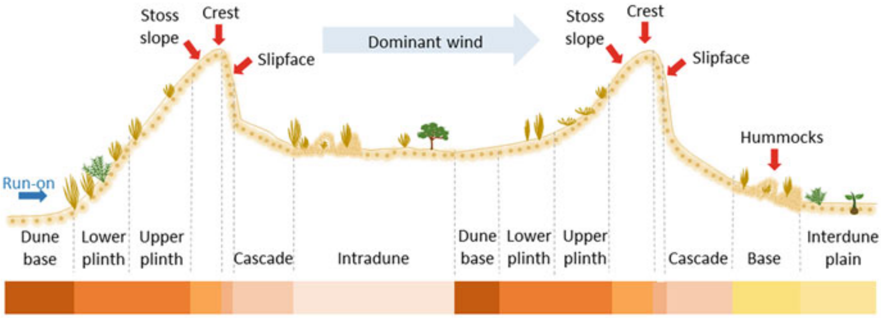
Sand can cover all low-growing vegetation (Danin 1996), while shrubs in the outer edge trap airborne sand grains on the leeward side of the depression to form hummocks (nebkas/hillocks). Unique microhabitats are created in the accumulated sand and hummock fields that are distinctive features around saline depressions. Over prolonged arid periods these hummock fields may grow into substantial lunette dune systems.

In less saline systems, such as freshwater playas and the endpoints of ephemeral rivers in endorheic basins or against topographical obstructions, very similar zones of progressively denser and more diverse vegetation develop. The inner unvegetated mudflats, subjected to occasional flooding, are fringed by a zone of shallow-rooted vegetation. This inner margin transforms into an outer zone of progressively higher and more diverse shrubs and phreatophytes. Waterlogged areas at endpoints of perennial or semi-perennial rivers can support a few dominant species of monocot perennials like reeds and sedges that form dense stands inhibiting the germination of other species. A special set of habitat types occur at oases, where subsurface flow resurfaces due to geological phenomena such as dykes. At such locations submerged and emergent macrophytes and isolated stands of dense relict or adventive phreatophytes may be found. Many oases are today associated with human habitation, and natural vegetation has been replaced by cultivated plants or weeds. More cosmopolitan, wide-ranging species occur in salt marshes and other saline coastal habitats (Shmida et al. 1986). However, these ecosystems and associated habitats are not representative of typical ecological processes in hot deserts.

1.3.5 Sand Plains and Sand Dunes

Aeolian sand plains and dune systems (Fig. 1.11) represent only some 20% of deserts (Pye and Tsoar 1990). These sand biotopes are dominated by a low diversity of psammophytes, predominantly grasses (Bowers 1982). Where water relations improve, some geophytes and chamaephytes that can cope with the nutrient-poor and easily perturbed substrate surfaces occur, with a limited number of deep-rooted perennial phreatophyte species where local conditions allow access to subterranean water. However, even relatively modest increases in rainfall have a positive feedback effect on vegetation and psammophilous biota (Boyer 1989).

Aeolian sand substrates have poor water-holding capacity, rapidly absorb water, are nutrient deficient, have low levels of organic content, and are usually composed of well-sorted, fine-grained particles without much clay content. Most psammophilous plant species require rainfall for germination and seedling establishment; thus, there is a direct correlation between vegetation and rainfall. In sand



Dune base	*Psammophiles (dominant), occasional pheatophytes, endogenic species (ecotone)*
Plinth	*Psammophiles, endogenic species*
Stoss slope	*Depauperate*
Slipface	*Endogenic, psammophile specialists*
Cascade	*Psammophiles (dune specialists), endogenic species*
Intradune	*Psammophiles, occasional perennial phreatophytes, endogenic species*
Base/Hummocks	*Psammophiles, chamaephytes, endogenic species*
Interdune plain	*Psammophiles, geophytes, grasses, annuals and amphiphytes, endogenic species*

Fig. 1.11 Habitats associated with sand plains and sand dunes (modified from Robinson and Seely 1980)

biotopes, vegetation also contributes organic matter and assists in stabilising surfaces that promote the development of microbiotic crusts (Danin 1996), while increased aeolian activity and other forms of mechanical erosion such as bioturbation or excessive trampling have an inverse correlation with vegetation cover and surface stability (Danin 1996). Non-rainfall moisture, such as dew and fog, only has a notable effect on macrobiotic life once vegetation has established through rainfall.

