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Chapter 1: Natural History and Evolution of the World's Deserts

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The Desert Biome: A Global Perspective

Looking at a satellite image of the whole earth it is easy to spot a series of conspicuous ochre, vegetation-barren areas that run parallel to the equator, in both the northern and southern hemispheres, along two East-West fringes at 25-35° latitude (Figure 1.1). They are the mid-latitude deserts of the world, lying some 2 000-4 000 km away from the equatorial rainforests. In the northern hemisphere, the succession of mid-latitude subtropical deserts is formed by (1) the Mojave, Sonoran, and Chihuahuan Deserts in North America, (2) the Sahara's immense swathe in Northern Africa and the Somali-Ethiopian deserts in the Horn of Africa, and (3) the deserts of Asia, including the Arabian, Mesopotamian, Persian, and Thar deserts that stretch from West Asia into Pakistan and India, as well as the Central Asian deserts in Uzbekistan, Turkmenistan, and the Taklimakan and Gobi deserts in China and Mongolia. In the southern hemisphere, the chain is formed by (1) the Atacama, Puna, and Monte Deserts in South America, (2) the Namib and the Karoo in southern

Africa, and (3) the vast expanse of the Australian deserts (Allan and others 1993, McGinnies and others 1977, Pipes 1998, Ricciuti 1996).

There are many criteria to define a desert but perhaps the most important one is aridity — the lack of water as the main factor limiting biological processes. One of the most common approaches to measure aridity is through an estimator called the Aridity Index, which is simply the ratio between mean annual precipitation (P) and mean annual potential evapotranspiration (PET , the amount of water that would be lost from water-saturated soil by plant transpiration and direct evaporation from the ground; Thornthwaite 1948). Arid and hyperarid regions have a P/PET ratio of less than 0.20; that is, rainfall supplies less than 20 per cent of the amount of water needed to support optimum plant growth (UNEP 1997, FAO 2004). Aridity is highest in the Saharan and Chilean-Peruvian deserts, followed by the Arabian, East African, Gobi, Australian, and South African Deserts, and it is generally lower in the Thar and North American deserts. Although the aridity indices vary in the different deserts in the world, all of them fall within the arid and hyperarid categories (Table 1.1).

Figure 1.1: Vegetation - barren areas of the world



The vegetation-barren areas of the desert biome are clearly discernible in this satellite image of the earth, both north and south of the equator.

Source: NASA 2004

Table 1.1: Classification of hyperarid and arid regions of the world

The hyperarid and arid regions of the world — defined as those areas with an aridity index (P/PET) lower than 0.20 — cover in total some 36.2 million sq. km, and occupy almost 20 per cent of the terrestrial surface of the planet. Potential evapotranspiration (PET) is calculated from Thornthwaite's (1948) equations as a function of mean monthly temperatures and mean monthly number of daylight hours, while precipitation (P) is measured directly from weather stations.

Classification	Aridity Index (P/PET)	Area (km ² × 10 ⁶)	Area (%) of world total
Hyperarid	< 0.05	10.0	7.5
Arid	0.05–0.20	16.2	12.1

Source: UNEP 1997

Thus, the global map of arid and hyperarid regions can be used as a good approximation to the boundaries of the Desert Biome (Figure 1.2a).

A bio-ecological criterion can also be used to map the world's deserts, by lumping together all the ecoregions of the world that harbour desert vegetation (identified by the xerophilous life-forms and the general desert-adapted physiognomy of the dominant plants). The resulting set of biologically desert-like ecosystems, modified from Olson and others (2001), provides a second approximation to the Desert Biome (Figure 1.2b; see also Appendices 1 and 2).

A third criterion can be derived from AVHRR-satellite images of the world. Using a land-cover index (NDVI, or Normalized Difference Vegetation Index) the earth has been classified into different land-cover categories (GLOBIO 2005, USGS 2005). The global map of deserts and semideserts, defined as large uniform regions with extremely low vegetation cover, may be used as an alternative approximation to the Desert Biome (Figure 1.2c).

Although each approach may have its own sources of error and the three differ in their definition of what is a desert, it is surprising how the three alternative maps coincide (Figure 1.3). The Desert Biome, in short, is formed by a set of geographic regions characterized by (a) extremely high aridity, (b) a large proportion of bare soil, and (c) plants and animals showing well-defined adaptations to survive in extremely dry environments. A desert, then, is a region with very little vegetation cover and large surfaces of exposed bare soil, where average annual rainfall is less than 20 percent of the amount needed to support optimum plant growth, and where plants and animals show clear adaptations for survival during long droughts.

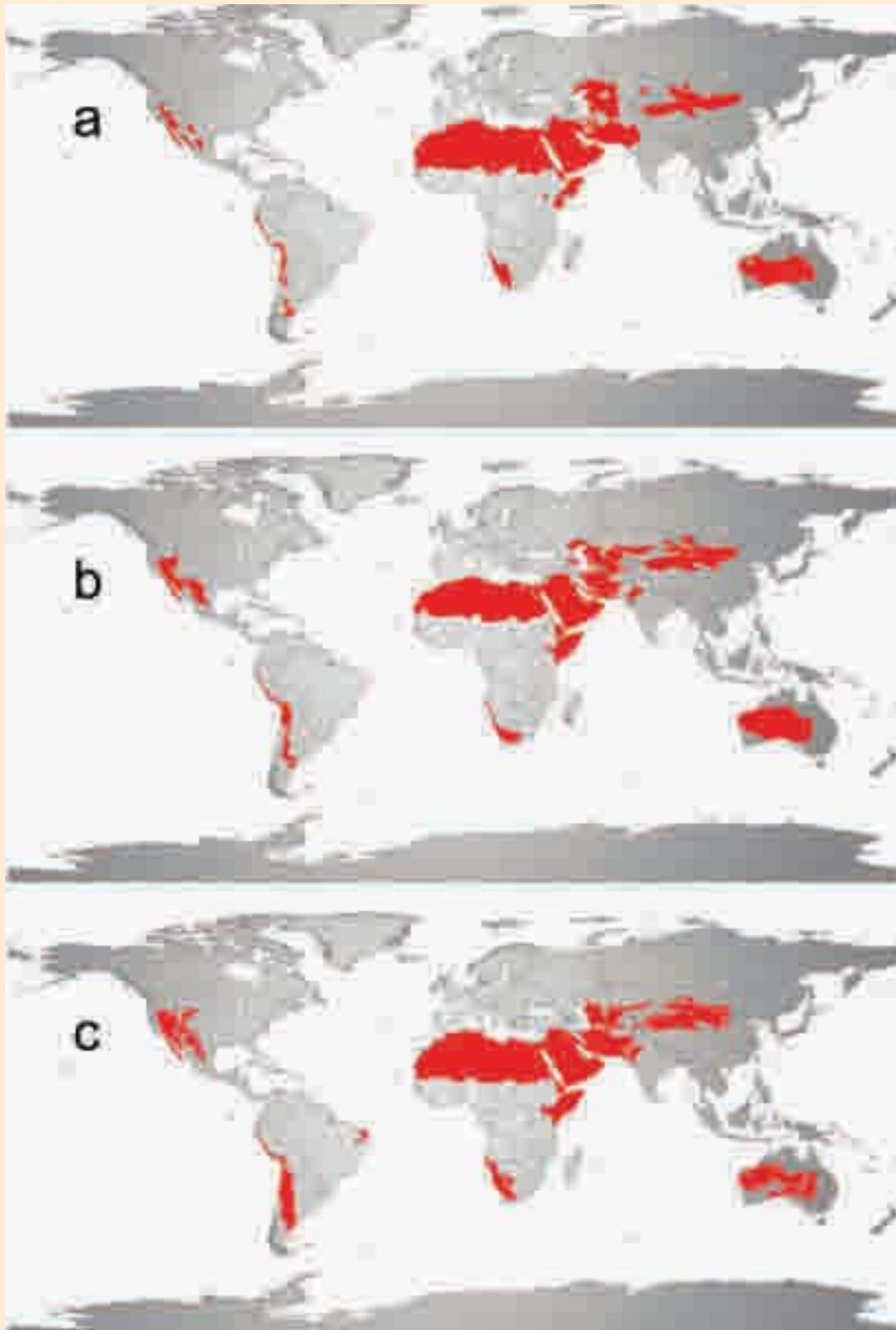
LATITUDINAL DESERT BELTS

Deserts occur in specific latitudes (25–35° north and south of the equator) because of the general thermodynamics of our planet. Solar radiation hits the earth with highest intensity near the equator. Because the earth's axis is tilted 23.5° with respect to the plane of its orbit, during part of the year the zone of maximum solar interception shifts northwards, towards the Tropic of Cancer, and during part of the year it moves southwards, towards the Tropic of Capricorn. Thus, the warm tropics form a belt around the equator from latitude 23° north to latitude 23° south, where the tropical heat generates rising, unstable air. As it climbs, the air condenses the moisture evaporated from the warm tropical seas and forests, and produces the heavy downpours that characterize the wet tropics. As it moves away from the equator at high altitudes, the air cools again and eventually starts descending towards the mid-latitudes, some 3000 km away from the equator both north and south. The air masses heat in their descent and, having lost their moisture during their tropical ascent, they become extremely dry. Thus, by contrast with the equatorial forests, the mid-latitude arid fringes that run alongside the tropical belt have a more stable atmosphere. These are the “horse” latitudes, where calm, dry air often dominates. Additionally, because of the stable atmosphere, not only are winds slack, but rainstorms seldom develop. For this reason most of the world's large deserts occur along the belt that separates the tropics from the temperate regions (Goudie and Wilkinson 1977).

CONTINENTALITY AND INLAND DESERTS

The sheer size of continents may be in some cases a direct source of aridity. Because most of the water in the atmosphere is ultimately derived from evaporation from the seas, there is often an aridity

Figure 1.2: Alternative definitions of the desert biome



The Desert Biome, as defined by three alternative criteria: (a) Arid and hyperarid regions of the planet as defined in the World Atlas of Desertification (UNEP 1997); (b) global ecoregions of the world (Olson and others 2001; Appendices 1 and 2) that harbour desert vegetation; and (c) contiguous regions of extremely low vegetation cover derived from AVHRR satellite images of the world (USGS 2005).

Figure 1.3: The desert biome defined by combined criteria



One of the first actions undertaken in the preparation of this report was to define the boundaries of the world's deserts. Deserts are commonly defined climatologically as the arid and hyper-arid areas of globe; biologically, as the ecoregions that contain plants and animals with clear adaptations for survival in arid environments; and physiologically, as large contiguous areas with low vegetation cover and ample extensions of bare soil. Overlaying the areas defined by each of the three criteria yields a composite definition of global deserts, occupying almost one-quarter of the earth's land surface — some 33.7 million square kilometres — inhabited by over 500 million people. The intensity of the red colour on the map indicates congruence in the three criteria: areas in intense red correspond to regions where the three criteria coincide, areas in intermediate red highlight regions where two criteria coincide, and areas in pale red show regions where only one criterion operates.

