A tale of two deserts

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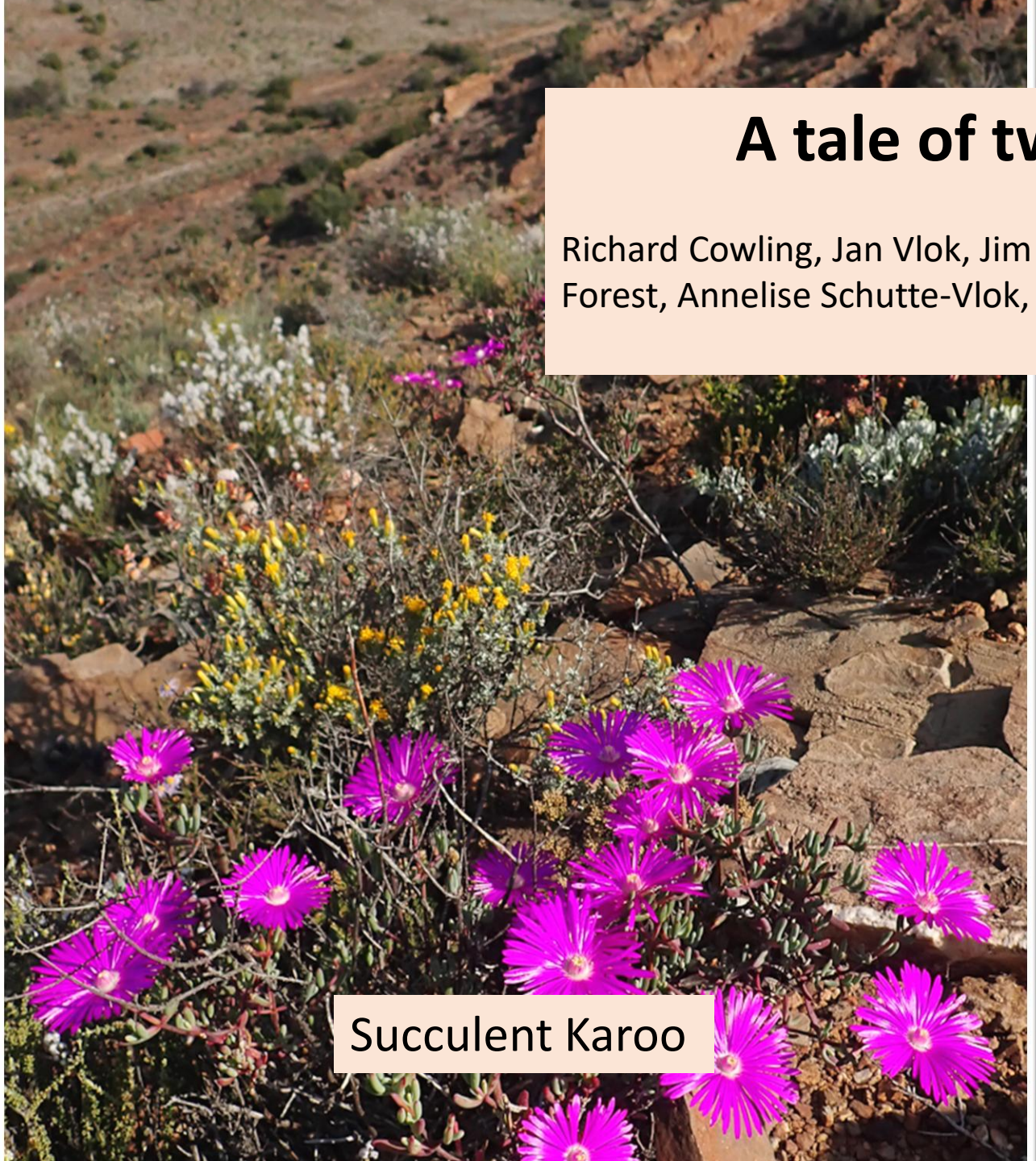


Vistas in the Succulent Karoo (top) and the Mojave Desert (bottom) show a striking similarity in appearance. However, this outward convergence belies the differences in these ecosystems – the stuff of evolution.

Introduction

Different parts of the world with similar climates and landscapes show strong similarities in plant growth forms and in the vegetation they occupy. This analogy of plant form and function occurs even though the floras from these distant regions have very different origins i.e. they are phylogenetically unrelated. Convergence theory predicts that similar selective regimes produce similar evolutionary outcomes in unrelated plants and animals and their associated ecosystems.

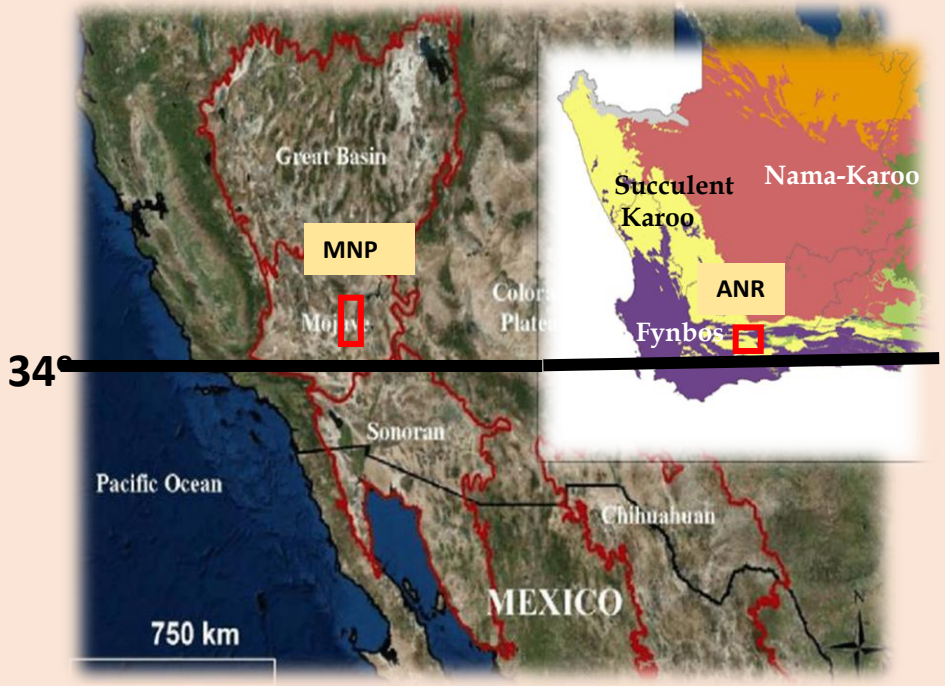
In this essay, we delve into the plant life of two warm temperate, desert regions: the Succulent Karoo of southern Africa and the Mojave Desert of North America. In both deserts, most rain falls in the cooler months, winters are cool, summers are hot, and the topography is rugged. Given the similar selective regimes of the two deserts, convergence theory predicts similarities in their plant forms, functions and the ecological and evolutionary processes that underpin them. The theory further predicts similar species diversities and growth forms, and similar patterns of diversification within shared plant forms.