Short-lived, episodic wet conditions often transform stable sand surfaces such as sand sheets, sandy plains, and dune bases into lush stands of therophytes (Seely and Louw 1980), sprinkled with the flowers and leaves of cryptic geophytes that emerge when conditions are favourable. Even during such highly productive episodes, the species composition typically consists of monocultures of relatively few species. These temporal changes may, however, trigger large-scale emergence of the reproductive stages or migration of a surprisingly high diversity of herbivores and secondary consumers. As is the case with perennial vegetation, therophyte abundance, species richness, and cover are positively correlated with rainfall.

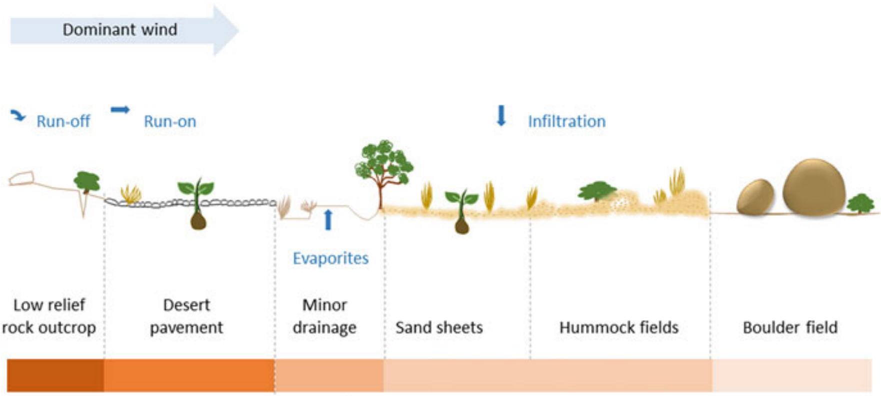
The surface topography of sand biotopes is affected by soil moisture and vegetation cover. Sand sheets and plains are usually uniform and relatively flat. Perennial vegetation occurs at distinct locations where water relations and surface stability allow colonisation, but plant cover is mostly too low to define communities. Where it does occur, low-growing perennial vegetation captures wind-blown sand and increases structural complexity through hummock, coppice, or nebkha formation. The canopy density, height of the canopy above the surface, and number of stems impose changes on the velocity and direction of wind and associated sand movement, which determine patterns of deposition, erosion, and growth in hummock fields.

In contrast, sand dune habitats (Fig. 1.11) have a typical structure that imposes order and zonation patterns (Robinson and Seely 1980; Seely 1990) on associated psammophilous macrobiota. The transition area at the dune base is often defined by more robust stands of perennial grasses and occasional phreatophytes (Danin 1996; Jürgens et al. 1997) exploiting the internal gravity flow of moisture absorbed by the dune sand. Annual grasses and herbs may also emerge at this transitional area after rain. Specialist perennial grasses, and occasionally other vegetation that can cope with erosion and abrasion by wind-blown sand, may colonise the plinth, becoming progressively sparser higher up. The same perennials are often also adapted to recover from burial and occur in the lee, at the base of the cascade, where they are subjected to sand cascades and slumping. The root systems of these grasses often have well-developed rhizosheaths (Marasco et al. 2018) to cope with the very low nutrient content (Buckley et al. 1986) in desert dunes. These perennials, augmented by therophytes, some geophytes, and occasional phreatophytes, may also be found further down the base or in depressions between successive crests of complex or braided dunes. Only transient psammophiles occur on the highly dynamic and severe abrasion zone near the crest on the stoss slope, though specialised biota may exploit the slipfaces and the cascades and slumping features in the lee of a dune crest. This zonation becomes more pronounced and distinctly colonised with increased rainfall, ascribed to differential stresses in the internal moisture regime of dunes, surface stability, interspecies competition, and abiotic stressors (Yeaton 1988).

1.3.6 Desert Plains and Pediplains

Desert plains are the most common biotope of deserts (Fig. 1.12). These extensive landscapes are usually sparsely vegetated with low-growing, arid-adapted, long-lived dwarf shrubs and subshrubs (xerophilous chamaephytes). The substrate is relatively level and stable, commonly protected by desert pavement. Desert or stone pavement typically consists of a dense cover of larger pebbles and stones embedded in a finer matrix, forming a coarse mosaic on the surface (Cook et al. 1993), restricting moisture penetration and consequently further limiting plant productivity. The shallow stony soils frequently have a subsurface rock-like horizon, or basement, which is water-repellent and which plant roots find difficult to penetrate (Gibson 1996; Walter 1983).