This analysis has also revealed that the population density in the desert cores (areas covered by all three definitions) is still low, while the edges of deserts (areas covered by only one or two definitions) are faced with higher pressures from human activities. Biological data also demonstrate that deserts are not simply barren lands but complex arrangements of diverse and fragile assemblages of species of flora and fauna. Located in the transition between deserts and semi-arid ecosystems, some of the desert fringes include several of the most endangered terrestrial ecoregions of the world.

	Figures in this report	Land area (1 000 km ²)	Protected area ³ (% of area)	Hotspots ⁴ (% of area)	Human Population		Distribution of land area (%) by degree of population pressure ⁵		
					Total (1 000)	Density (persons/km ²)	Low	Medium	High
Deserts defined by:									
Aridity	Fig. 1.2a	25 714	4.5	9.0	354 976	14	94.1	3.82	2.1
Ecoregions	Fig. 1.2b	25 270	5.1	9.8	254 860	10	95.1	3.21	1.7
Landcovers	Fig. 1.2c	28 819	5.8	10.7	283 400	10	94.6	3.96	1.5
Deserts (strict)¹	Fig. 1.3	19 467	4.6	6.7	143 670	7	96.4	2.43	1.1
Deserts (broad)²	Fig. 1.3	33 688	5.5	12.1	502 232	15	92.9	4.77	2.3
World Total		130 483	9.9	12.0	6 081 528	47	79.6	12.4	8.0

Note:

1. Deserts (strict) — The area classified as desert by all three definitions simultaneously.
2. Deserts (broad) — The area classified as desert by at least one of the three definitions.
3. Protected Area — The proportion of the area under environmental protection, following IUCN's definition, namely, "an area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means." (Mulongoy and Chape 2004)
4. Hotspots — The proportion of the area occupied by biological "hotspots", defined as the earth's biologically-richest and most endangered terrestrial ecoregions (Mittermeier and others 1999)
5. Population pressure — Low population pressure: < 25 persons square kilometre; Medium population pressure: 25–100 persons per square kilometre; High population pressure: > 100 persons per square kilometre.

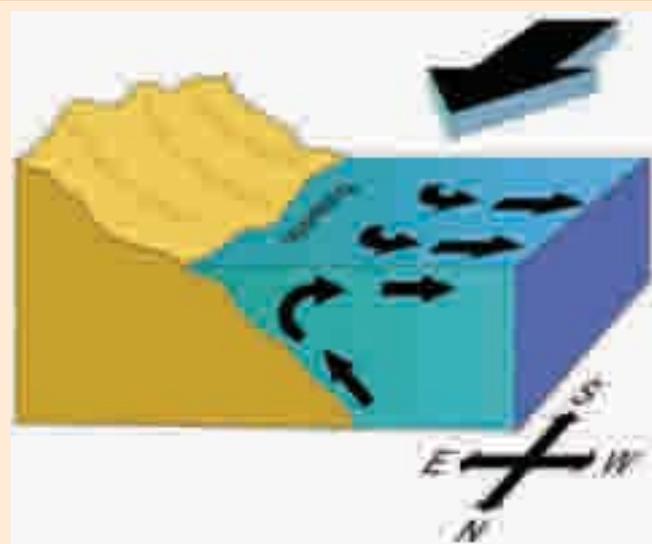
Source: San Diego Natural History Museum for image production, UNEP/GRID-Sioux Falls for table calculations

gradient in large continents: the land closer to the sea often receives a larger share of this ocean-derived water and, as air moves inland, it gets depleted of moisture and precipitation drops. Thus, regions lying deep within a continent may become deserts simply because air currents reaching them have already traversed vast land distances and lost most of the moisture they originally carried. Continentality is a major factor driving arid conditions in the Monte Desert in South America (see Figure 1.4), in the central deserts of Australia, in the Great Basin in North America, and especially in the central East Asian deserts, the Taklimakan and the Gobi.

COASTAL DESERTS: THE EFFECT OF MARINE UPWELLINGS ON DESERT DISTRIBUTION

The latitudinal explanation, however, is only partial. Around the mid-latitude belt, only the western side of continents is normally occupied by deserts, while the eastern side is covered by forests. The reason for this has to do with the global circulation of ocean currents: gravitation from the sun and the moon pulls air and water on the earth's surface

Figure 1.5: The upwelling phenomenon



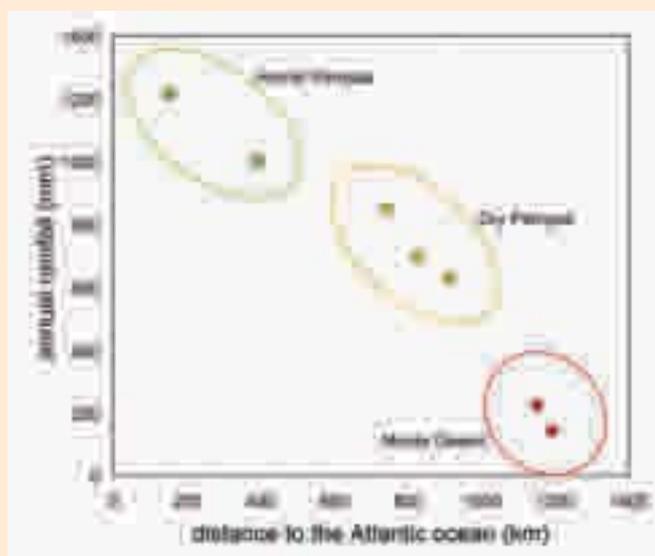
Wind and currents running parallel to the coast toward the equator are deflected westwards by the rotational movement of the Earth (the Coriolis effect). As the top layer of ocean water moves away from the coast, cold, nutrient-rich water from the bottom is brought to the surface. These waters generate immensely fertile ocean coasts but also create a cool and stable coastal atmosphere with very low rainfall.

and tends to make them lag behind, relative to the earth's rotational movement. The gravitational drag is greatest in the equator, where the centrifugal speed of the earth is fastest. Thus, as the earth turns, ocean currents and winds flow in the equator from east to west, tugged by universal gravitation, forming the equatorial currents and the easterly trade winds. As the westbound surface waters move away from the continents, they pull cold, nutrient-rich waters to the surface that generate a cool, stable coastal atmosphere, with little evaporation from the sea and very low rainfall other than morning fogs (Figure 1.5). In the coasts neighbouring these oceanic upwellings, typical coastal fog deserts tend to develop, forming some of the driest ecosystems on earth. Thus, the large-scale circulation of the ocean is the main reason why coastal deserts are always found on the west side of continents, such as the Namib in Africa (Figure 1.6), Atacama in Chile, the Atlantic Coastal Desert of Morocco, or the deserts of Baja California (Figure 1.7).

RAIN SHADOWS AND TROPICAL DESERTS

Topographic heterogeneity also contributes to the formation of deserts, especially of those that occur outside the mid-latitude belts. In the tropics, for

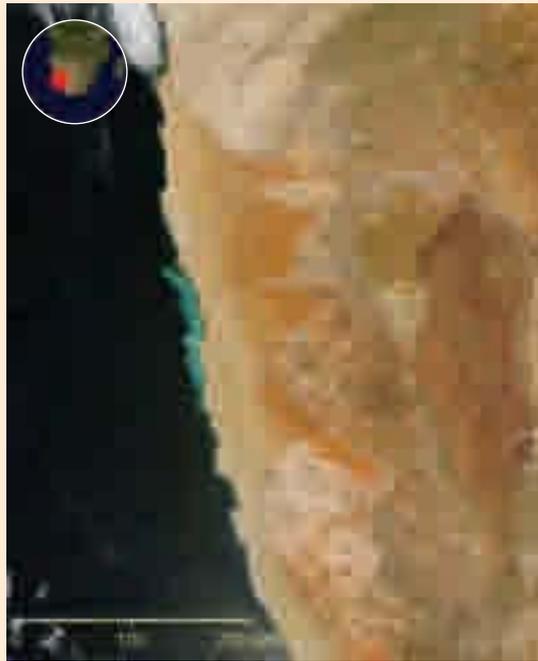
Figure 1.4: Continentality and aridity



Following a transect along the flat Argentine Pampas from the Atlantic coast to the foothills of the Andes, mean annual rainfall decreases as a function of the distance to the coast at a mean rate of -1 mm/km . Because the high Andean Cordillera stops any moisture coming from the Pacific, the continental distance to the Atlantic coast is the single best predictor of precipitation. The colours indicate local weather stations in the humid Pampas (green), the dry Pampas (yellow), and, finally, the Monte Desert (red) in the extreme west.

Source: Servicio Meteorológico Nacional, Argentina; online statistics at <http://www.meteofa.mil.ar/> for the following stations from east to west: Buenos Aires, Pergamino, Río Cuarto, Villa Mercedes, San Luis, Mendoza, and Uspallata

Figure 1.6: The Namibian coast



The consequences of the upwelling of cold, nutrient-rich water from the Benguela current near the coast of Namibia are clearly visible in the greenish-white plume of sulphur emissions produced by decomposing phytoplankton accumulated after the winter productivity peak. To the right, the dunes of the Namib desert bear witness to the dramatic aridity of this coastal desert.