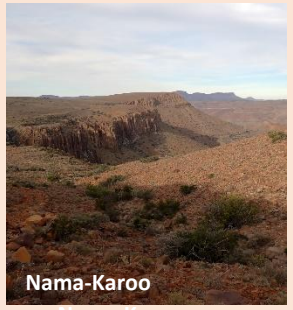
From a distance, Succulent Karoo and Mojave landscapes do, indeed, look similar. Wide vistas of plain and mountain covered sparsely by hardy shrubs. However, closer inspection reveals intriguing differences, for example the low diversity of annuals and high diversity of geophytes in the Succulent Karoo, while the opposite holds for the Mojave.

Confronting these non-convergences makes us think long and hard about the more subtle differences in the ecologies (or selective regimes) of the two deserts, both now and in the past. Such attention helps us to untangle the role of ecology and environmental history in governing diversity in more interesting ways than comparisons across biomes.

Our essay unfolds as follows: first we look at the selective regime of the two deserts, namely geography, landforms and climates; then we describe their vegetation; next we illustrate examples of the five major plants forms of both deserts, namely herbs, geophytes, succulents, shrubs and trees. Throughout the essay we allude to similarities and differences in the two deserts of their growth form mix, and explain these in terms of differences in climate and soils. Finally, we discuss our findings in terms of the predictions of convergence theory.

Desert endemics. Top: *Freesia speciosa* endemic to the SE Succulent Karoo. Bottom: *Phacelia calthifolia*, endemic to the NE Mojave.





Biogeographical context

The Succulent Karoo and Mojave Desert are found at similar latitude in the southwestern parts of Africa and North America, respectively. Both are warm-temperate deserts with predominantly winter rainfall. At 116 000 km^2, the Succulent Karoo covers a slightly smaller area than the Mojave Desert 's 135 000 km^2.

To the east and the north, the Succulent Karoo abuts the Nama-Karoo biome, a warm-temperate, grassy desert that occupies the dry, western part of the Highveld Plateau. Here most rain falls in the warmer months and heavy frosts occur in winter. To the south and the southwest, Succulent Karoo borders on the fire-driven Fynbos biome, usually abruptly with the transition to infertile sands derived from Cape quartzites, but more gradually on shale-derived soils. In the southeast, it grades, along with increasing summer rainfall, into the Subtropical Thicket biome, characterised by tree succulents and spiny, evergreen shrubs of tropical affinity.

The Mojave Desert is geographically transitional between the lower-lying, subtropical Sonoran Desert – with its charismatic tree cacti - to the south, and the higher-lying, cold-temperate Great Basin desert to the north. The latter receives most of its precipitation as winter snow; there in no equivalent of the Great Basin desert in southern Africa where altitudes in desert areas seldom exceed 1 800 m. The western part of the Sonoran Desert receives most of its rain in winter, grading eastward into a bimodal (summer and winter) regime. West of the Mojave lies the fire-driven Chaparral biome.

Thus, both deserts are transitional between warmer and cooler deserts, both border on subtropical deserts, and both abut fire-prone Mediterranean-climate ecosystems. However, only the Mojave grades into a cold-temperate flora, which extends over vast areas of North America and beyond.

Another important difference is the degree of continental influence in the two deserts. While the Mojave forms part of a huge land mass extending northwards to polar climes, the Succulent Karoo occupies a subcontinent bounded on three sides by ocean. Thus, given similar altitude, the Mojave has greater temperature extremes than the more oceanic Succulent Karoo.

The Succulent Karoo and Fynbos biomes correspond to the Greater Cape Floristic Region, which is the richest centre of plant diversity and endemism outside of the tropics. Succulent Karoo floras are the richest desert floras globally.

Phytogeographically, the Mojave Desert is considered part of the Madrean Floristic Region which occupies arid or semiarid areas in the southwestern United States and northwestern Mexico. It includes the California Floristic Province, a globally recognized hot spot of diversity.

In the remainder of this essay we will focus on two areas of the deserts well known to us, with broadly matching physiographies and climates. These are the Anysberg Nature Reserve (ANR) in the western Klein Karoo in the and the Mojave National Preserve (MNP) in the south-eastern Mojave Desert.

Physiography and land forms

The Anysberg Nature Reserve (ANR) is embedded in the Cape Folded Belt, a massive sandwich of sediments violently folded some 280-215 million years ago. The Cape mountains were then buried under Mesozoic sediments, and re-emerged and deeply dissected after the breakup of Gondwana in the Cretaceous, starting 140 million years ago. Thereafter, more than a hundred million years of tectonic stability produced a vast peneplain (the African surface) that extends into south central Africa. Uplift in the Mio-Pliocene scoured out the sediment-filled Cretaceous canyons and dissected the African surface to create the scenery we see today: parallel, east-west trending fold mountains comprised of erosion resistant quartzitic sandstones, alternating with softer shales that form the intermontane valleys.

Overall, topography is much more subdued in the ANR (as well as elsewhere in the Succulent Karoo) than in the Mojave National Preserve (MNP), but the former has older and more finely dissected landscapes. Mountains in this part of the Klein Karoo reach heights of about 1500 m and the valley floors and plains range between 400-800 m. In these lowlands, where desert vegetation prevails, shale ridges are replaced downslope by rocky colluvial fans, and below them, the walls of shallow valleys which merge into alluvial, saline bottomlands. Except for the alluvium, all soils are shallow, clay-rich and rocky.

Landscapes of the Anysberg Nature Reserve showing (top) view southwards from Anysberg range showing quartzites of the Cape Folded Belt. The flat-topped surfaces of the gently sloping plain in the background represent remnants of the African surface, which has been incised by Mio-Pliocene uplift, producing rocky colluvial fans, steep valley walls and alluvial bottomlands. The bottom photo shows the northern slopes of the Anysberg range (1500 m) in the background and a remnant African surface (800 m) in the foreground. Note the canyons incised into the erosion resistant quartzites, a legacy of the fragmentation of Gondwana.

The Mojave National Preserve (MNP), like the rest of the Mojave Desert, forms part of the Basin and Range geomorphic province of western North America's Great Basin. Located in a tectonically active region where land masses are shearing apart, Basin and Range topography is relatively young. Rifting, which started about 30 million years ago, has reduced crust thickness below the Mojave Desert to the lowest globally, resulting in a high tectonic instability. Indeed, mountain building and rifting continues today. Consequently, mostly igneous rocks make up the Mojave's impressive mountain ranges, some of which exceed 3500 m in elevation.

The topography of the MNP comprises north-south trending mountain, alternating with internally drained basins. Mountains reach heights of over 2000 m while bottomlands range between 800 and 1000m. Large interconnected and coarsely-grained alluvial fans (bahadas) flank the mountains, merging into plains with finer-grained soils and finally draining into seasonally wetted playas or pans. Wind blown sand derived from these playas form impressive dunes in the southwest of the MNP. The mountains have rocky, shallow soils; elsewhere, soils are mostly deep with decreasing grain size downslope.