Grasses are the dominant plants across desert plains where summer rainfall prevails. Some grasses may be annual or perennial (amphiphytic) depending on local conditions. Perennial grasses can remain dormant for many years until favourable conditions return. In contrast, annual grasses and herbs (therophytes) live for one growing season and survive as seeds until the following growing season. Usually occurring in mixed-species groups, these ephemerals can transform plains into fleeting floral carpets after a moisture pulse. Usually, the ephemeral vegetation



Low relief rock outcrop	*Petrophiles, chasmophytes, pheatophytes, cryptic species*
Desert pavement	*Petrophiles, therophytes, geophytes, epilithic, hypolithic, and cryptic species*
Minor drainage	*Phreatophytes, endolithic species*
Sand sheets and hummock fields	*Psammophiles, geophytes, endogenic and cryptic species*
Boulder field	*Petrophiles (epipetric, hypopetric, endopetric)*

Fig. 1.12 Habitats associated with desert plains and pediplains

is unevenly distributed in rivulets and depressions, while a patchy occurrence may be due to very localised rain showers. Features differ between summer and winter annuals, e.g. plant height and leaf morphology (Ward 2009), as well as species composition.

Where they occur, boulder fields and localised rock outcrops (Fig. 1.12) provide moister, cooler microclimates for plants growing around and between the boulders and in rock crevices. Low-relief bare rock surfaces are kept clear of sand and gravel by the wind and support low-growing plant life, often cryptic and succulent, rooting within crevices. Some rock types with the capacity to hold water at shallow depths, such as sandstones or exfoliating granite, support a different flora than the surrounds (Gibson 1996).

Geophytes, many of which produce leaves and flowers at different times (hysteranthous), are a common lifeform in desert plains. In sandier areas, geophytes may have contractile roots drawing the underground organs deeper into the substrate, a strategy triggered by erosion, predation, and soil disturbance. Extended flats of gravel plains accumulate wind-borne materials (Hegazy and Lovett-Doust 2016) in surface sheets. As the sheet becomes deeper, more plant species appear, and support psammophiles that can resist sand-blasting or endogenous faunal species.

Dense, dome-shaped chamaephytes are found in wind-swept areas, with canopies close to the soil surface. This growth form minimises direct exposure of the foliage to sunlight (Hegazy and Lovett-Doust 2016), traps organic debris, and inorganic particles and provides moister shaded microclimates for other taxa. In areas with greater sand movement, shifting sand is often deposited where grass tussocks or the lower branches of woody and succulent chamaephytes inhibit aeolian transport to form wind-heaped hummocks around and downwind of plants. Dispersed summer-active herbaceous, geophytic, and low caudiform vines escape the strong dry winds associated with hot deserts by hugging the surface.

Due to their low-relief and poorly developed topography, shallow drainage channels are a notable feature of most desert plains. These channels are often visible as linear vegetative patterns along their extent. Chamaephytes and woody phreatophytes are commonly found along their edge, where subsurface moisture can be directly tapped. Plant growth within the channel is often constrained by exposed evaporites and episodic water flows and may be absent from channels with frequent or high-energy flows.

Across desert plains, autotrophic microbial organisms, or biological soil crusts, occur commonly in the bare spaces between higher plants (Ward 2009). As they increase infiltration and nitrogen fixation, reduce erosion, and contribute to soil organic matter, they contribute positive local effects on plains with sparse vegetation.

1.4 Desert Soils

1.4.1 Semi-arid and Arid Soils

Given the lack of water and leaching, very shallow or absent weathering fronts, limited chemical alteration, and clay production, very little soil formation takes place in most drylands. Soil formation is more pronounced on desert margins and stable surfaces away from steep uplands and dunes. Several soil types can nevertheless be found (Dunkerley and Brown 1997) and include entisols, which are widespread, but are merely unaltered sediments with little sign of post-sedimentary modification, occurring at the heart of continental desert regions, such as the Sahara and in Australia. Aridisols are slightly more evolved and depict very limited leaching or evaporation, and can promote the minor accumulations of calcium, silica, gypsum, and salts in their profile. Mollisols are associated with plains and grasslands, particularly in North America and Central Asia. They may feature a thin organic layer, along with calcium accumulations, and are fertile, but also prone to deflation, if stripped of their vegetation cover. Mollisols in part produced the dustbowl, during the great depression in the USA (Lee and Gill 2015). Alfisols, the most evolved dryland soils, are located in the semi-arid margins, towards temperate and equatorial regions in Europe, South America, Africa, and Australia. They are moderately leached, featuring a clay-enriched subsoil, which also leads to a higher productivity, but are also prone to erosion by water (Cogle et al. 2002). Opportunities for microbes in desert soils exist especially in low-lying, run-on areas which may accumulate sediments, weathering products, nutrients, and water and with time may form a subsurface habitat.