Source: NASA 2004

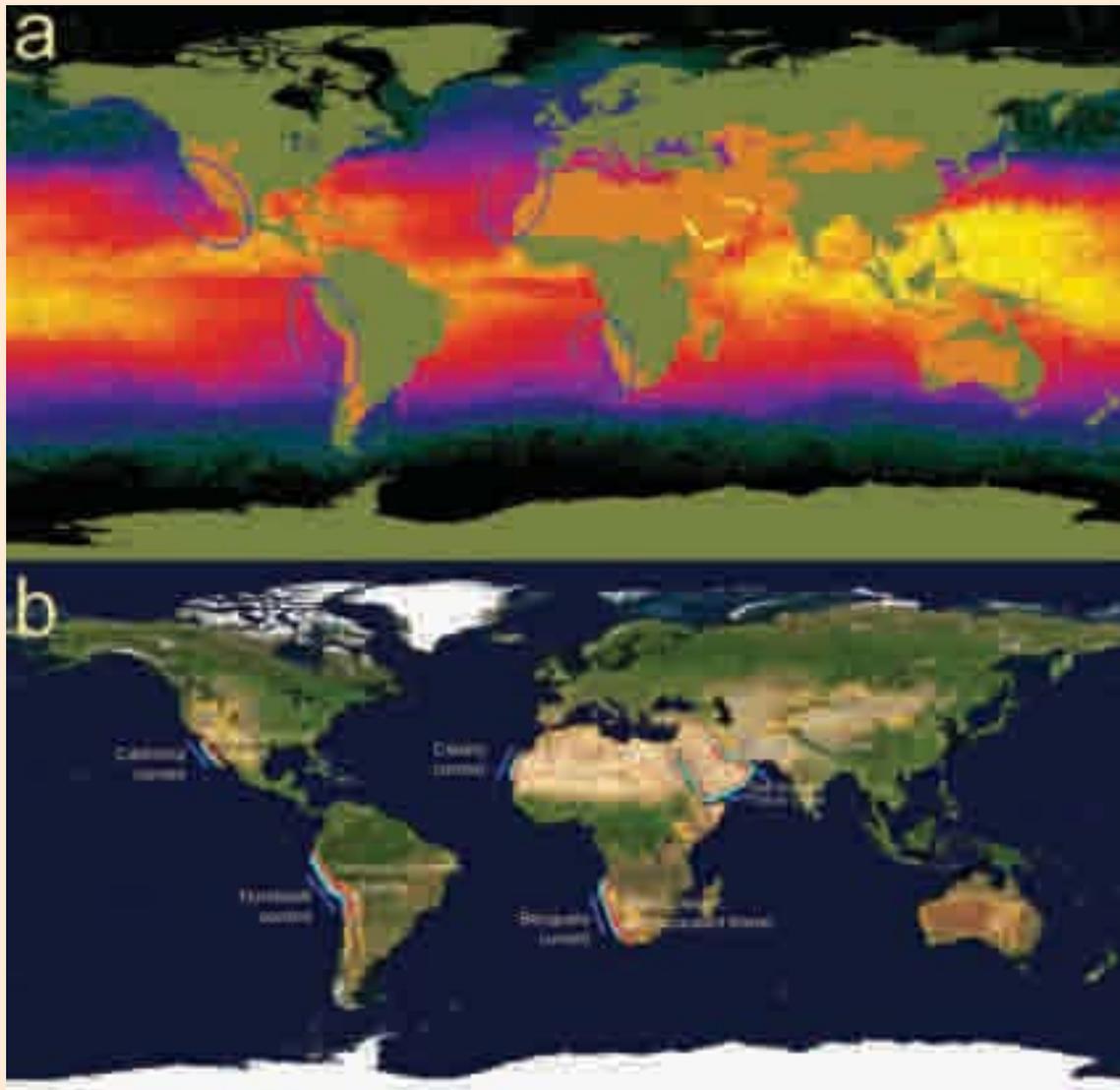
example, when the moisture-laden tropical trade winds reach continental mountain ranges they cool as they ascend, condensing fog and drizzle that feed montane cloud forests. Once the winds pass the mountain divide, they start compressing and warming-up again in their descent, but, having left behind their original moisture, they become hot and dry. Thus, while the windward slopes of most tropical mountain ranges are covered by cloud forests, the leeward part, known as the “rain shadow” of the mountains, is covered by arid scrub. The rain shadow effect is largely responsible for many tropical arid lands that seem to defy the rule that deserts are only found in the earth’s mid-latitude reaches, such as the Sechura Desert in Peru and Ecuador, the Caatinga scrub in equatorial Brazil, or the Tehuacán Valley desert in southern Mexico, a hotspot for cactus biodiversity. They are also responsible for some high-latitude cold deserts, such as the Great Basin, Patagonia, and the deserts of Central Asia.

DESERT LANDFORMS

The landforms of deserts, like those of high mountains and the polar areas, are much more visible than those of more vegetated landscapes. Bareness also allows much more active surface processes in all these areas, but in different combinations. Deserts suffer much more wind erosion than any other environment. Additionally, if slopes are steep and when the rain does fall, they also experience very fast water erosion. Desert landscapes come in two categories: (1) “shield” deserts and (2) “mountain-and-basin” deserts (Cooke and others 1992, Mabbutt 1977).

Shield deserts have developed on very ancient crystalline basements; that is, rocks that have been folded and faulted and hardened by heat and pressure over many millions of years. Granites, injected originally deep within the earth, have been unearthed by erosion and form steep-sided hills in many places (as at Uluru in Australia). The Sahara, the Arabian deserts, the southern African deserts, and the Australian deserts are in this group. Though very tough, the basement has been folded into gently-sloping swells and basins, and the basins have been filled over millions of years with sediments eroded from the swells, although these sediments have remained virtually unfolded themselves. They contain the best supplies of groundwater in the deserts, as in the northeastern and southern Sahara, and in Australia; and in some areas they are also rich in oil. Here and there recent volcanic rocks have overflowed at the surface, as in the Ahaggar and Tibesti mountains of the central Sahara. In their long lives these landscapes have experienced many different climates (partly because they were moved round the earth by continental drift) and many features formed in the different climates survive. There are even ancient glacial features in parts of Arabia and the Sahara; there are many more ancient river gorges, and ancient soils like silcretes or even laterites — ancient soils that formed under wet tropical conditions. The deep rotting of the rock in wetter times penetrated further in softer than harder rocks, and when the loose rotted material was stripped off, the uneven surface of the sub-soil landscape was revealed: a process appropriately called etching.

Figure 1.7: Sea surface temperatures and coastal deserts



(a) Sea surface temperatures during 2–9 June 2001, measured by NASA's Moderate Resolution Imaging Spectroradiometer (MODIS). Cold waters are black and dark green; blue, purple, red, yellow, and white represent progressively warmer water. Note the plumes of cold water along the Pacific coasts of North and South America (Baja California and Peru), as well as along the Atlantic coasts of Africa in Morocco and Namibia. (b) Distribution of the coastal fog-deserts of the world and the associated cold ocean currents: the California, Canary, Humboldt, and Benguela streams. Other coastal and fog deserts are also found around the Arabian Peninsula, in both the Red Sea and the Oman coast, associated with the strong tidal currents in these narrow water bodies and straits.

Water is the main agent of erosion only on the few hills of the shield deserts, and cuts deep gullies on their edges. Elsewhere low gradients mean that water erosion is not very effective, and this leaves the field free to the wind: the great plumes of dust travel from the Sahara over towards Europe, southwest Asia and the Americas, removing much more sediment than do rivers from the same area, and have taken even more dust in recent geological periods. With the dust winnowed out, sand is left behind, and most of it collects in dunes,

which cover 20–30 per cent of these landscapes. Some of the larger “sand seas” cover more than 300 000 square kilometres; their median size is 123 000 km².

Mountain-and-basin deserts are those in the much more recently folded and faulted rocks of the earth's active tectonic belts. Up-faulted mountains alternate irregularly with down-faulted basins. The American deserts, both North and South, are all of this kind, as are the deserts of Central Asia

(where some of the basins, however, cover many hundreds of thousands of square kilometres). Water erosion in the mountains cuts deep, steep-sided valleys and gorges, and takes the debris out into the basins, where the broadening and shallowing of the ephemeral washes (called *arroyos* in the Americas and *wadis* in Northern Africa and West Asia) first cause the coarser debris to be dropped in broad “alluvial fans.” Occasional extreme storms may carry huge boulders onto these as well. Further down, the alluvial fans coalesce into a long slope of finer alluvium — the *bajada*. Sand may be winnowed out of the alluvial deposits and form dunes (and in Central Asia, even a few sand seas). Only the finest debris (silt and clay) reaches the bottom of the basin, where it is deposited in ephemeral lakes or *playas*. The salts carried in the waters also accumulate there.

Climatic Variability and Rainfall Pulses

In deserts, rainfall events trigger short periods of high resource abundance which, despite the overall scarcity of rain, can saturate the resource demand of many biological processes for a short time. Thus, although deserts are often characterised by their mean climatologic conditions (as in the case of the Aridity Index described in the previous section) they are really driven by a succession of short pulses of abundant water availability against a background of long periods of drought. And, because rain storms are also frequently very localized, deserts are extremely patchy environments in their resource availability, both in space and in time. Rainfall pulses are really the driving force structuring desert ecosystems, and plants and animals have developed very specific adaptations to cope with ephemeral abundance, especially with regard to growth, population dynamics, and the cycling of organic matter and nutrients (Sher and others 2004). Within a desert, rainfall events may vary significantly from one pulse to the next: some spells may occur in winter, others in summer; some events may bring very little precipitation, others may bring intense showers; and the period between pulses may also vary substantially.

Each organism’s response threshold is often determined by its ability to make use of moisture pulses of different durations and infiltration depths. For example, brief and shallow pulses have an important effect over surface-dwelling organisms with fast response times and high tolerance for low resource levels, such as soil micro-organisms. Short precipitation pulses are important to the survival of annual plants, but deep-rooted perennial plants may respond only to longer, more intense precipitation events. Thus, the diversity of pulses also promotes a diversity of responses in life-forms, migrations, or population cycles in different species. To a large extent, it is the heterogeneity of pulses that drives the surprisingly high biodiversity of desert ecosystems (Chesson and others 2004).

But what commands pulses in deserts? Why are seasons, and even decades, so different from each other, and often so unpredictable? To a large extent, pulse-type variations in desert environments are linked to global atmospheric and oceanic phenomena. Large-scale drivers of regional precipitation patterns include the position of the jet streams, the movement of polar-front boundaries, the intensity of the summer monsoon, El Niño Southern Oscillation events, and even longer-term ocean cycles, such as the Pacific Decadal Oscillation (Loik and others 2004). Driven by these large-scale forces, the intensity of mid-latitude continentality, ocean upwellings, and rain shadows — the major factors modulating the distribution of arid lands — is not constant but may vary from one year to the next. As a result, the intensity and frequency of rain pulses at a local scale may vary substantially with time, and in a seemingly unpredictable fashion.

The influence of large-scale drivers on local desert conditions was noted many years ago by the fishermen and the farmers of the coastal desert of Peru, who realized that during some years the normally cold waters of the Pacific became warmer. In these years, they noted, the abundance of sardines decreased but abundant rainfall soaked the land and made the desert flourish. Because this phenomenon was normally observed around the month of December (a time of the year in which Christians commemorate the birth of the Christ child — *El Niño* in Spanish), they called the phenomenon

the “El Niño” ocean current. During El Niño years, the trade winds and the west-bound equatorial currents slow down, and the upwelling of nutrient-rich waters in the coasts of the American Continent decreases. The sea becomes less productive while the coastal fog deserts of the Pacific Ocean become drenched in the abundant rainfall that originates from the now-warm sea waters (Holmgren and others 2001; see also Chapter 4).

These pulses of abundance and scarcity of resources are a major force in the ecological organization of many deserts of the world. During pulses of bounty, the fragile seedlings of desert plants can germinate, establish, and prepare for long droughts burying their roots deep into the desert soils. Ephemerals can replenish their seed banks (Figure 1.8), desert toads can reproduce in extraordinary numbers before entering again into their waterless torpor, and granivorous rodents, such as North American kangaroo rats, Australian hopping mice, and African jerboas, can stock up their underground caches. The desert becomes renewed, and ready to face again decades of extreme hardship.