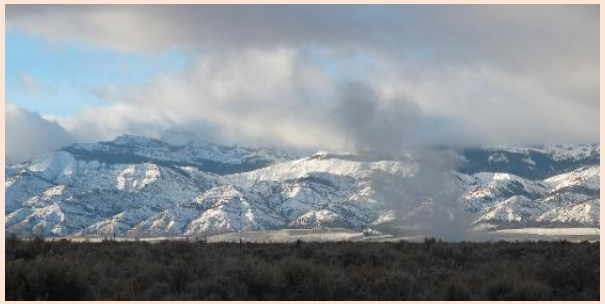
Typical Mojave Desert scenery (top) showing coalesced alluvial fans (bahadas), plains and a playa in the distance. The bottom photo shows a similar sequence in the Mojave National Preserve, but with the magnificent Kelso dunes. The snow-covered mountains in the far distance near Death Valley, exceed 3000m in altitude.

Climate present and past

Our focus here is on the desert climates of the Anysberg Nature Reserve (ANR) and Mojave National Preserve (MNP), since it is these landscapes that harbour desert vegetation. Montane climates are considerably wetter and cooler than the lowland ones.

Both regions are rain shadow deserts: mountains intercept much of the rain that comes with the westerly fronts that strike land in the cooler months, or with moist, tropical air that arrives in the warmer months. Annual rainfall is slightly higher in the ANR (167-363 mm) than the MNP (72-387 mm).

Both areas have bimodal rainfall regimes; however, each has a different periodicity. In the ANR, rainfall peaks in autumn and winter whereas the MNP shows a pronounced mid-summer and a lesser winter peak. The proportion of rain falling in the cool season (Apr-Sep/Oct-Mar) and the warm season (Oct-Mar/Apr-Sep) is similar for both deserts (ca 55% vs ca 45%). In every month of the year, the reliability of rainfall in the MNP is lower than in the ANR, but especially so in winter when rainfall reliability is two to three times lower in the MNP. Warm-season rainfall is also less reliable in the MNP than the ANR, probably because it is largely associated with a few, intense thundershowers, whereas in the ANR, much of the rainfall at this time falls in gentle showers associated with post-frontal events in the Indian Ocean; by comparison, thundershowers are rare.



Temperatures in the MNP are more extreme than in the ANR, and indeed elsewhere in the Succulent Karoo. Temperatures frequently fall below zero during winter and early spring in the MNP, but not so for the ANR. The mean minimum of the coldest month for the latter region is 4°C, and for the former it is 0°C. MNP summers also experience more extreme temperatures: mean midsummer minima (12-15°C) are about 7°C cooler and maxima (34-37°C) are about 5°C warmer in the MNP than ANR. Extreme maxima in the MNP can reach 43°C whereas in the ANR these seldom exceed 30°C. Overall, the ARN experience a milder and more predictable climate than the MNP.

The glacial climates that prevailed over the past million years or so, were much colder and wetter in the Mojave than the Succulent Karoo. Under these conditions, Mojave desert vegetation was replaced by Great Basin vegetation, comprising piñon (*Pinus osteosperma*), Utah juniper (*Juniperus osteosperma),* bitterbush (*Purshia mexicana*) and mountain mahogany (*Cercocarpus ledifolius*). The now barren playas were transformed into impressive lakes and desert vegetation retreated to steep equatorward slopes and the lower reaches of the Colorado valley.

In the Succulent Karoo, glacial climates were only slightly cooler than at present and the proportion and amount of winter rainfall did not fluctuate widely. Thus, desert vegetation was not banished to refugia, but persisted over much of its present range, albeit with shifts in species distributions, throughout the Pleistocene.

Top: Cape mountains impeding the penetration of moist frontal rain into the Klein Karoo. Middle: A rare summer thunderstorm in the ANR. Bottom: Snow-clad mountains in the Mojave.

Floristic features

The desert vegetation of the Anysberg Nature Reserve (ANR) i.e., excluding the fynbos of the Anysberg mountain) support 753 species, 58% of which are endemic to semi-arid vegetation of the Greater Cape Floristic Region and 21% endemic to the Succulent Karoo part of it. Eleven species are endemic to the ANR.

The five largest largest families are the Asteraceae (151 spp), Aizoaceae (124 spp), Crassulaceae (43 spp), Scrophulariaceae (36 spp) and Hyacinthaceae (34 spp). The five largest genera are *Crassula* (Crassulaceae) (33 spp), *Hermannia* (Malvaceae) (22 spp), *Mesembryanthemum* (Aizoaceae)(20 spp), *Pteronia* (Asteraceae) (20 spp) and *Asparagus* (Asparagaceae) (14 spp).

Uniquely for warm deserts, succulent shrubs comprise 26%, and geophytes 15% of the ANR desert flora. Perennial herbs constitute 12% of the flora, while non-succulent shrubs, 60% of which are low in stature (>1m), comprise 36% of the flora. Trees, at 2%, are poorly represented. Also uniquely for deserts is the low proportion of annuals, which - at 7% - is almost seven times fewer than found in the Mojave, where this plant form has massively diversified.

Desert vegetation of the Mojave National Preserve (MNP) has 687species of plants, 64% of which are endemic to the Madrean Floristic Region and 8% endemic to desert vegetation of the southwest. Four species are endemic to the MNP.

Unique for warm deserts, geophytes and succulent shrubs together comprise more than half the Succulent Karoo flora. Shown at the top is the dwarf succulent *Gibbaeum heathii*, a species endemic to quartz patches in the Anysberg Nature Reserve. Bottom is a spring bloom of Mojave annuals comprising species of *Papaver, Phacelia and Mentzelia.*

The five largest families are Asteraceae (120 spp), Poaceae (61 spp), Fabaceae (36 spp), Boraginaceae (34 spp) and Polemoniaceae (28 spp). While the first three families are common in warm deserts worldwide, the last two families are essentially Boreal in distribution and are centred in the western North America. The largest genera are *Phacelia* (Hydrophyllaceae) (18 spp), *Eriogonum* (Polygonaceae) (17 spp), *Gilia* (Polemoniaceae) (16 spp), *Mentzelia* (Loasaceae) (13 spp) and *Cryptantha* (Boraginaceae) (11 spp).

The two deserts share 36 families and 17 genera. However, even in large shared families (Asteraceae, Fabaceae and Poaceae) most of the component species in each desert are associated with distantly related lineages. Furthermore, for many shared families there is a clear asymmetry in species number, e.g. Crassulaceae and Aizoaceae hugely overrepresented in the ANR and Boraginaceae underrepresented there.

Unlike the Succulent Karoo, a massive 75% of the MNP flora comprises herbaceous species of which most (86%) are annuals. Only 4% of species are succulents and a mere 2% (15 spp) are geophytes. Shrubs, most of which are tall (>1m), comprise about 18% of the flora and trees 3%.

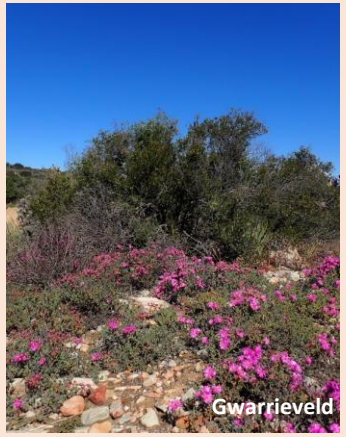
The life form spectrum of the MNP is similar to that recorded in the winter-rainfall desert of Israel where ca 50% of species are annuals and only 8% are geophytes. The ANR and the MNP differ from this desert in the relatively high incidence succulent species, although the large proportion of low, leaf-succulent shrubs is a unique feature of Succulent Karoo floras, as is the diversity of non-succulent shrubs.