1.4.2 Introduction to Unconsolidated Porous Media

There are several advantages for microbial life below the surface (Table 1.2), since temperature fluctuations are less pronounced and water in its liquid form may be available and has the ability to retain nutrients. Especially an unconsolidated porous subsurface media and associated pore geometry provide biochemical reactions and interactions, which shape the microbial habitat while providing shielding from UV radiation. It has been shown that pore geometry, access to organic material, and microbial diversity are linked (Rabbi et al. 2016). However, prolonged water evaporation may promote salt accumulation, which can create more extreme conditions in shallow groundwater settings also (Fig. 1.10). Abiotic properties of unconsolidated porous media are found in Table 1.2.

Table 1.2 Fundamental abiotic properties of unconsolidated porous media which moderate the subsurface environment

	Property	Consequence for microbial life
Physical	Low UV radiation transmittance	Protects against solar radiation. UVA and UVB radiation penetration varies between minerals; however, it is typically less than 0.5 mm (Carrier et al. 2019)
	Poor conductor of heat	The temperature regime below the surface is less extreme than at the surface (Hillel 2004)
	Retains water either through surface adsorption or capillarity This ability is enhanced with decrease in particle size (increase in surface area)	The propensity of water to change phase decreases compared to free water. More energy is needed to evaporate water from a porous medium If a sufficient number of micropores are present, the medium will exhibit the ability to retain water against gravity (Hillel 2004)
Chemical	All mineral surfaces carry charge Variable or pH dependable charges are more common; however, a select group of 2:1 phyllosilicates additionally have permanent negative charge in their crystal structures The more finely divided the material is, the greater the sum surface charge per mass of material	Chemical reactivity is imparted to the medium This, in turn, results in mineral surfaces that: 1. Interact with polar constituents, for example, cations, anions, water, and other mineral particles (Essington 2015) 2. Induce surface precipitation 3. Interact, transform, and protect organic compounds (Kleber et al. 2005, Barré et al. 2014) The net effect of abovementioned is the ability to accumulate life essential elements

1.4.3 The Desert Pedoderm

Desert sediments and soils provide a critical but marginal microbial habitat. We will focus on the “pedoderm”, a term originally proposed by Brewer et al. (1970), in reference to the top few millimetres or centimetres of the terrestrial surface. It defines a distinct microenvironment that is physically, chemically, and mineralogically diverse (Fey et al. 2006). The pedoderm pore geometry regulates gaseous exchange as well as water and nutrient acquisition, storage, and movement (Young and Crawford 2004; Rabbi et al. 2016) and requires relatively stable conditions to form and prevail. The following section will examine the physical, chemical and biological characteristics associated with the desert pedoderm, which vary significantly across landscapes and landforms and would be more developed on stable run-on surfaces (Burket et al. 2012) (second column of Table 1.3).

The bare single-grained pedoderm (S) (Table 1.3 and Fig. 1.13b) is associated with a high content of sand-sized particles found in dunes and sandy plains (Fig. 1.11). Due to high rates of mobility, no crusting or aggregation are observed. The formation of WSA requires colloidal organic material, iron oxides, and secondary clay minerals to bond larger particles into stable units (Tisdall and Oades 1982; Fernández-Ugalde et al. 2013). As a result, WSA are more common on dryland margins. Clay minerals, associated with such intermediate stages of weathering (so-called 2:1 clays), include smectite, vermiculite, and chlorite mineral groups (Essington 2015). However, smectite and vermiculite are also particularly susceptible to dispersion by cations like sodium (Na^+), because of their high cation exchange capacity (CEC) (Itami and Kyuma 1995; Ruiz-Vera and Wu 2006) and hence prone to decay. Water-unstable aggregates (WUA) with a high silt content lack the cohesion of clay and iron oxides (Shainberg et al. 2003; Warrington et al. 2009) and are common in drylands.