WINTER AND SUMMER RAINFALL PATTERNS

Two important weather systems bring precipitation to the world’s deserts. The horizontal transport by wind of moist air from the sea into the land (known as advective transport) during winter, when

the land becomes colder than the sea, causes atmospheric condensation over the cold continents and generates winter rains. Because this particular pattern of summer droughts and winter rains dominates the coasts around the Mediterranean Sea, the areas of the world that show this type of seasonal variation are called “Mediterranean” regions. In summer, in contrast, a different weather system is the main driver of rainfall pulses in arid lands: as the continents become hot they generate low-pressure centres with rapidly ascending warm air; and as the air ascends vertically (a phenomenon known as convective transport) the atmospheric mass cools rapidly and condenses large amounts of air moisture, which pour down in the form of summer thunderstorms. In many parts of the world this rainfall pattern is known as the “monsoon.”

Most of the large deserts of the world lie between these two weather patterns: the large mid-latitude deserts share their boundary with winter-rain ecosystems in their higher latitudes, and with monsoon regions near their tropical reaches. The Sahara Desert, for example, is dominated by winter rains in its northern Mediterranean limit, and by summer rains in its more tropical Sahelian border. The Sonoran Desert, in North America, receives mostly winter rains in its northwestern reaches, near the Mojave, and is fed by the Mexican summer monsoon in its tropical southern reaches (Dimmit 2000). In South America, the Monte Desert receives mostly winter rains in its cold Patagonian austral limit but is dominated by summer thunderstorms near the Tropic of Capricorn (Ezcurra and others 1991).

Plants in winter-rain deserts have a rather narrow window of opportunity for growth. During winter, moisture accumulates in the soil but the weather is often too cold for plant growth. During summer, temperature may be adequate but the soil is parched and waterless. Only during spring, when temperatures start to rise and moisture is still present in the ground, can plants flourish. For perennial plants, retaining the leaves from the previous year gives the shrubs an early start and a competitive edge during the short spring. But in order to keep the foliage on until the next year

Figure 1.8: Ephemeral plants in the Gran Desierto



During rainy years, the sand dunes of the Gran Desierto — the driest desert in North America — become lush with the growth of ephemeral plants.

Source: Patricia Robles-Gil

the leaves have to survive the dry desert summer, when no rains occur and the soil is bone-dry. To avoid water loss during the hot season, many evergreen desert shrubs have developed small leaves, or leaves with a thick, leathery epidermis, and few, small stomata (the pores through which leaves breathe and fix carbon dioxide). Thus, evergreen shrubs with small and/or tough, leathery leaves are the dominant life form in winter-rain deserts.

Tough leaves, however, are not the only mechanism through which plants can efficiently use the short desert spring season. The winter-rain deserts of the world are also amazingly rich in short-lived spring ephemerals. These plants survive the scorching summer in the form of seeds, bulbs, or tubers, and quickly sprout during the narrow window of opportunity that the desert spring provides. In contrast with the evergreen shrubs, their leaves are soft and tender, and their stomata are large, allowing the plants to grow very fast when conditions are favourable. One of their most astonishing traits is the lack of any evident adaptations to aridity other than fast growth. Because desert ephemerals complete their life cycles during short periods of abundance, natural selection has favoured fast growers and even faster reproducers.

In monsoon deserts, in contrast, rainfall pulses coincide with adequate temperatures for plant growth. Because moisture becomes available at a time in which plants can grow fast, leaf retention is rare and drought-deciduousness is a dominant trait in shrubs and trees. In these deserts, perennial plants often show extensive networks of shallow roots, and many plants compete to extract water from the soil immediately after the rain has fallen. Giant fleshy trunks or cactoid succulent stems, adapted to accumulate water, are thus common in summer-rain deserts.

Evolution, History and Biogeography

GLACIAL PERIODS AND THE EVOLUTION OF MODERN-DAY DESERTS

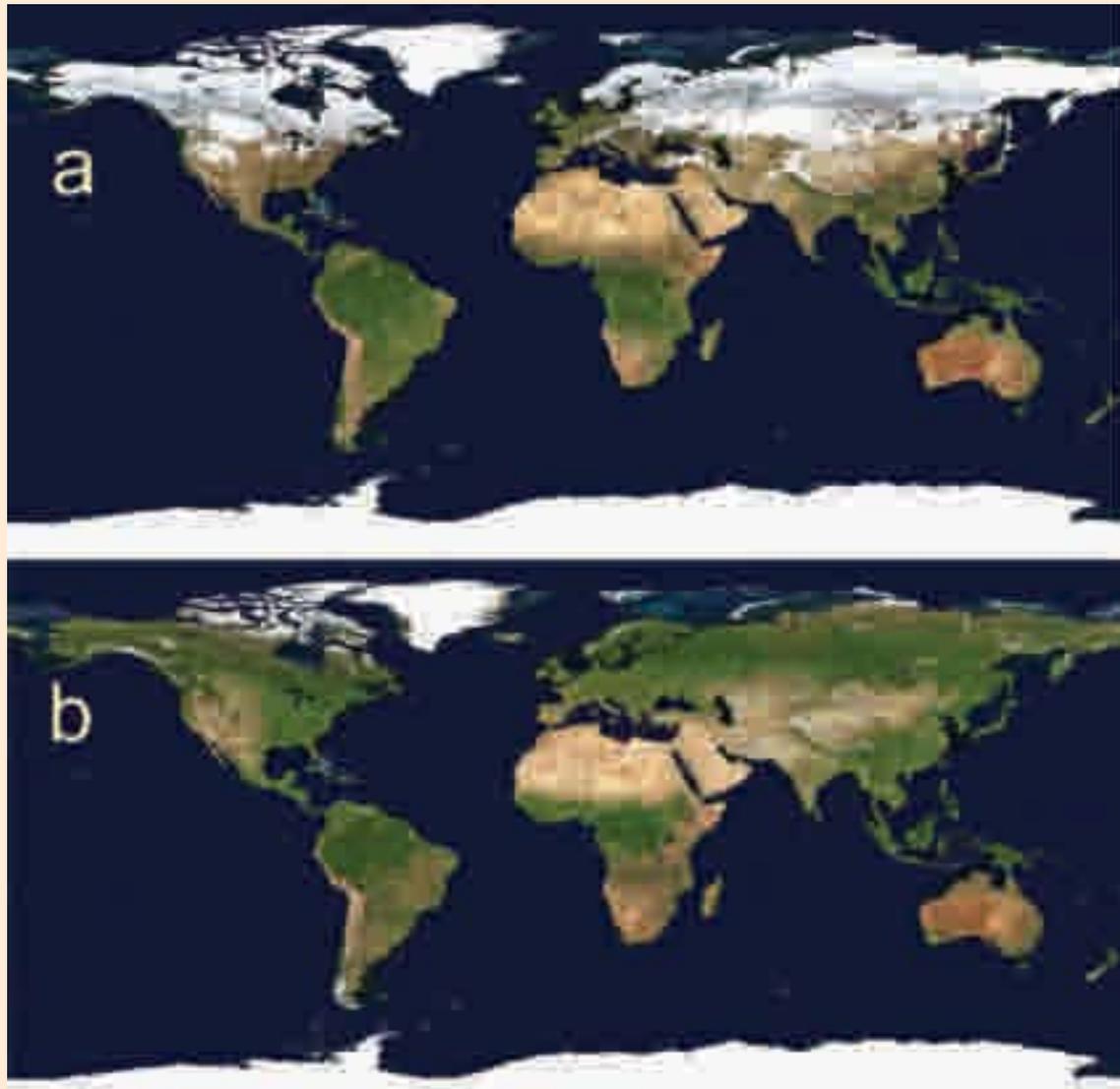
During the last two million years — the Pleistocene period — the earth underwent a series of alternate

cycles of cooling and warming, induced by variations in the planet's orbit and in the inclination of its axis. During the colder periods — known as the “Ice Ages” — most of the high-latitude regions of the world became covered by massive glaciers, and temperate ecosystems such as cold grasslands and conifer forests moved towards the equator. Because of the higher proportion of land-mass in the northern hemisphere, this phenomenon was more conspicuous in North America and Eurasia (Figure 1.9).

From the late Pleistocene glacial period to present times significant changes occurred in the climate and ecosystems of the planet. During the Last Glacial Maximum (LGM) period, (25–17 000 years before present [yBP]), the presence of large ice sheets and lower concentration of atmospheric CO₂ had given rise to a colder climate and a reduced summer monsoon resulting in low global forest cover. The tropical belt narrowed and the deserts moved towards the equator, shrinking in the mid-latitudes, where they were replaced by grasslands, semiarid scrubs, open woodlands, or cold steppes. The ancestors of the modern-day desert biota found refuge in what are now dry subtropical habitats, especially in places where arid conditions persisted under the rain shadow of large mountain ranges, or in areas that are now covered by dry tropical savannas which, lacking intense monsoons, were then more arid than at present. The last glaciation ended around 15 000 years ago, when the glaciers retreated, giving place to the warm interglacial period that followed: the Holocene, our current global climate.

As a general rule, during the LGM, the high-latitude borders of the world's deserts became colder and wetter than they are at present, while the tropical fringes became drier than they are today. Thus, during the LGM large dunes developed in the southern Sahara-Sahel zone and in the Thar Desert of India, while the Mediterranean coast of Algeria and Morocco became wetter and colder. Similarly, during the late Pleistocene the Chihuahuan Desert of North America witnessed woodlands of piñon pines, junipers, and oaks, while the tropical dry woodlands of central Mexico became drier, evolving the rich cactus flora that characterizes the region today.

Figure 1.9: Continentality and glacial dynamics in the northern and southern hemispheres



While snow and ice cover a large proportion of the temperate terrestrial areas during the northern hemisphere winter (January 2004, top) and all but disappear in summer (July 2004, bottom), the advance and retreat of the ice sheet in the southern hemisphere is much less pronounced because of the buffering effect of large oceanic masses. A similar effect occurred during the Pleistocene glaciations, when the ice sheet covered most of the northern hemisphere, forcing deserts north of the equator to retreat into the tropics. In the southern hemisphere, in contrast, because of the lower landmass and higher oceanic influence, the advance and retreat of the glaciers was less pronounced.

Source: NASA 2004

During the warm early to mid-Holocene (8 000–5 000 yBP), the global climate that resulted from glacial retreat brought an increase in the intensity of the monsoon throughout the sub-tropical arid lands. Lake Chad became a freshwater inland lake bigger than today's Caspian Sea, in an area that has again become a complete desert. Tropical forests and dry woodlands around the equator expanded north and south, while deserts moved into the mid-latitudes. During that period, the southern Sahara and the Sahel were much

wetter than today, with extensive vegetation cover, thriving animal communities, and numerous human settlements.

Sometime between 6 000 and 5 000 yBP, there was again a transition to more arid conditions. Mesic vegetation communities disappeared rapidly, lake levels declined dramatically, and highly mobile pastoralist cultures started to dominate and replace sedentary lacustrine and riparian traditions. The Liwa region of the United Arab Emirates, for

example, experienced phases of sand deposition that lead to the formation of a large (up to 160 m high) mega-dune. A similar transition towards more arid conditions occurred in North America, where the Holocene brought the arrival of Mojave, Chihuahuan and Sonoran desert scrub elements from the south, such as the agaves, cacti, ocotillos (*Fouquieria*), and creosote bushes that characterize the area today.