Anysberg desert vegetation


Ranteveld


Apronveld

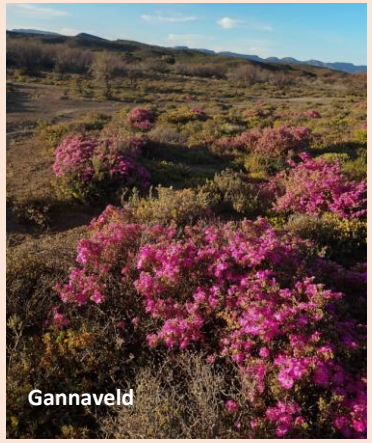

Quartz apronveld


Gwarrieveld


Scholtzbosveld

Note that all vegetation type descriptions list only dominant shrubs. Ranteveld is found on ridges of shale bedrock. Despite the harshness of the environment, these habitats are home to numerous dwarf succulents. Dominant species are *Berkheya cuneata, Eriocephalus ericoides, Chrysocoma ciliata* and *Hereroa gracilis.* Apronveld occupies the colluvial fans that accumulate on hillslopes. It includes Quartz apronveld, which is associated with weathered quartz veins and is home to a diverse dwarf succulent flora. Dominant species in Apronveld include *Eriocephalus* spp, *Berkheya* spp., *Hirpicium alienatum* and *Pteronia* spp. Gwarrieveld, which is found on rocky valley sides and mountain foothills, is characterised by the widespread abundance of *Euclea undulata* (gwarrie), a low, multistemmed tree of tropical affinity. Other dominant species include *Nymania capensis, Pteronia* spp and *Crassula* spp. Scholzbosveld, which grows on flat-topped hills where a shallow, loamy soil overlies calcrete, is dominated by *Pteronia pallens* (scholtzbos); subdominant shrubs include *Berkheya spinosa, Pentzia incana* and *Ruschia spinosa.*


Kalkveld


Gannaveld


Quartz gannaveld


Riparian woodland

Kalkveld, which is restricted to calcrete bedrock and is largely confined to the ANR, comprise a sparse shrubland with many by dwarf species, mostly succulents, including several local endemics. Dominant species include *Pteronia incana, Eriocephalus ericoides, Pentzia sphaerocephala* and *Ruschia* spp. Gannaveld occupies the deep, alluvial and saline soils of flood plains in the ANR. Despite the uniform habitat and high salt content of the soils, Gannaveld is rich in species. Included in this types is Quartz gannaveld, where weathered quartz is associated with hypersaline soils, and a highly adapted flora of dwarf, succulent shrubs. Dominant species in zonal Gannaveld include *Salsola aphylla, Eriocephalus* spp, *Mesembryanthemum* spp and *Drosanthemum* spp. Riparian woodland fringes the water courses in the ANR and elsewhere in the Klein Karoo. Dominant trees are *Vachellia karroo* and *Searsia lancea.*

Mojave desert vegetation


Creosote bush scrub


Mixed succulent scrub


Grassland savannah

Creosote bush scrub occupies the lower reaches (300-800 m in elevation) of the MNP where it grows in deep, gravelly sand on flats and gentle slopes. Most of the 80 – 160 mm of annual rain falls in winter. Co-dominant shrubs are creosote bush (*Larrea tridentata*) and *Ambrosia dumosa.* Other common species include *A. salsola, Encelia farinosa* and *Senna armata.*

Mixed succulent scrub grows at higher elevations (800-1600 m) with higher rainfall (100-200 mm) than Creosote bush scrub. Topography is also more rugged, and soils rockier. The vegetation is structurally diverse and lacking in dominance. Succulents are more diverse and abundant here than in any other vegetation type in the MNP. Most species are Cactaceae (species of *Cylindropuntia, Opuntia*, *Ferocactus*, *Echinocereus*). Common shrubs include *Yucca shidigera, Y. jaegeriana, Coleogyne ramosissima, Larrea tridentata* and *Cylindropuntia acanthocarpa.*

Grassland savannah, ranging from 800 to 1600 m in elevation in the northeastern part of the MNP, receives more of its 160-220 mm annual rainfall in summer than the rest of the Preserve. While rock type and topography vary greatly, soils are often more clay-enriched. Vegetation comprises a dense cover of perennial C4 grasses, including species of *Bouteloua, Hilaria* and *Stipa.* The open canopy of tall shrubs is dominated by species of *Juniperus* and *Yucca.*

Sand ramps and dunes, a habitat not found in the ANP, comprise about 10% of the MNP where they occur in the northwest, at elevations of 300-900 m. Almost all of the annual rainfall of 80-130 mm falls in winter. Typical perennial grasses include *Hilaria rigida, Stipa hymenoides* and *Panicum urvilleanum.* Prominent shrubs growing on more stabilized dunes include *Croton californicus, Petalonyx thurberi, Larrea tridentata* and *Prosopis glandulosa.* Some 70% of the flora comprise annuals of which 20 species are confined to the Mojave dunes habitats.

Wetlands, while concentrated in bottomlands, range up to 1500 m in elevation as springs and riparian corridors. The playa lake basins are seasonally wet bottomlands dominated by saltbush scrub, a sparse shrubland of low species richness, comprised of largely halophytes, several in the genus *Atriplex.* Playa margins support perennial grasses, sedges and rushes, including four species of *Juncus.* Numerous springs and riparian corridors throughout the MNP support high diversity wetlands species iincluding several rare species. Riparian zones, including canyon drainages and washes, may have well developed woodlands comprised of *Populus fremontii, Salix gooddingii, S. exigua* and *Chilopsis linearis*, a much richer flora of woody riparian species than that of the ANR.


Sand ramp


Wetlands

The desert vegetation of the MNP grows on deeper, less rocky soils and extends to higher elevations than the ANP. However, the ANP supports a greater diversity of desert vegetation types than the MNP, possibly a consequence of its higher meso-scale ecological heterogeneity, a legacy of its older, more dissected landscapes. Only Mixed succulent scrub among the MNP desert types resembles the vegetation of the ANR, with its higher cover and diversity of succulents, relatively low stature, and lack of shrub dominance. Wetland vegetation in the MNP is more diverse in habitats and species than in the ANR, a consequence of the Basin and Range topography of the Mojave, and consequent internal drainage patterns.