Salt crusts (SC) occur, where net evaporation is very high and often results in the formation of physical crusts (PC). These may entail a biological component as well as hydrated salts. Desert pavements (DP) on the other hand offer among the hardest protection layers, the result of silt deflation and pebble armouring at the surface. (Fig. 1.8). Clearly, factors which support a stable pedoderm are patchy in dryland areas.

Biological soil crust (BSC) can also establish on surfaces and decrease water infiltration. The microbiology of BSCs is described in Chap. 3. This is attributed to surface densification and the entrapment of silt-sized particles over coarser underlying material (Felde et al. 2014) and the development of hydrophobicity when polysaccharides, excreted by cyanobacteria, dry out (Mazor et al. 1996; Eldridge et al. 2000). The flora of BSC can be diverse ranging from cyanobacterial dominated crusts (BSC_{cyan}), crusts with multiple species (BSC_{muli}), to algal dominated BSC (BSC_{alg}). Additional pedoderm classes are worthy of note and include those with rock mulch (RM) trapped between large rocks, exposed cemented horizons (CEM), and erosion pavements (EP), the result of denudation (Table 1.3).

Table 1.3 Pedoderm classification of arid environments and their possible genesis

Pedoderm classes of Burket et al. (2012)		Possible genesis
1. Characteristics the result of abiotic processes	*Bare single-grained soil (S).* The pedoderm consists of particle in the sand fraction range and exhibit negligible particle aggregation.	The result of limited weathering and/or the net removal of finer particles by wind or /and water. Sand plains and sand dunes (Fig. 1.11)
	Water-unstable aggregates (WUA). Aggregates at the soil surface which easily disintegrate upon wetting and/or raindrop impact	Aggregates lack strong bonding agents. Associated with high silt and low organic material content. Slaking susceptibility increases, with increasing Na^+ content
	Water-stable aggregates (WSA). Well-formed or distinct aggregates at the soil surface which does not slake upon wetting	Combination of clay, iron oxides, and organic material results in aggregates that exhibit resistance against physical and chemical dispersion. The dominance of flocculating cations (e.g. Ca^{2+}) rather than dispersive cations is also a feature
	Rock mulch with stable soil (RM). Material is trapped and protected by closely spaced and partially embedded rock fragments	Rough surfaces on windward slopes improve dust and nutrient acquisition run-off will result in particles sorting, possibly favouring the removal of colloidal-sized particles. RM is most likely associated with uplands, inselbergs, and rocky outcrops (Fig. 1.8)
	Physical crust (PC). Usually platy or massive, no substantial biological component	The disintegration of especially WUA that leads to in situ structural crust development in areas where run-on occurs. Aggregate breakdown driven by raindrop kinetic energy transfer and wetting rate (mm h^{-1}) (Agassi et al. 1981; Shainberg et al. 2003)
	Cemented horizon exposed at surface (CEM)	Areas that experience run-off, erosion exposing petrogypsic, petrocalcic, petroduric horizons
	Salt crust (SC) of fine to extremely coarse evaporite crystals or visible whitening	Areas experience where shallow water table is present.

(continued)

Table 1.3 (continued)

Pedoderm classes of Burket et al. (2012)		Possible genesis
	on the soil surface. May include biological components	Saline basins, playas, and river endpoints (Fig 1.10)
	Erosion pavement (EP). The erosion of finer soil material left rock fragments that occur in a dense uniform pavement. Individual fragments may be displaced during run-off events	Run-off areas that experience net loss of material
	Desert pavement (DP). A concentration of closely packed and varnished rock fragments at the soil surface, embedded in a vesicular crust	Vesicular crust develops as a result of dust acquisition; however, platy structure is also associated with it. Low hydraulic conductivities are the norm because of these features (Turk and Graham 2011). DP is associated with desert plains and pediplains (Fig. 1.12)
2. Characteristics the result of both abiotic processes and biological soil crusts (BSC) formation	*Physical–biological crust (PBC)*. Few cyanobacterial sheaths with no darkening from cyanobacteria	Currently unclear if nutrient and fine particle enrichment associated with BSC is solely the result of particle acquisition and entanglement. Or if BSC establishes preferentially where nutrient and fine particle enrichment in the landscape occurs. Then afterward, BSC aid in preventing fine particle export However, with increased dominance, the stronger will the influence of BSC be on the pedoderm properties.
3. Characteristics predominantly the result of BSC	*Biological soil crust dominated by cyanobacteria* (*BSC_{cyan}*). Dense cyanobacterial sheaths that form a smooth or dimpled crust of variable darkness. It can include algae, lichen, moss	
	Biological soil crust with multiple structural groups (*BSC_{multi}*). Two or more structural groups (cyanobacteria, algae, moss, lichen) form a rugose, pinnacled, or rolling crust	
	Biological crust dominated by algae (*BSC_{alg}*). Rubbery algal crust, with or without lichen showing *cracking or curling*	
4. Characteristics imparted by vegetation	*Duff (D)*. Non-decomposed to fully decomposed plant and organic matter located above the A horizon (a patchy or continuous O horizon)	This pedoderm class will occur where extensive vegetation can be supported, for example, drainage systems (Fig. 1.9)