An explanation for these climatic variations is that changes in incoming solar radiation, associated with slow shifts in the Earth's orbit, enhanced the strength of the summer monsoon rains at the beginning of the Holocene. These rains, in turn, increased the extent of vegetation cover and wetlands, and this had two major effects — a reduction in surface albedo (reflectance) and an increased ability to recycle water back to the atmosphere through evapotranspiration. Both effects helped fuel the monsoons with additional energy and moisture, increasing the summer rains. In Africa, the climate-vegetation system maintained a “green Sahara” climatic regime through the middle Holocene, when a sudden transition occurred to a “desert Sahara,” the regime that we know at present. The aridization trend of the mid-Holocene fed back into the deserts themselves by decreasing vegetation cover, reducing local inputs of moisture into the atmosphere, and further increasing the dry conditions.

MOUNTAIN SKY-ISLANDS AND CLIMATES OF THE PAST

When the ice sheets started to retreat, some 20 000 years ago, most of the temperate flora and fauna slowly migrated back into higher latitudes and the Desert Biome gradually expanded across the mid-latitudes to its current extent. A subset of the temperate biota, however, stayed behind in the rugged and cool mountain ranges that emerge from the desert plains. Establishing higher-up with each passing generation as the climate warmed, the ice-age organisms were able to persist in the cool mountain environments, where conditions are similar to the ones they had enjoyed in the lower plains during the Ice Ages. As they ascended into the isolated desert mountains, the communities of the desert “sky-islands” became separated from other mountains by harsh desert plains. Like prehistoric castaways,

the Ice Age species now survive high-up in the cool refuges of the desert mountains; a biological memory of past evolutionary history subsisting high-up in the mountains like ghosts of climates past. And, because they have been reproducing in isolation for 15 000–20 000 years, many of their populations have developed unique genetic traits and have evolved into new species. Thus, in a similar fashion to evolution in remote oceanic islands, the biota of the desert sky-islands is composed by a large number of endemic species and has immense value for biological conservation (Axelrod 1950).

As the effect of the Ice Ages was more severe in the northern hemisphere, which is mostly covered by continental land masses, than in the more oceanic southern half of the globe (Figure 1.9), most of these Pleistocene montane relicts are found north of the equator. In North America, where the desert relief is highly folded, mountainous sky-islands dapple the central part of the Sonoran and the Chihuahuan Deserts, and of the Great Basin. All these ranges contain endemic pines, oaks, madrones, and chaparral species, remnants of the “Madro-Tertiary” flora, a unique temperate ecosystem that covered much of the now-dry North American deserts during the last six million years.

In Africa, similar relict mountains emerge from the harsh Saharan plains: near the Mediterranean coast, the Atlas Mountains in northern Morocco shelter rich pine and oak forests. Further south, the Ahaggar and Tassili-n-Ajjer ranges of south-eastern Algeria and the Air massif in northern Niger harbour a number of endemic and rare Mediterranean species such as the tarout, the wild olive, and the Saharan myrtle. To the east, the Tibesti mountains in southern Libya hold some Mediterranean as well as some tropical relicts. These Saharan mountains also provide prime habitat for migratory birds and a key refuge for threatened wildlife.

In the Somali Peninsula, and across the Gulf of Aden in the southern part of the Arabian Peninsula, high mountain ranges shelter similar temperate relicts: along the northern Somalian coast, in the tip of the Horn of Africa, the Somali Montane Woodlands thrive along the coastal ranges fed by

moisture brought in from the sea. A biogeographic refuge and centre of endemism, these mountain habitats harbour many endemic species of both plants and animals. The higher parts of the ranges contain an evergreen scrub quite similar to the Mediterranean *maquis*, with species such as kadi, mountain box, Ethiopian pistachio, and remnants of ancient juniper forests.

Across the Aden Straits, and overlooking the coast of the Red Sea, the high Asir mountains of Yemen and Saudi Arabia give shelter to an even richer relict montane ecosystem with juniper, bramble, and zaytoon olive. Fed by the coastal fogs of the Red Sea, the region shelters more than 170 endemic plants, and is a critical refuge for a large number of endangered animals such as the Arabian leopard and the Hamadryas baboon. Finally, in the eastern part of the Arabian peninsula, near the coast of the Gulf of Oman, the Al Hajar Mountain range forms a spectacular wall of mountains that rise almost 3 000 m from the surrounding deserts, providing an important refuge for endemic and relict species of plants of Mediterranean and Indo-Iranian origin, often growing in the vicinity of tiyu (a carob relative) and other trees of African ancestry. The endemic Arabian tahr, a type of wild goat, is still common on these precipitous slopes.

These mountains, and many others, play an immensely important role in the maintenance of desert diversity and in the conservation of desert biota. Sharp ecotones exist between arid plains and island-like, desert-surrounded mountains. In these slopes, altitudinal change reflects evolutionary time and in their intense transitions it is possible to explore the evolutionary history of deserts during the Pleistocene (Figure 1.10).

Biological Adaptations to Aridity

At its origins, life evolved in water, and water is the most crucial element for the survival of all living organisms. Thus, it is no surprise that some of the most remarkable adaptations for survival are found in desert species, that is, in the environments where water is most scarce (Louw and Seely 1982). The short pulses of abundance that

Figure 1.10: The Maderas del Carmen range



The Maderas del Carmen range in the Chihuahuan Desert is a prime example of a montane Pleistocene relict, or desert “sky-island”. The lowlands are covered by creosote bush (*Larrea tridentata*) and prickly pears (*Opuntia* sp.), two hardy desert perennials, but high-up in the mountains the ancient pine forests that once covered a large part of the region still survive.

Source: Jaime Rojo

contrast sharply with the background condition of aridity and scarcity are the major force that has driven evolution, natural selection, and adaptation in desert biota. Plants and animals are adapted to these seasonal strokes. Natural selection and evolution have moulded in very precise ways the life-forms of desert organisms in their harsh and unpredictable environment. Furthermore, because most deserts of the world have developed in relative isolation from each other, many of their constituent species have evolved from different ancestors (Morton 1979). Thus, deserts are prime ecosystems to study and understand the phenomenon of convergent evolution — the development of similar growth forms and adaptations derived from different ancestors (Table 1.2, Figure 1.11).

ADAPTATIONS OF PLANTS TO ARIDITY

Most desert species have found remarkable ways to survive by evading drought (Robichaux 1999). Desert succulents, such as cacti or rock plants (*Lithops*) for example, survive dry spells by accumulating moisture in their fleshy tissues. They have an extensive system of shallow roots that allows them to capture soil water only a few hours after it has rained. Their photosynthesis is modified to exchange gases and fix CO₂ during the night, when evaporative demand is low, and to accumulate the fixed carbon in the form of malic

Table 1.2. Convergent evolution of animal guilds in four hot deserts of the world

In spite of their different phylogenetic origin and their different biogeographic histories, many of these animals look strikingly similar in appearance

Guild	Deserts			
	North American	Australian	North African	South African
Bipedal rodent granivores ⁽¹⁾	<i>Dipodomys</i>	<i>Notomys</i>	<i>Jaculus</i>	
Quadrupedal rodent granivores ⁽¹⁾	<i>Chaetodipus</i> <i>Perognathus</i>		<i>Taterillus</i> <i>Pachyuromys</i> <i>Gerbillus</i> <i>Sekeetamys</i>	<i>Gerbillus</i> <i>Tatera</i> <i>Gerbillurus</i>
Small mammalian insectivores ⁽¹⁾	<i>Onychomys</i> <i>Notiosorex</i>	<i>Antechinus</i> <i>Sminthopsis</i> <i>Antechinomys</i>	<i>Crociodura</i>	<i>Crociodura</i> <i>Elephantulus</i> <i>Macroscelides</i>
Mid-sized herbivores ⁽¹⁾	<i>Lepus</i> <i>Sylvilagus</i>	<i>Onychogalea</i>	<i>Lepus</i>	<i>Pedetes</i>
Mammalian carnivore ⁽²⁾	<i>Vulpes</i>		<i>Fennecus</i>	
Ant eating reptile ⁽²⁾	<i>Phrynosoma</i>	<i>Moloch</i>		
Horned snakes ⁽²⁾	<i>Crotalus</i>		<i>Cerastes</i>	<i>Bitis</i>
Open space, long-legged lizard ⁽³⁾	<i>Callisaurus</i>	<i>Amphibolurus</i>		
Medium-sized, lizard-eating lizard ⁽³⁾	<i>Crotaphytus</i>	<i>Varanus</i>		

Sources: (1) Mares 1980; (2) Schmidt-Nielsen 1964; (3) Pianka 1986.

Figure 1.11: Convergent Evolution



The Australian horny devils (*Moloch horridus*, shown in this picture taken in Alice Springs, Australia) are surprisingly similar the North American horned lizards (*Phrynosoma coronatum*, in Baja California) in both their feeding habits and their ecology. Their similarity, however, is due to convergent evolution in distant deserts, as they belong in different families and are taxonomically unrelated.

Source: Patricio Robles-Gil and Brad Hollingsworth

acid, which is later used by the plant as a building block of more complex organic molecules (this photosynthetic pathway is called “Crassulacean Acid Metabolism” or CAM).

Additionally, many cacti and other stem-succulent plants of hot deserts present columnar growth, with leafless, vertically-erect, green trunks that maximize light interception during the early and late hours of the day, but avoid the midday sun, when excessive heat may damage, or even kill, the plant tissues. Thus, erect columnar plants may avoid drought by (a) accumulating water, (b) exchanging gases at night, and (c) morphologically avoiding midday exposure to solar radiation (Zavala-Hurtado and others 1998). Instead of having developed succulent stems adapted for water storage, other CAM plants such as aloes and agaves have developed ground-level rosettes of succulent leaves. Because of the funnel-shape of their leaf-whorls, these plants seem to be adapted to collect dew from morning fogs in desert mountains, hillslopes, and ocean coasts, accumulating the water thus harvested in their fleshy leaves and central bud (Martorell and Ezcurra 2002).

Woody desert trees, such as acacias, cannot store much water in their trunks but many of them evade drought by shedding their leaves as the dry season sets in, entering into a sort of drought-induced latency. Many of these desert species also have deep taproots that explore deep underground water layers. Other trees have convergently evolved a mixture of these strategies: they can store water in gigantic trunks and have a smooth bark that can do some cactus-like photosynthesis during dry periods; but, when it rains they produce abundant green leaves and shift their metabolism towards that of normal-leaved plants. This group is formed by trees with famously “bizarre” trunks, such as the African baobab (*Adansonia*), the Baja-Californian Boojum-tree (*Fouquieria columnaris*) and elephant-trees (*Bursera* and *Pachycormus*), and the South African commiphoras (*Commiphora*), bottle-trees (*Pachypodium*), kokerbooms (*Aloe dichotoma*, Figure 1.12) and botterbooms (*Tylecodon*).