Non-desert vegetation

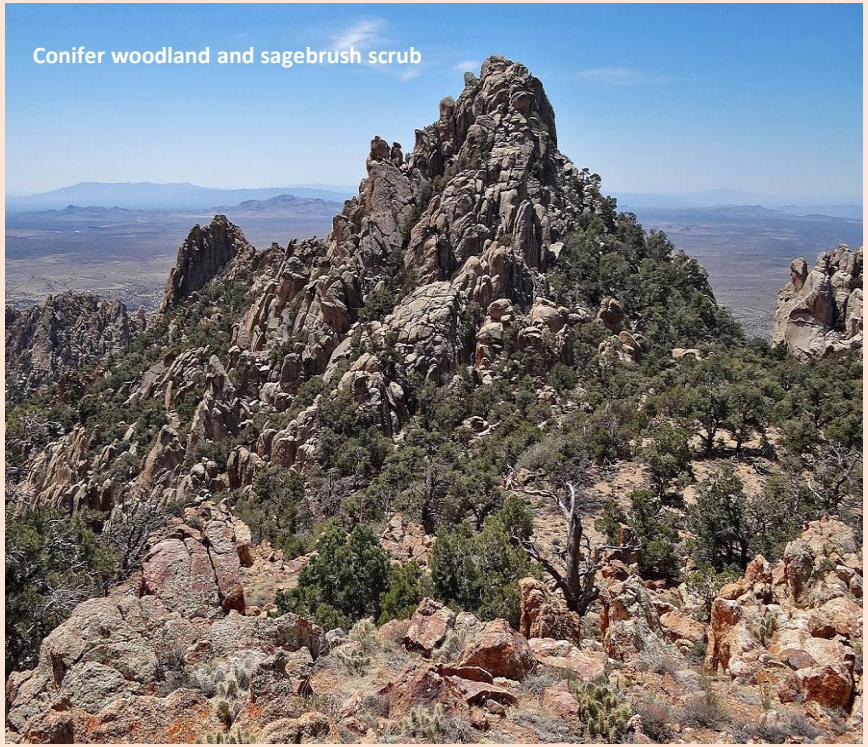

Fynbos

The MNP differs from the ANR in that desert vegetation extends into mountainous terrain, up to elevations of 1500 m. In the ANR, it is the quartzitic sandstone geology that determines the abrupt change from Succulent Karoo to Fynbos biome vegetation, even at rainfall amounts that support karoo on the adjacent shale substrate. Fynbos is a fire-loving and species-rich shrubland and comprises the richest flora in the Greater Cape Floristic Region. In the ANR, is contributes 45% of species to the park's tally, while occupying just 16% of its area. Fynbos, comprising three vegetation types (Mesic Proteoid, Arid Proteoid and Arid Asteraceous) extends from the sandstone-shale interface at the base of the Anysberg, to its highest peaks at ca. 1400 m. Annual rainfall varies from 200 mm on the lower slopes to 300 mm on the higher slopes. Topography is rugged and rocky; soils are skeletal and nutrient poor. The richest families in ANR fynbos are Ericaceae (45 spp., all in *Erica*), Restionaceae (44 spp.) and Proteaceae (24 spp.). Eight species are endemic to the Anysberg mountain.


Erica plukenetii


Protea laurifolia

In the MNP, the transition to non-desert vegetation occurs at about 1600 m, with the appearance of Conifer woodland and sagebrush scrub which extends up to the highest peaks at about 2400 m. This highly diverse vegetation complex is associated with complex topography and geology and receives an annual rainfall 200-280 mm and regular winter snow. The woodlands are dominated by shrubby trees of *Pinus, Juniperus, Quercus* spp. and large shrubs such as *Cerocarpus intricatus, Ribes* spp., *Yucca baccata* and *Arctostaphylos* spp. *Artemisia* spp dominate Sagebrush scrub, often accompanied by *Ericameria nauseosa, Purshia stansburyana, Chrysothamnus viscidiflorus*, and many others. With over 100 species of conservation status as rare and endangered, the combination of geographic isolation and unique soils in this vegetation type supports high levels of endemism and rarity unparalleled elsewhere in the California Mojave.

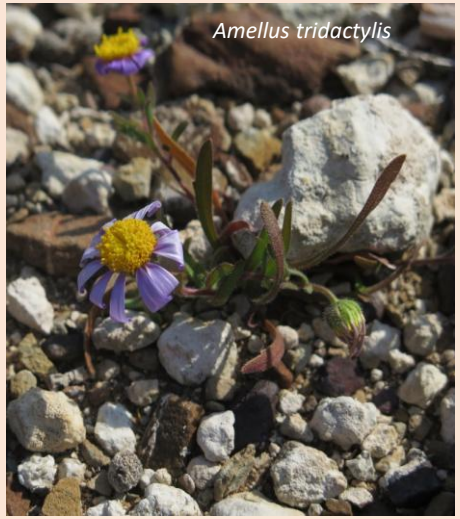

Conifer woodland and sagebrush scrub


Arctostaphylos pungens


Penstemon palmeri


Juniperus osteospema

Anysberg herbaceous flora


Amellus tridactylis

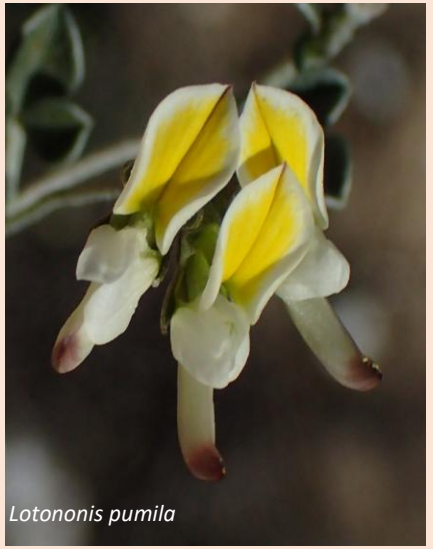

Arctotis sp nov


Mesembryathemum stenandrum


Dianthus bicolor


Gazania lichtensteinii


Mesembryathemum subtruncatum


Lotononis pumila

The herb flora (excluding geophytes and graminoids) of the ANR comprises 120 species of which annuals make up 53%. By contrast, the MNP supports 439 herbaceous species of which 74% are annuals, five times richer than the annual flora of the ANR. In both deserts, daisies (Asteraceae) dominate the herbaceous floras, but the lineages on each continent are unrelated: ANR genera are centred in southern Africa and MNP genera in North America. Several herbaceous daisies from the ANR are perennials, persisting through the dry summer as buried, fleshy rhizomes (e.g. *Gazania* spp.). A distinctive feature of the ANR herb flora is the abundance of succulent annuals and weak perennials in the Aizoiaceae, most being species of *Mesembryanthemum*. Brassicaceae (*Heliophila*) and Scrophulariaceae (*Diascea, Nemesia*) contribute importantly to the annual flora but Fabaceae (e.g. *Lotonis pumila)* are poorly represented), unlike in the MNP where annual lineages of *Lupinus* and *Atragalus* are richly diversified. All ANR annuals are winter growers.

Mojave herbaceous flora

Two spreads are required to showpiece this diverse flora. Note that in the caption below some species noted there are shown in the overleaf spread.


Mojavea confertifolia


Amsinckia tessellat


Diplacus rupicola


Abronia villosa


Eschscholzia glyptosperma


Psathyrotes annua


Oenothera deltoides


Mentzelia laevicaulis


Lupinus arizonicus


Phacelia distans

The diverse herbaceous flora of the MNP is its most remarkable feature. A rare superbloom – the synchronous flowering *en masse* of spring annuals – is spectacle of extraordinary beauty. Ninety per cent of the MNP annual flora is winter growing, but at 33 species, the summer annual flora is significant. In addition to a rich daisy flora (e,g, *Psothyrates annua, Enceliopsis nudicaulis, Monoptilon belliodes* and *Pectis papposa* – a summer annual), MNP annuals are found in another 16 families, many of them absent from the ANR and the rest of Sub-Saharan Africa.