Adapted from Burket et al. (2012)

Fig. 1.13 A well-aggregated soil (**a**) versus a sandy, single-grained soil (**b**). The details of these pedoderm classes can be found in Table 1.3. A surface crust that developed because of a lack of basal cover, leaving the soil surface exposed to raindrop impact and surface crust formation (**c**). The layered nature of a surface crust (**d**) (credit: P de Jager)

1.4.4 Impeded Infiltration

The ability for soils to absorb water is highly variable at the slope scale. With the losses from run-off areas, run-on areas become subsequently enriched, with particle-bonded nutrients, such as phosphate and dissolved constituents, inorganic ammonium, nitrate, and sulphate. This further increases the spatial heterogeneity of nutrient distribution. The additional process of densification can accentuate the heterogeneity of spatial water and nutrient distribution further, which is a common and natural process in deserts. In fact, many of the characteristics of the pedoderm classes in Table 1.3 are prone to densification. The exceptions are single-grained, rock mulch, and erosion pavements. For example, if void spaces of rock mulch or erosion pavements are filled in with finer material, the porosity of the inter-rock space decreases and in essence densifies. This is best explained with the basic equation for bulk density (ρ_b):

$$_{\mathrm{b}} = M_{\mathrm{solid}}/V_{\mathrm{total}} \tag{1.1}$$

where M_{solids} is the mass of solids (kg) and V_{total} is the volume the solid particles occupy (m^3) (Hillel 2004)

Surface and soil densification caused by soil compaction (and causing soil degradation) is common in anthropogenically impacted environments (e.g. in urban environments and agriculture). This is the result of a static and/or a dynamic force applied to the surface (e.g. trampling, vehicles), which results in the packing of the particles in a smaller space (V_{total} decrease). However, the bulk density of a porous medium can also be decreased if the numerator (M_{solids}) increases, as in the case of void spaces that are filled with finer particles. The natural densification of desert surfaces is most likely a combination of M_{solid} increase and denominator (V_{total}) decrease.

Apart from direct densification, the layering of material at the surface may further impede water infiltration. The abrupt widening of conductive pores in a porous medium is as disruptive to water movement as the sudden narrowing of pores. An example of abrupt widening of pores can be found in vesicular subsurface structures associated with desert pavement. As a result, decreased water infiltration, with increasing vesiculation, is commonly reported (Brown and Dunkerley 1996). Finer material that abruptly transitions to coarser material represents another example where the continuity of pores is often disrupted. More detail on the impact of pore geometry changes and water conductivity can be found elsewhere (Hillel 2004). The consequence of this for run-on areas is that under desert conditions this can concentrate water-soluble constituents at or near the surface.

1.4.5 Organic and Inorganic Carbon in Desert Soils

Organic carbon, apart from being an important energy source for heterotrophic organisms, also contributes to aggregate stability (Tisdall and Oades 1982). Deserts have lower levels of organic material (above and below ground) compared to other regions, illustrated by the southern African pedoderms, with lower organic carbon content of the driest country in the region (Namibia) relative to wetter countries (Table 1.4).

Organic matter decomposition in deserts is high and rates are comparable to tropical climates have been reported (Steinberger and Whitford 1988). This has been linked to photo-oxidation by UVB radiation resulting in fast surface litter decomposition rates and the creation of a direct CO_2 release to the atmosphere and the circumvention of soil and microbes (Austin and Vivanco 2006).