A third group of plants, the “true xerophytes” or true desert plants, have simply adapted their morphology and their metabolism to survive extremely long droughts. These species have remarkably low osmotic potentials in their tissue, which means that they can still extract moisture from the soil when most other plants cannot do so. True xerophytes, such as the creosote bush (*Larrea*), are mostly shrubs with small, leathery leaves that are protected from excessive evaporation by a dense cover of hairs or a

thick varnish of epidermal resin. Their adaptive advantage lies in their capacity to extract a fraction of soil water that is not available to other life-forms. However, because their leaves are so small and protected from transpiration, their gas-exchange metabolism is very inefficient during rain pulses when moisture is abundant. In consequence, these species are extremely slow growers, but extremely efficient water users and very hardy.

Finally, one of the most effective drought-survival adaptations for many species is the evolution of an ephemeral life-cycle. A short life and the capacity to leave behind resistant forms of propagation is perhaps one of the most important evolutionary responses in most deserts, found not only in plants but also in many invertebrates. Desert ephemerals are amazingly rapid growers capable of reproducing at a remarkably high rate during good seasons, leaving behind myriad resistance forms that persist during adverse periods. Their population numbers simply track environmental bonanzas; their way to evade critical periods is to die-off, leaving behind immense numbers of propagules (seeds or bulbs in the case of plants, eggs in the case of insects) that will restart the life cycle when conditions improve. These opportunist species play an immensely important role in the ecological web of deserts: myriad organisms, like ants, rodents, and birds, survive the dry spells by harvesting and consuming the seeds left behind by the short-lived ephemeral plants. Granivory (the consumption of seeds) and not herbivory (the consumption of leaves) is at the base of the food chain in most deserts, as those few plants that maintain leaves during dry spells usually endow them with toxic compounds or protect them with spines. The onset of rainy periods brings to the desert a reproduction frenzy of desert ephemerals, and a subsequent seed-pulse that drives the entire food web for years.

From the information above it can be seen the survival strategies of desert plants are classifiable along a gradient ranging between two extreme categories: (a) adaptation for quick use of ephemerally abundant resources, or (b) adaptation for the efficient use of poor but more permanent resources (Shmida 1985). The first category, typically exhibited by desert ephemerals, represents

Figure 1.12: Fleshy-stemmed trees



The fleshy stems of the kokerbooms (*Aloe dichotoma*)—one of Africa’s many giant, fleshy-stemmed trees — are true landmarks in the otherwise barren landscape of the Namib Desert.

Source: Patricia Rojo

a “maximum variance” behaviour that consists essentially in tracking environmental variation, while the second category, exhibited by true xerophytes and cacti, is a “minimum variance” behaviour that consists in adapting to the worst possible conditions. Drought-deciduous perennials and grasses represent a compromise between these two extreme behaviours. Attributes necessary for the quick use of water include rapid growth (often at the cost of low water-use efficiency) and abundant seed production. Attributes for survival with little water include high water-use efficiency, slow growth, and passive cooling. Drought deciduousness, as an intermediate strategy, requires the capacity to shed leaves and to quickly recover them when moisture conditions improve.

The survival strategies of desert plants present some of the most striking cases in nature of evolutionary convergence: plants from widely different families and from divergent evolutionary origins have developed, in the different deserts, life-forms so similar that it is sometimes difficult to tell them apart. Such is the case of the succulent cactoid growth form, evolved in Africa from the families Euphorbiaceae, Asclepadiaceae, and Aizoaceae, and in the Americas from the family Cactaceae. Similarly, bottle trees in Africa evolved from the families Apocynaceae, Aloeaceae, and Crassulaceae, while in the New World they belong to the Fouquieriaceae, Anacardiaceae, and Burseraceae.

ADAPTATIONS OF ANIMALS TO ARIDITY

Behavioural adaptations

To the physiological, anatomical, and morphological adaptations of plants, animals can add adaptive behaviour. Many birds and most large mammals, like pronghorn antelopes or wild sheep, can evade critical spells by migrating along the desert plains or up into the mountains. Smaller animals cannot migrate such long distances, but regulate their environment by seeking out cool or shady places. In addition to flying to other habitats during the dry season, birds can reduce heat loads by soaring. Many rodents, invertebrates, and snakes avoid heat by spending the day in caves and burrows, and procuring food during the night. Even diurnal animals may reduce their activities by resting in the shade during the hotter hours of the day. Fossoriality, a lifestyle based in burrows, is the

Figure 1.13: The sidewinder snake



The characteristic crawling pattern of the sidewinder (*Crotalus cerastes*) leaves a tell-tale trail in the dunes of the Gran Desierto. Its perfect matching to the colour of the sand protects it from predators such as kestrels and falcons.

Source: Patricia Robles-Gil

norm for small animals in all deserts, as it allows them to stay away from the gruelling heat during the hotter part of the day and it also provides them a warm refuge during the cold desert nights. Additionally, humidity inside burrows (ca. 30–50 per cent) allows desert animals to preserve water. When the normal mechanisms to keep body temperature within acceptable limits fail, many small rodents and some desert tortoises (*Testudo*) salivate to wet the chin and throat and allow evaporative cooling. Such mechanisms have a high cost in water and are used only as emergency measures to prevent death.

At dawn, the dry desert ground may approach freezing temperatures and at midday it may heat up into an 80°C inferno. A few inches above the ground, variations in air temperature are much less pronounced, and, just a few inches below the surface, underground temperatures are almost constant between day and night. For this reason, thermoregulation is a particularly challenging problem for small surface-dwellers and especially for reptiles, which cannot regulate their body temperature metabolically. Most desert reptiles have developed peculiar ways of travelling over hot sandy surfaces. Side-winding, a form of lateral movement in which only a small part of the body is in contact with the surface, is employed by many sand snakes (Figure 1.13). Many lizards and some ground birds avoid overheating by running rapidly over the hot desert surface while maintaining their

bodies well separated from the ground (Safriel 1990). Some lizards assume an erect, bipedal position when running, while others regulate their contact with the hot desert pavement by doing “push-ups” with their forelegs.

Many large mammals that cannot avoid being in the sun during a large part of the day orient their bodies so as to reduce the incidence of the sun’s rays. By standing upright, ground squirrels reduce solar incidence upon their bodies. The African ground squirrel *Xerus inauris* even orients towards the sun and shades itself with its tail when foraging (Figure 1.14). The jackrabbit *Lepus californicus* warms its body in the early morning by exposing its large, highly vascularised ears perpendicular to the sun’s rays, using them as a form of solar collector. Similarly, it cools at midday by keeping in the shade and putting the ears parallel to the incoming solar radiation, thus minimizing exposure while keeping the same radiative surface.

Figure 1.14: The African grand squirrel



Using its tail like a parasol, the African ground squirrel (*Xerus inauris*) protects itself from the sun in the Namib Desert.

Source: Patricio Robles-Gil

Figure 1.15: Ostriches in the Namib



Despite the gruelling heat and extreme drought, a family of ostriches (*Struthio camelus*) survives and thrives in the Namib Desert.

Source: Patricio Robles-Gil

Morphological and anatomical adaptations

In mammals, desert fur coats are short, hard and compact, but at the same time well-ventilated, to allow sweat to evaporate directly from the skin. Birds, in addition, can fluff or compact their feathers to regulate heat exchange. In the ostrich, a desert dweller, the uncovered head, throat, legs and abdomen allow for radiation and convection cooling, while the feathers on the back protect the larger part of the body from direct solar radiation (Figure 1.15). Bipedalism, a common trait in small desert mammals such as kangaroo rats, allows for fast travel in open spaces and also keeps the body separated from the extreme temperatures of the ground surface. Indeed, bipedal desert rodents use open microhabitats much more frequently than their quadrupedal relatives, who restrict their activities to sheltered habitats.

Sand-dwellers have evolved several traits that allow them to survive in dunes, including fleshy foot-pads in camels, scaly fingers in certain lizards and digital membranes in some geckoes. Additionally, camels have long dense lashes that protect their eyes and they can close their nostrils to protect them from wind-blown dust. Many snakes have upwardly-turned nostrils that allow them to burrow rapidly in loose sand; others are flat and can bury laterally. Many other reptiles also show adaptations that protect their eyes, nose, and ears from sand

and dust, and many insects have specially-adapted legs that allow them to bury themselves rapidly and to walk efficiently on hot sand.

Physiological adaptations

The most basic physiological problem of desert animals is to maintain their water balance by maximizing water intake and/or minimizing water loss. In deserts, free-standing water is scarce, found only in isolated oases and reservoirs. Camels and wild asses, for example, can drink large quantities of water in a very short time causing a dramatic dilution of the bloodstream, sufficient to cause death in other animals. In coastal deserts, animals obtain water by licking fog-drenched rocks. Desert amphibians can absorb water through the skin from humid underground dens by accumulating urea in their blood and raising its osmotic pressure.

Most herbivores, like eland and oryx, obtain water from the foliage of the shrubs that compose their diet, often feeding at night when the plants are turgid. Some succulent plants have high salt contents, toxic compounds, or spines that deter their consumption. Herbivores, however, have found their way around these obstacles: some reptiles and birds have developed efficient salt-excreting glands, and many mammals have kidneys that can cope with salty water. White-throated packrats (*Neotoma albigula*), which feed almost exclusively on juicy cacti, have metabolic adaptations to prevent poisoning from the oxalates contained in these plants.

Animals lose water through urine, faeces, respiration, and transpiration. Desert rodents have kidneys that are capable of producing highly concentrated urine, with an electrolyte concentration many times higher than that of blood plasma. Reptiles, birds and insects excrete uric acid, which requires less water, and sometimes complement the excretion process with specialized excretion from salt glands. Amphibians produce little urine, and can store large amounts of urea within their bodies, drastically reducing water loss. In droughts, some rodents can produce dry faeces, efficiently reabsorbing liquids in the rectum.

Metabolism produces CO₂ and water as by-products of respiration. In most animals, this

metabolic water is exhaled through the lungs, but many desert animals, including invertebrates, reptiles, and mammals, possess physiological and anatomical adaptations to reduce respiratory water loss, including modifications in the morphology of the nasal passages and the capacity to reabsorb water along the respiratory tract. One of the most extreme examples of this is given by the kangaroo rat (*Dipodomys*), which can survive on a diet of perfectly dry seeds.

In addition to the mechanisms that reduce water loss, many desert animals are extremely tolerant to dehydration, a condition that causes a fatal increase in blood viscosity in non-desert dwellers. In order to achieve this, camels, for example, are able to lose water selectively from tissues other than blood. In contrast, desert amphibians are tolerant to increased fluid viscosity, and some reptiles can excrete excess electrolytes through urine and salt glands, avoiding the thickening of the blood as they dehydrate. A problem related to dehydration is that of temperature regulation. In smaller animals the high surface area-to-body volume ratio makes sweating a dangerous enterprise and panting is the most common method of cooling. Even larger animals that usually sweat, like the oryx, begin to pant when their body temperature exceeds 41°C.