The intriguing *Mohavea confertifolia* as well as many species of *Penstemon* are members of the Plantaginaceae. Other families rich in annuals are Boraginanceae (*Amsinckia tessellata*), Phrymaceae (*Diplacus rupicola*), Nyctaginaceae (*Ambrosia villosa*), Papaveraceae (*Eschscholzia glyptosperma*), Onograceae (*Oenethera deltioides* – a perennial on dunes), Loasaceae (*Mentzelia laevicaulis*), Fabaceae (*Lupinus arizonicus, Astragalus phoenix*), Hydrophyllaceae (*Phacelia distans*), Brassicaceae (*Physaria tenella, Dithyrea californicai*), Polemoniaceae (*Loeseliastrum matthewsii*) and Orobanchaceae (*Catillja exerta*).


Pectis papposa


Physaria tenella


Astragalus phoenix


Loeseliastrum matthewsii

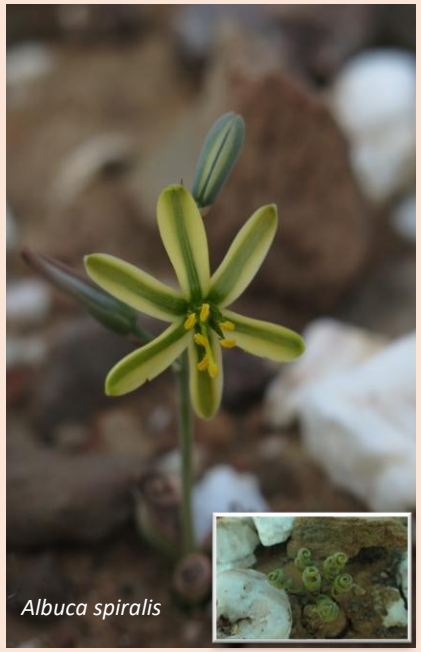

Catillja exerta


Dithyrea californicai


Monoptilon belliodes

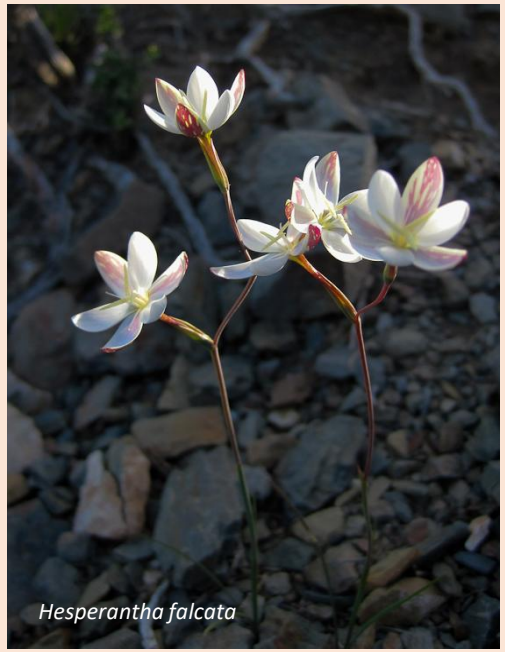

Enceliopsis nudicaulis

The high diversity and endemism of annuals in the warm desert and chaparral biomes of southwestern North America is a floristic phenomenon of global significance. Indeed, much of the diversity of these biomes is associated with their herbaceous floras. The large number of infraspecific taxa in the regions – and notably in the Mojave Desert – is suggestive that speciation is recent and ongoing. It seems reasonable to speculate that rapid climate change since the onset of the Holocene some 12 000 years ago, is the stimulus underpinning this impressive diversification.


Albuca spiralis


Oxalis obtusa


Lachenalia obscura


Hesperantha falcata


Ferraria crispa


Ornithoglossum viride


Tritonia pallida


Babiana cuneata


Tritonia securigera ssp watermeyeri

Anysberg geophytes

The Greater Cape Floristic Region in which the ANR is embedded, has the richest geophyte flora globally, comprising about 2100 species, 84% of which are endemic. Geophytes are perennial herbs with below-ground storage organs.

The ANR is home to 113 species of geophyte amounting to 15%. These are distributed across many families, but notably Hyacinthaceae, Iridaceae and Asphodelaceae. Most geophytes are spring flowering but several lineages – mainly Amaryllidaceae and some species of *Eriospermum* (Ruscaceae) – flower in the warm months long after the winter foliage has withered.

Like most other Cape geophytes, ANR species produce colourful floral displays to attract pollinators - mainly insects - during the cool and windy spring. Shown here are members of the Iridaceae (*Hesperantha, Ferraria, Tritonia,* and *Babiana*) Hyacinthaceae (*Albuca, Lachenalia*), Oxalidaceae (*Oxalis*) and Colchicaceae (*Ornithoglossum*).

Mojave geophytes


Allium fimbriatum


Calochortus striatus


Hesperocallis undulata

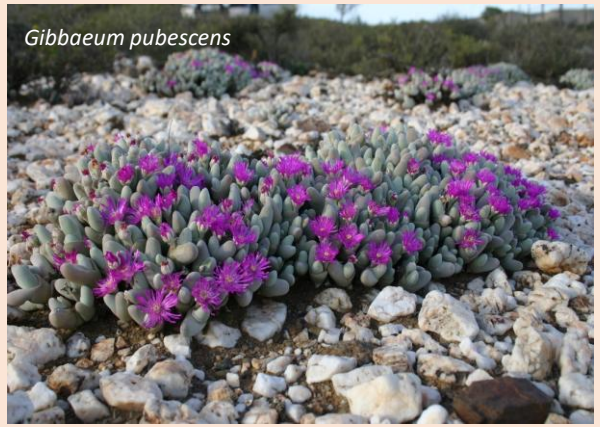

Calochortus kennedy

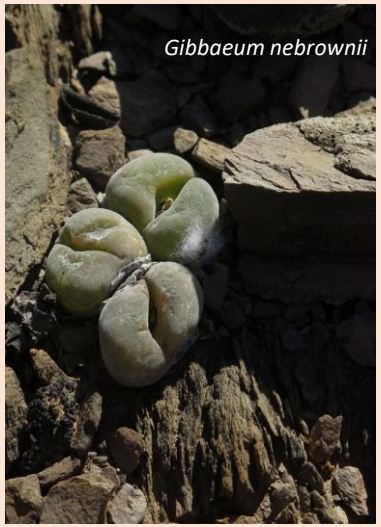
Unlike the ANR, the MNP has a small geophyte flora comprising 15 species distributed in four families, namely Amyrillidaceae (*Allium*) Calochortaceae (*Calochortis*), Asparagaceae (including the Mojave endemic *Hesperocallis undulata*) and Melianthaceae (*Toxicoscordion*).

Why then, amongst the herbaceous flora should the ANR have so few annuals and so many geophytes, while the opposite holds for the MNP? Could it be that the less reliable winter rain in the MNP selects for annuals which produce an abundance of hard-coated seeds that survive the dry summers? The large soil seed bank and dormancy patterns would buffer the species form “false starts”, where early season rainfall that stimulates germination, is not followed up by sufficient rain for flowering.

On the other hand, the more reliable rainfall of the ANR enables the persistence over the dry months of the storage organs of geophytes, most of which are very small and fleshy. The frequency of winter-rainfall failure in the MNP would select against geophyte diversification.