The nature of organic material in desert soils is also variable, since organic compounds derived from plants differ from that of microbes. For example, plants impart lignin which has a slow decomposition rate because of its structural complexity and an abundance of aromatic carbon (Thevenot et al. 2010). Plant

Table 1.4 Pedoderm organic carbon content (%)[a] of various Southern African countries from the hyper-arid west to the semi-arid interior and tropical east

	Country				
	Namibia	Botswana	Zambia	Zimbabwe	Mozambique
Climate[b]	Largely warm desert (BWh) with warm semi-arid (BSh) in northeast	Largely warm semi-arid with warm desert in southwest	Predominantly humid subtropical (Cwa)	Semi-arid to humid subtropical	Tropical savannah (Aw), in the south, inland is warm semi-arid
n	117	89	101	47	104
Mean	0.39	0.65	1.05	0.96	0.92
Median	0.29	0.55	0.98	0.82	0.81
Standard deviation	0.47	0.48	0.49	0.54	0.49
95% Confidence interval[c]	0.31–0.48	0.55–0.75	0.95–1.14	0.80–1.12	0.83–1.02

[a]Oxidisable carbon determined by dichromate method of Walkley-Black (Nelson and Sommers 1996). This method reasonably isolates lower oxidation state organic carbon from inorganic carbon (carbonates), which is carbon at its highest oxidation state, C(+4)
[b]Based on Köppen-Geiger climate classes reported by Beck et al. (2018)
[c]The 95% confidence interval for a Student's *t*-distribution, chosen because of relatively small samples for some countries

polysaccharides also differ from microbial polysaccharides, with the latter lacking pentoses (Essington 2015).

Carbon accumulation in the form of CaCO3 can be 10–17 time greater than organic carbon accumulation in desert soils (Díaz-Hernández et al. 2003), particularly given their high accumulation in inorganic carbonate ion CO_3^{2-}. Globally, areas receiving <250 mm of precipitation have the highest soil inorganic carbon (SIC) with accumulation exceeding 32 kg C m^{-2} (Zamanian et al. 2016). Arid environments therefore appear to strongly drive the oxidation of organic carbon and the accumulation of inorganic carbon.

1.4.6 Nitrogen Dynamics in Desert Soils

Nitrogen is critical for life, and understanding the environmental processes that direct its movement is important. In natural systems, atmospheric N_2 enters the pedoderm either through abiotic processes, for example N deposition, or through microbiological N fixation. The fraction not assimilated by living organisms are subjected to oxidation to nitrate (NO_3^-), the most leachable form of N. N biogeochemical cycling in hot deserts is further detailed in Chap. 7.

Subsurface accumulation of nitrate (NO_3^-) is commonly reported for arid environments of North America (Walvoord et al. 2003; Graham et al. 2008), Namibia (Stone and Edmunds 2014), and Australia (Barnes et al. 1990). Graham

Table 1.5 Pedoderm N content (%)[a] of various southern African countries from the hyper-arid west to the semi-arid interior and tropical east

	Country				
	Namibia	Botswana	Zambia	Zimbabwe	Mozambique
Climate[b]	Largely warm desert (BWh) with warm semi-arid (BSh) in northeast	Largely warm semi-arid with warm desert in southwest	Predominantly humid subtropical (Cwa)	Semi-arid to humid subtropical	Tropical savannah (Aw), in the south, inland is warm semi-arid
n	117	89	101	47	104
Mean	0.05	0.06	0.09	0.09	0.08
Median	0.03	0.04	0.08	0.08	0.07
Standard deviation	0.08	0.06	0.04	0.07	0.04
95% Confidence interval[c]	0.03–0.06	0.06–0.07	0.08–0.10	0.08–0.10	0.07–0.09

[a]Catalysed high temperature combustion (Dumas method) (Bremner 1996)
[b]Based on Köppen-Geiger climate classes reported by Beck et al. (2018)
[c]The 95% confidence interval for a Student's *t*-distribution, chosen because of relatively small samples for some countries

et al. (2008) reported nitrate levels equivalent to 8.9–12.7 tons N ha^{-1} at fairly shallow depths (<1 m) below desert pavement in the Mojave Desert, California, and attributed this to NO_3^- entering the soil in areas of the landscape where appreciable infiltration occurs. NO_3^- then moves and accumulates under desert pavement because of its exceedingly low hydraulic conductivity that prevents water from further transporting it. Walvoord et al. (2003) also attributed NO_3^- subsoil accumulation in desert soils to the fact that it is moved beyond biological reach.