Nocturnal hypothermia, exhibited by some large mammals like the eland, allows them to reduce their metabolic rate and to exhale air with less humidity during the night. Diurnal hyperthermia allows animals to reach body temperatures that would be normally lethal for non-desert vertebrates and to save on water needed to prevent overheating. Camels and elands, for example, can reach body temperatures of 44°C with no harmful consequences, and save as much as 5–10 litres of water during extremely hot days. Hyperthermal species have a special disposition of veins and arteries that allows their brains to remain at a temperature lower than that of the overheated body.

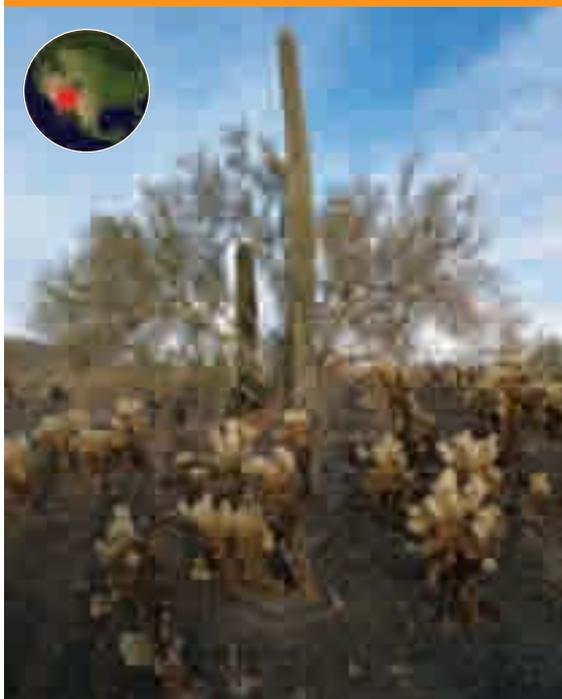
Like ephemeral plants, many smaller desert animals can also evade drought by entering into a dormant phase: desert butterflies and grasshoppers thrive in huge numbers when

conditions are good and survive dry spells in the form of eggs or pupae. Spade-foot toads (*Scaphiopus*) spend most of their lifetime buried in dry mud and become active only after rains refill their ephemeral pools. Many other organisms go into some form of torpor during dry periods.

INTERACTIONS BETWEEN SPECIES

The harsh conditions of desert ecosystems has promoted the evolution of a complex set of relations among desert organisms, a surprising number of which are positive interactions (Cloudsley-Thompson 1996). Desert shrubs in general and woody legumes in particular, create microhabitats that are critical for the survival of other species. Small animals seek the shade of desert trees and shrubs, birds find refuge and nesting sites in their canopies, and many small plants recruit their juveniles under the nitrogen-rich canopy of desert woody legumes such as acacias, carobs, and mesquites. Because of their crassulacean acid metabolism, desert succulents such as agaves, aloes, and cacti

Figure 1.16: Nurse plants



Giant saguaro cacti (*Carnegiea gigantea*) in the Pinacate mountains of the Sonoran Desert establish and grow under the protective shade of a palo verde (*Parkinsonia microphylla*), a legume species that generates true islands of fertility in the harsh desert environment.

Source: Patricio Robles-Gil

Figure 1.17: Seed dispersal



A Gambel's quail (*Callipepla gambelii*) forages on the ripe, red, juicy fruits of the saguaro. After digesting the sweet pulp it drops the seeds, often under the protective shade of nurse plants, where the cactus will be able to germinate and establish.

Source: Patricio Robles-Gil

are poor thermoregulators as young seedlings, and cannot survive the harsh ground-level midday temperatures. For this reason, they can successfully germinate and establish only under the protective shade of shrubby “nurse plants” that act as true cornerstone species in desert conservation (Figure 1.16). If the desert trees and shrubs are cut, all the accompanying biota soon disappears.

Additionally, many desert plants have very specific requirements in terms of their pollinators and seed dispersers (Figure 1.17). Although some desert ephemerals are truly unspecific in their requirements and produce thousands of seed with only wind-pollination, the slow-growing desert perennials are frequently highly specialized in their reproductive habits, and depend strictly on co-evolved animals to help them out in their sexual and reproductive processes. Many African cactoid plants (euphorbs and asclepias) produce foul-smelling flowers that attract carrion insects as pollinators. New World giant cacti and agaves produce sugar-rich nocturnal flowers that engage the pollinating services of nectar-feeding bats, while the sweet pulp of their fruits lures birds to disperse

the seeds miles away. The red tubular flowers of many desert shrubs attract hummingbirds and giant sphinx-moths.

HUMANS IN THE DESERT

“Co-evolution” is a term evolutionary theorists use to describe ecological intimacy, when the evolution of one organism is shaped by and in turn shapes the evolution of another (Ehrlich and others 1988). It is interesting to consider the evolutionary trajectories of desert biota and of human beings in that light. Relative to the time-scales of the geologic and atmospheric processes that created desert conditions, the advent of humans is a very recent event. Nonetheless, the effect of humans on deserts — and of deserts on humans — is pronounced.

Desert landscapes and desert biota have had profound effects on human cultural evolution. Humans display remarkable behavioral and cultural adaptations to the aridity and unpredictability of deserts, and traditions derived there have influenced human and biological communities far beyond the desert edge; that the three “religions of the book” had their origins in these environments well-illustrates that fact (see Chapter 2). Plants and animals from these harsh landscapes have also played an important role in the evolution of modern

human societies. Dryland biota provided much of the “raw material” for species that could and did become domesticated, which helped usher in the dawn of pastoral and agricultural societies. The early domestication of ungulates (cattle, sheep, and goats) began in the drylands of West Asia, on the edge of the Arabian Deserts, some 9 000 years ago (Davis 2005), and the domestication of llamas and alpacas took place in the Andean Puna of South America some 6 000 years ago just north of South America’s “arid diagonal” formed by the Atacama, Dry Puna, and Monte deserts (Table 1.3). In many regions of the world, dryland annuals have been at the base of the plant domestication process and drylands have been the cradle of agricultural societies. The first records of cultivated wheat and barley (two dryland ephemerals) come from the Fertile Crescent of West Asia some 7–9 000 years ago. In the American Continent the first agricultural records come from the Tehuacán Valley in southern Mexico, a hot tropical dryland where corn and squash (two annual, drought-tolerant fast growers) were first domesticated some 6 000 years ago. Not too long after that, gatherers in the Andean Puna started domesticating two other dryland ephemerals: the quinoa (*Chenopodium*, a fast-growing annual) and the potato (*Solanum*, a tuber ephemeral).

Table 1.3. Domestic mammals evolved from wild dryland ancestors

Domestic form		Wild progenitor		First domestication		Distribution of wild progenitor
Common	Scientific	Common	Scientific	Date	Place	
Perissodactyla						
Donkey	<i>Equus asinus</i>	African ass	<i>Equus africanus</i>	4000 BC	Egypt	North Africa, possibly West Asia
Artiodactyla						
Llama	<i>Lama lama</i>	Guanaco	<i>Lama guanicoe</i>	4000 BC	Peruvian Andes	South American drylands
Alpaca	<i>Lama pacos</i>	Guanaco	<i>Lama guanicoe</i>	4000 BC	Peruvian Andes	South American drylands
Dromedary	<i>Camelus dromedarius</i>	Dromedary	<i>Camelus</i> sp.	3000 BC	West Asia	Asia, possibly North Africa
Bactrian camel	<i>Camelus bactrianus</i>	Bactrian camel	<i>Camelus ferus</i>	3000 BC	Central Asia	Central Asia
Goat	<i>Capra hircus</i>	Wild goat	<i>Capra aegagrus</i>	7000–8000 BC	West Asia	West Asia
Sheep	<i>Ovis aries</i>	Mouflon	<i>Ovis orientalis</i>	7000–8000 BC	West Asia	West Asia

Source: FAO 2002

Box 1.1: Desert Soils — *It's not all the same out there!*

Old and young desert landscapes, landform/soil/hydrology interactions

Soil is the earth's living skin — the stuff from which plants grow, shelter for myriad animals and microorganisms, and the surface that partitions rainfall into run-off, “green” water held in the soil accessible to plants, and drainage to groundwater. Life, the atmosphere, surface and groundwater, soils and landforms have evolved together.

Soils are formed by climate, topography, and life acting on the parent material over time. They are not all the same; each individual soil shows a record of its development in the soil profile — seen in a vertical slice down from the surface. Because rain is rare in deserts, chemical weathering of the parent material and leaching of weathering products such as clay, lime and soluble salts hardly takes place; rather, evaporation drives the upward movement of water and dissolved salts which accumulate at, or close to, the surface.

Desert terrain determines the distribution of soil and water: in steep lands, erratic rains and erosion restrict the soil to a thin, patchy cover; light showers merely wet the surface and the water evaporates where it falls; rare torrents produce flash floods that carry water, mud and dissolved salts to footslopes and depressions.

Where soil and water accumulate, vegetation takes hold — generating organic matter that, in turn, sustains animals and microorganisms. Decomposition of organic matter produces CO₂ and organic acids that dissolve carbonate and silicate minerals. Materials in solution — soluble salts, gypsum, lime, silica, manganese, iron — may then be redistributed within the soil profile and in the landscape.

Time, as a soil-forming factor, denotes no absolute age but refers to the accumulated time in which soil formation could take place. Desert soils may be very old in years, but they usually show only weak signs of alteration of the soil parent material, because chemical weathering and biological activity are only spasmodic. Evidence of redistribution of sparingly soluble materials is generally more pronounced in the deserts of old continental shield areas than in younger formations. Thick, hard crusts of silcrete, lime and/or gypsum characteristic of old desert areas were once formed at some depth below the surface, but have been exposed by erosion; areas into which deserts have expanded in more recent times often preserve these relics of past wetter conditions.

Desert soils

The most extensive soils of deserts are the stony, rocky soils of the uplands, windblown sands, and other soils that have only surficial profile development. Although typical of true deserts, they are not strictly confined to deserts and may be found also in other drylands. These soils include *Leptosols* (Greek *leptos*, thin), which are shallow soils over hard rock, *Arenosols* (Latin *arena*, sand), developed in loose sand, and *Regosols* (Greek *reghos*, blanket), developed in other un lithified materials. They exhibit only a surface layer which, in deserts, is hardly different from the underlying parent material.

The most characteristic desert soils are those that exhibit significant accumulations of soluble salts: gypsum, calcium carbonate, or silica. These include *Solonchaks* (Russian *sol*, salt; *chak*, salty area), characterized by high levels of soluble salts which accumulate naturally in closed depressions; Solonetz (Russian *sol*, salt; *etz*, strongly expressed), highly alkaline, sodium rich soils which are very slippery when wet; *Gypsisols*, or gypsum soils; *Calcisols* (Latin *calcarius*, chalky or limy), characterized by accumulation of calcium carbonate, and *Durisols* (Latin *durus*, hard), showing a hard pan cemented by silica.