But why so few annual species in the ANR, since would these not also benefit from a more reliable rainfall?





Anysberg succulents

The ANR, like other parts of the Succulent Karoo, harbours a rich succulent flora comprising 195 species or 26% of its flora. Typically for a Succulent Karoo flora, most species (65%) are members of the Aizoaceae, followed by the Crassulaceae (22%) and both are mainly leaf succulents. Eight other families include succulent species, notably Apocynanceae, Euphorbiaceae (both stem-succulent), Asteraceae and Asphodelaceae (both leaf-succulent). Many succulents have small geographic ranges and thus contribute markedly to patterns of local endemism in the Succulent Karoo.

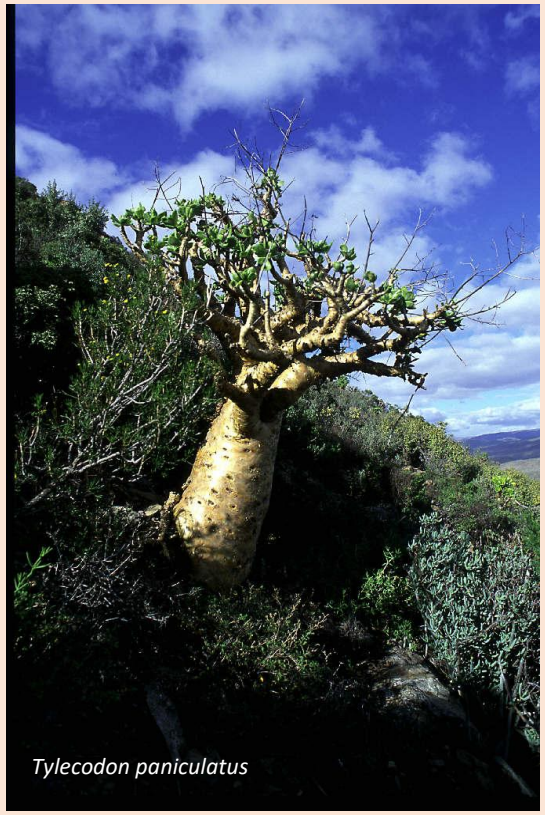
Unique amongst succulent floras globally are the large number in the Succulent Karoo - and the ANR - of dwarf forms: species that seldom exceed 10 cm in height and have very low moisture storage capacity. A sample of these species are illustrated in this spread.

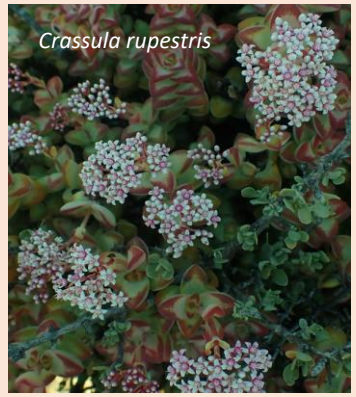
Five of these dwarf species belong to the Aizoiaceae (*Gibbaeum, Trichodiadema, Tanquana*), all of which are endemic to the Klein Karoo, as is *Euphorbia pseudoglobosa* and *Avonia papyracea* (Anacampserotaceae). Succulent crassulas, while very diverse, tend to have wider distributions than most other succulent groups.

Also shown here is *Haworthia truncata* (Asphodelaceae), a Klein Karoo endemic that is confined to a few populations east of the ANR.

Even the larger-bodied succulents of the ANR are of relatively low stature, seldom exceeding 0.5 m in height. One of the larger species in the ANR is T*ylecodon paniculatus* (Crassulaceae), a stem succulent with drought-deciduous, fleshy leaves. Asphodalaceae are represented in the spread by *Aloe variegata,* a species widespread in the drier parts of southern Africa, and *Astroloba corrugata,* endemic to the southern Succulent Karoo. Both *Euphorbia multiceps* and *Crassula rupestris* are widely distributed in the Succulent Karoo.

Of the three Aizoaceae shown, only *Drosanthemum chrysum* is endemic to the Klein Karoo. *Lampranthus haworthii* extends northwards from the Klein Karoo to southern Namaqualand and *Ruschia spinosa* is widespread in both the Succulent Karoo and Nama-karoo biomes.


Tylecodon paniculatus

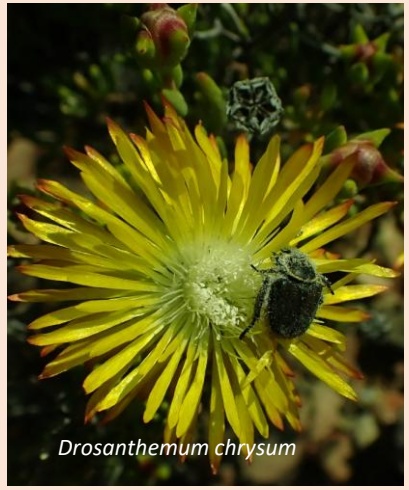

Crassula rupestris

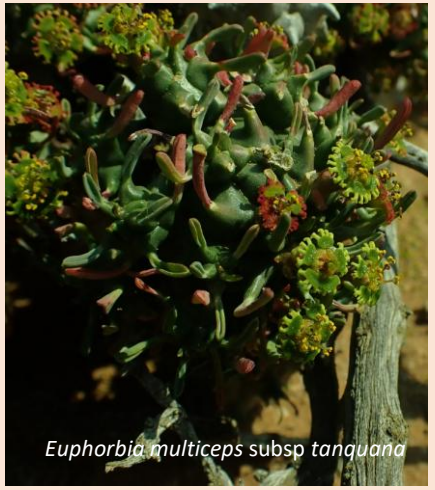

Aloe variegata


Astroloba corrugata


Ruschia spinosa


Lampranthus haworthii


Drosanthemum chrysum


Euphorbia multiceps subsp *tanquana*


Ferocactus cylindraceus


Echinocereus triglochidiatus ssp *mojavensis*


Mammillaria dioica


Opuntia basilaris


Escobaria vivipara var *rosea*


Optuntia polyacantha


Opuntia chlorotica

Mojave succulents

The succulent flora of the MNP is much poorer than that of the ANR and is home to only 27 species (4% of the total), 18 of which are Cactaceae, the remainder belonging to the Agavaeae (e.g. *Yucca*) and Crassulaceae (e.g. *Dudleya*). Other than the iconic Joshua tree (*Yucca brevifolia*), the Mojave lacks endemic succulents; most species have ranges that extend deep into the Sonoran Desert.

What the MNP lacks in succulent diversity, it makes up for in the size and grandeur of its species, notably its cacti. The Cactaceae, like the Aizoaceae, is a huge family of succulents, comprising 125 genera and 1800 species, most of them found in Central and South America. Unlike the Aizoaceae, cacti are mainly stem succulents.

This spread shows a sample of the genera found in the MNP. Included are two species (*Escobaria vivipara* and *Mammillaria diocea*) which resemble in stature the dwarf succulents of the ANR. However, most species are taller and more bulky than the ANR succulents. Moreover, all are fiercely protected by spines, a feature also common in many Succulent Karoo stem-succulent euphorbias and stapeliads (Apocynaceae).