Returning to the pedoderm, the alkalinity of arid surfaces increases the propensity of nitrogen from biological origin to volatilise. Westerman and Tucker (1978) reported that 70% of NH_4 applied to desert soils is lost to the atmosphere. This was confirmed by Peterjohn and Schlesinger (1990) who reported that up to 77% of N inputs was lost in the dry Southwestern USA. It must be, however, noted that this later study was published before the quantification of subsurface nitrate in these areas.

Similar to organic carbon, when the pedoderm N content of southern Africa is compared, Namibia again exhibits the lowest levels with a confidence interval stretching over a lower range compared to other countries (Table 1.5). Michalski et al. (2004) estimated NO_3^- atmospheric deposition for deserts of the southern hemisphere to range from 21 to 84 mg N m^{-2} a^{-1} (0.21–0.84 kg N ha^{-1} a^{-1}) with a reported mean of 0.43 kg N ha^{-1} a^{-1}. The N content confidence interval for Namibia equates to 47.5–88.8 kg N ha^{-1}, assuming a 1 cm depth and bulk density of 1400 kg m^{-3}. The deposition rates appear minor when directly compared to the pedoderm N content. However, in theory, it will take only 226–423 years to reach the measured surface N levels based on the conservative deposition estimate (0.21 kg N ha^{-1} a^{-1}) and 108–202 years based on the mean deposition rate. If the biological N fixation is taken as double the conservative atmospheric deposition rate (0.42 kg N ha^{-1} a^{-1}), as estimated by Peterjohn and Schlesinger (1990), the rate at which the pedoderm acquires N totals 0.63 kg N ha^{-1} a^{-1}. The time frame to accumulate current N pedoderm levels then decreases to 75–141 years. If ammonium deposition, or any other N additions, is added, it will require even less time to reach the measured pedoderm N levels. These rudimentary calculations highlight the transient nature of N in the Namibian pedoderm.

1.5 Conclusion

Globally rainfall is not equally distributed in both space and time and the varied surface geomorphology does not equally store and channel the resulting surface water and subsurface moisture. Hence. opportunities for desert microbes are not equal either. At the local scale, the most defining variables for microbial ecology are moisture and substrate stability, while microbial species richness is defined by microhabitat moisture regimes, stability, and diversity of nutrient sources. The dominant climate, geomorphology, and soil type are primary determinants of microbial ecology in deserts, while macrobiotic colonisation, diversity, population densities, endemism, life histories, and rate of species turnover are dependent on nutrient pools and hydrology of shallow surface soils associated with desert habitats. Low and erratic rainfall accentuates relatively small differences in moisture retention and nutrient mobilisation, which have cascading effects on the suitability for colonisation and development of microbial communities. The relatively high biotic diversity and microtopographic heterogeneity typical of desert mountains and hills result in complex microbial mosaics at minute spatial scales, which contrasts with more homogenous microbial communities associated with extensive desert plains. Similarly, switches between dry terrestrial conditions and aquatic and semi-aquatic settings are associated with ephemeral streams and drainage. However, at the microbial scale, other desert habitats experience similar changes after rainfall events, though for briefer periods. One of the more significant influences of ephemeral rivers on microbial ecology is the introduction of propagules for colonisation during flood events, though drainage systems also homogenise propagules to directionally disperse downstream. Wind and opportune settling of propagules are the more likely dispersal agents in other desert habitats. Microbial communities are more depauperate, and often more specialised, where the salient features of the system enhance desiccation such as in saline habitats, impenetrable clay or rock surfaces, or expanses of sand dominated by a homogenous, unstable, and nutrient-poor substrate with rapid infiltration and poor water-holding capacity. At a microbial scale, habitat islands such as vegetation that impart stability, nutrients, and organic matter (Danin 1996) are important for promoting diversity and providing ecological refuges (Pointing and Belnap 2012; Chaps. 3, 5, and 8). Soil pore spaces many opportunities if and where they are present. In general, soils are more mature on desert margins than in interiors. Run-off and run-on settings determine the accumulation and accretion of material at the local scale of geomorphic contexts and habitats. The pedoderm regulates the exchange between the atmosphere and subsurface soil and is dependent among other factors on crusts, cover, and compaction—all of which translate into variable carbon and nitrogen levels in the subsurface environment. In conclusion, opportunities for microbes vary globally as a function of spatial and temporal rainfall patterns and local moisture availability, which is modified by geomorphic conditions and the resulting habitats. At the scale of soil samples, pedoderm development and soil pore geometry act as additional fine-scale controles. Integrating and interpreting microbial field observations, across such a varied scales and settings, remains a formidable challenge.

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