Accumulation of salts in desert soils affects plant growth in two ways: (1) the salts aggravate drought stress because electrolytes create an *osmotic potential* that opposes uptake of water by plants; (2) dissolved sodium depresses the uptake of potassium and calcium, and magnesium depresses potassium. Thus, the vegetation of *solonchaks* is highly specialized: several species — called halophytes or salt-plants — have evolved fleshy leaves with large vacuoles in their cells, where they



The desert topographic sequence clearly visible at the Laguna Salada in the Mexican Sonoran Desert. The upland mountains (a) discharge their run-off onto alluvial fans of the terraced foothills (b); downstream, the water flows in the bajada (c) coalescing into larger streams dotted by mesquite and other phreatophytes (plants that extract water from the deep aquifer), and finally the run-off and drainage water with all its accumulated salts arrives in the valley bottom playa (d), where it evaporates leaving the salts behind. Thus, the playa salt flat is fringed by a belt of halophytes, or salt-tolerating plants. Along these desert topographic sequences, there is an inverse texture effect as compared to wetter regions: soil texture becomes finer towards the valley bottom where the clay is transported by water. The hillslopes are rocky, the foothills are stony, the bajadas are formed by sand and loam, and the playas by clay.

Source: Google Earth image browser

dispose of the excess ions that are taken up by the roots, and characteristic red algae develop in the hypersaline substrates of the valley-bottom *playas*.

Dissolution of calcite (CaCO_3) and its subsequent precipitation in a deeper calcic (soft) or petrocalcic (hard) accumulation layer is controlled by (a) the CO_2 -pressure of the soil air and (b) the concentrations of dissolved ions in the soil water. The mechanism is straightforward: the partial pressure of CO_2 is high where root activity and respiration by soil microorganisms produce CO_2 , so calcite in the topsoil dissolves as Ca^{2+} and HCO_3^- ions which move down in percolating water. Evaporation of water and a decrease in CO_2 -pressure deeper in the soil (fewer roots and less soil organisms) cause saturation of the soil solution and precipitation of calcite. Calcite, like gypsum, does not precipitate evenly within the soil matrix; fissures, root channels and burrows that are connected with the outside air act as ventilation shafts in which the CO_2 -pressure is much less than in the soil matrix. When carbonate-rich soil water reaches such a channel, it loses CO_2 and calcite precipitates on the channel walls. Narrow channels become entirely filled with calcite *pseudomycelium*. Other characteristic forms of calcite accumulation are soft or hard *nodules*, *pendants* or *beards* below stones, and platy layers of hard calcrete.

Where is the water?

Landforms and soils, jointly, determine hydrology and, in turn, ecology.

Variations of soil and terrain from steep and rocky land to mobile dunes to fans and *playas*, with soils ranging from shallow patches of earth on hard rock to thick sand or clay, many with hard cemented layers close to the surface, some with a high concentration of salt at the surface — all determine the distribution and availability of water and footholds for life in deserts. The variety of life-forms and life strategies has evolved to exploit these specialist opportunities.

Rainfall in deserts can be heavy; it just happens infrequently. This means that plant cover is usually sparse so the rain batters an unprotected soil surface. Most of the soils yield rapid run-off — thin, rocky soils of the steeplands and thicker soils of footslopes slake on wetting and do not allow rapid infiltration. Run-off causes erosion; it quickly gathers as muddy torrents that carve steep *wadis* or *arroyos* in the uplands and, then, deposit fans of alluvium where they emerge on the footslopes. In tectonically active regions, these landforms are commonly disrupted; sections of fans and floodplain may be raised as terraces along the flanks of mountain chains, valleys are offset along fault lines. These features are very visible, because there is little vegetation to conceal them, and they remain fresh because erosion and deposition by water is infrequent.

Streams are short-lived. On gentler slopes, the water soaks into its own alluvium, maintaining a groundwater table that may appear at the surface in the lowest parts of the landscape as springs, oases and lakes. Where the water-table is close to the surface, evaporation drives the upward movement of water and, with it, dissolved salts that accumulate as a surface efflorescence, salt lakes and saline groundwater. Towards the centre of any landlocked basin, surface and groundwaters tend to become increasingly saline though they may be fed by rain and snowmelt on the surrounding mountains.

The patterns of soils and vegetation reflect this hydrological and salinity gradient:

Uplands: Shallow, patchy soils (Lithosols); may be desert or not desert, even fed by snowmelt; generate run-off and deep drainage to groundwater — both fresh. In desert, vegetation is very sparse because water does not remain long enough to be useful.

Terraces: Terraces, often formed by the accumulation of coarse rocks, are found at the foothills of the desert mountains. Older terraces carry more mature soils, maybe with subsoil layers of carbonate or gypsum accumulation (Calcisols or Gypsisols) that may impede water percolation; subject to erosional run-off. Where there is reasonably regular rainfall, the thicker topsoil may support steppe or thorn/cactus scrub.

Bajadas (coalescing alluvial fans that may bury lower terraces in fresh alluvium): Variation in soil texture depending on the force of water flow, finer materials deposited on gentler slopes furthest out across the fan; surface water soaks into the alluvium. Vegetation follows the more regular water courses and deep-rooted perennials may exploit shallow groundwater.

Marl plain or playas: *Lacustrine* flats beyond the toe of the fans; springs where the water-table intersects the surface, commonly upwelling of deep seepage from the surrounding uplands providing a rich habitat; evaporation concentrates the seepage leading to a salinity gradient extending across the plain; least-soluble salts crystallize first so there is a sequence of carbonates (Calcisols), sulphates (Gypsisols) and, finally, the very soluble chlorides (*Solonchak/Solonetz*); vegetation has to be increasingly specialized.

Box authors: David Dent and Paul Driessen

That biota of drylands would be a source of such innovation is not surprising, given the life history of those plants and animals. Arid-land herbivores, in particular desert ungulates, are extremely hardy. They can use water very efficiently, they can withstand long periods without drinking, and when forage is plentiful they can quickly convert plant material into animal protein with very high efficiency. Furthermore, many of them are migratory and move naturally in herds following a leader, looking for new foraging grounds, and socially protecting themselves from predators. For all these evolutionary reasons, ungulates native to drylands were ideal candidates for domestication: hardy animals, efficient foragers, and amenable to shepherding, as social aggregation is a natural behaviour for them. Some of the same factors that made wild goats, mountain sheep, or guanacos evolutionarily adapted to desert environments are what drove early hunter-gatherers to start breeding their offspring and selecting them for desirable domestic attributes. As with desert ungulates, the same traits that have made some desert annuals apt to survive and thrive on ephemeral water pulses are what make them so apt for agriculture: fast growth, short life cycle, and the capacity to direct most of their metabolic budget towards the abundant production of seeds. Because dryland ephemerals grow so fast and produce so much seed in just a few weeks, they grow at an amazingly fast rate when planted at the desert's edge and make ideal grain plants, especially cereals and pulses.

The effect of humans on the ecology and the evolutionary trajectory of deserts can be similarly pronounced. The following ecological “anachronism” provides an illustrative example: some desert plants have seed dispersal mechanisms that reflect the existence of seed dispersers that are no longer present. Trees like the mesquites (*Prosopis*), for example, have pods with nutritious sweep pulp and extremely tough seeds which need intense scarification in order to germinate. Similarly, the tough seeds of the prickly pears (*Platyopuntia*) germinate successfully only when chewed and digested for a long time. During the Pleistocene period, this abrasion was provided by the digestive system of large ungulates, such as gomphotheres or giant ground sloths. At the

end of the last glaciation some 15 000 years ago, however, much of that Pleistocene megafauna went extinct — a fate that humans likely contributed to (Alroy 2001, Brook and Bowman 2004). Loss of that fauna resulted in the loss of seed dispersal and regeneration mechanisms for a number of plant species. Desert plant species with anachronistic seed dispersal have merely survived for the last millennia through vegetative growth and accidental abrasion of seeds in the deserts' sand and gravel, in the absence of their effective seed dispersers. Not surprisingly, when humans reintroduced ungulates — cattle — into the New World some five centuries ago, the population of many of these plant species rebounded to large numbers.

Humans continue to affect desert ecology, at times fundamentally. Being areas of such low productivity, deserts can be easily degraded — even irreparably — by the increasing intensity of human land and resource use. Desert soils, which are of generally limited profundity and high fragility (see Box 1.1), are highly susceptible to compaction, erosion, and salinization when exploited for agricultural, industrial, or recreational purposes. Invasive non-native plants, whether introduced intentionally (such as in the case of the planting of grasses for livestock forage, which have the effect of introducing a grass-fire cycle to an ecosystem that has no natural fire regime) or not (such as the case of the invasion of *Tamarix ramosissima* in Nearctic deserts, which can substantially alter desert hydrological regimes), can have cascading effects on ecosystem function and native species viability in deserts. Human industry in and beyond deserts alters not only desert weather patterns via anthropogenic climate change, but also desert nutrient cycling via atmospheric deposition. Paradoxically, fertilization of deserts through increased deposition of nutrients like nitrogen can favour the invasive dispersal of non-native species and reduce native diversity. Whether through direct or indirect pathways, humans clearly have a hand in determining the future course of desert evolution.

CONCLUDING REMARKS

To the untrained eye, deserts look barren, especially during dry periods. However, because of their evolution in relative geographic isolation, most deserts of the world are rich in rare and

endemic species, and are hence highly vulnerable to biological extinction and environmental degradation. In spite of their remarkable convergence in adaptation, deserts are different in their origin and their evolutionary history. Their incredible variation of the world's deserts in rainfall patterns, continentality, temperature regime, and evolutionary history have all contributed not only to their biological uniqueness, but also to their wondrous wealth of life-forms and adaptations, from some of the shortest-lived ephemeral plants, to some of the longest-lived giant cacti; from seed-eating rodents that do not need water to survive and depend on their burrows to regulate their metabolism almost as if the burrow was an extended part of their body, to amazing pollinators like nectar-feeding bats that migrate thousands of miles following the flowering seasons (Davis 1998). This adaptive diversity — what Darwin, strongly influenced by deserts himself, called “forms most beautiful and most wonderful” — is what makes deserts unique. In the hot deserts we may find

giant cacti and trees with mammoth fleshy stems coexisting with some of the toughest hardwoods; ground-creeping succulents side by side with fog-harvesting rosettes, incredibly fast-growing annuals together with the hardiest drought-resistant perennials; shrubs of enticing odours with some of the nastiest, spiniest plants ever. Very few parts of the earth contain a richer collection of natural adaptations.

The fragmented evolutionary history of the deserts of the world has been the driving force of their biological rarity, of adaptation to local conditions, and of specialization to isolated environments. After millions of years in isolation, the forces of evolution and fragmentation have yielded unique life-forms in each desert, strangely-shaped desert plants and extraordinary animals. The world's deserts are biological and cultural islands, lands of fantasy and adventure, habitats of surprising, often bizarre growth-forms, and territories of immense natural beauty.

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