Why should the MNP succulent flora comprise large-bodied species compared to the much smaller-bodied ANR flora? One possibility is that reliable rainfall of the ANR selects for succulents with small water storage capacity, since adequate replenishment occurs almost every year. Furthermore, the mild winters enable growth throughout the rainy season, meaning that there is scant selection for deep roots required for exploiting moisture for growing in the warmer spring and early summer months, when the water table has receded.


Agave deserti


Nolina parryi


Cylindropuntia echinocarpa


Agave utahensis


Yucca baccata


Cylindropuntia ramossisIma

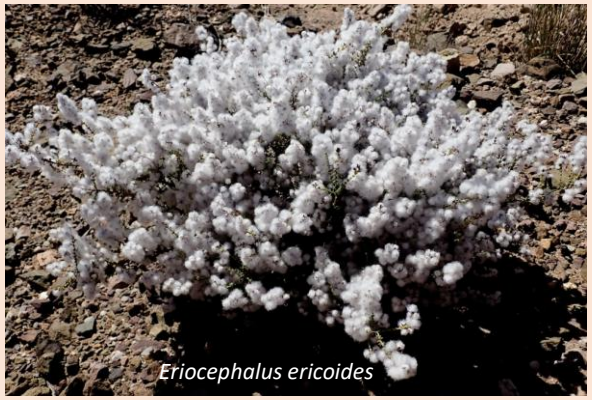
The larger succulents of the Mojave are represented by cacti - notably chollas (*Cylidropuntia* spp) - and agaves, nolinas and yuccas, all leaf-succulent members of the Asparagaceae.

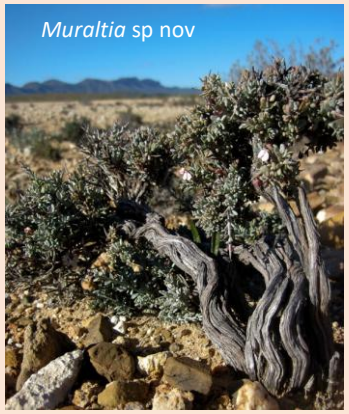
Agave is a large genus (250-300 species) distributed across the arid regions of North and Central America, including the Caribbaean. Agaves superficially resemble many aloes with their rosettes of succulent leaves with spine-tipped margins. However, unlike aloes, they produce massive flowering stalks, up to 4 m tall. In the case of *A. desertii,* this huge allocation to reproduction kills the plant. Up to two decades of vegetative growth is required before flowering occurs. Also, the yellow, lily-like flowers of yuccas are pollinated by bats whereas aloes are bird-pollinated.

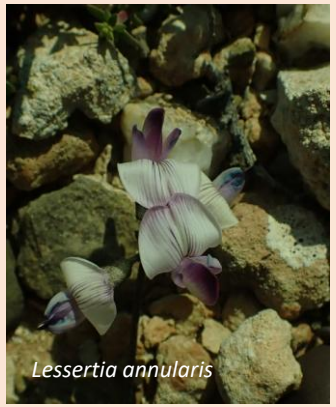
Yuccas, comprising about 50 species, have a similar global distribution to agaves. However, yuccas are not true succulents in that their rigid leaves do not store much moisture and they lack Crassuleacean Acid Metabolism (CAM), whereby carbon is fixed at night and metabolised during the day. MNP yuccas include *Y. brevifolia* (Joshua tree), *Y. baccata* and *Y. schidigera.* All species produce dense clusters of cream-coloured flowers which are pollinated exclusively by yucca moths (*Tegiticula* spp.).

Nolina is a genus of about 25 species that are found in arid North America. The MNP is home to two species, *N. bigelovii* and (shown here) *N. parryi.* Like yuccas, nolinas are not true succulents. Their pale-coloured flowers, borne on huge flowering stalks, are pollinated by a range of insects.

Interestingly, many cacti and some agaves are invasive in the arid and semi-arid parts of southern Africa, including the Succulent Karoo. These have either been planted for hedges and for soil erosion control (agave), or escaped from ornamental plantings and planted as fodder (cacti). Most of these invasives originate from South American species; none is a Mojave Desert species







Anysberg shrubs

In both deserts, non-succulent shrubs form the bulk of the biomass. Exceptions are on quartz patches and other edaphically marginal habitats in the ANR where leaf succulent dominate, and in rocky habitats in the MNP where cacti are abundant. Of the 271 shrubs species in the ANR (36% of the total flora), 72% are low in stature (<0.5) and 96% are evergreen. In contrast, only 28% of the MNP shrub flora comprises low-stature species, and only 43% is evergreen.

Asteraceae dominate the ANR shrub flora. Six daisy shrubs are illustrated in this spread. *Berkheya cuneata,* a Klein Karoo endemic, is common on rocky soils and, being highly palatable, is an indicator of well managed veld. Also highly palatable is *Osteospermum sinuatum*, which is widely distributed from across semi-arid southern Africa. *Dimorphotheca cuneata,* on the other hand, is unpalatable to game and livestock; its abundance is an indicator of overgrazed veld. *Eriocephalus ericoides,* another relatively unpalatable shrub that produces masses of fluffy fruits, is also widely distributed. *Euryops* sp nov is a recently discovered species endemic to a small patch of Kalkveld in the ANR. *Pteronia paniculata* is one of 20 species of this genus found in the ANR.

The species of *Lasiosiphon* (Thymeleaceae) and *Muraltia* (Polygalaceae) are both new to science, and endemic to ANR Kalkveld. *Muraltia* is a predominantly fynbos-centred genus of 109 species; the species shown here is the only occurrence of this genus in desert vegetation.

The remaining three species are dwarf shrubs in the Fabaceae (*Lessertia annularis*), Plumbaginaceae (*Plumbago tristis*) and Scrophulariaceae (*Aptosimum indivisum*). All have wide distributions in arid southern Africa.


Larrea tridentata


Ambrosia dumosa


Encelia farinosa


Lycium andersonii


Ericameria linearifolia


Salvia dorri


Ephedra nevadensis


Justicia californica


Peucephyllum schottii


Prunus fremontii


Psorothamnus arborescens


Eucnide urens

Mojave shrubs

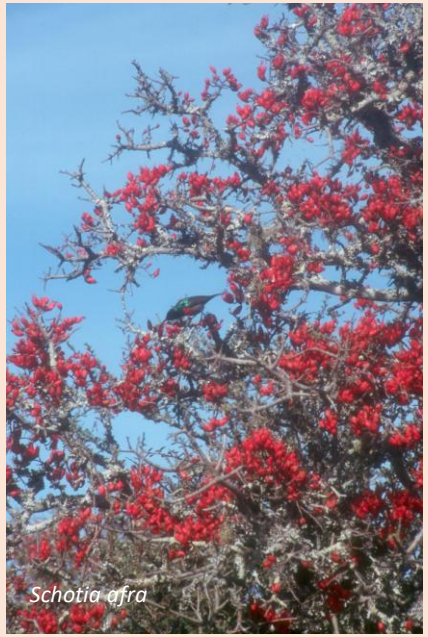
The MNP shrub flora comprises 130 species or 19% of the total. The most common shrub in the Mojave Desert and, indeed, in both the Sonoran and Chihuahuan deserts, is *Larrea tridentata* (Zygophyllaceae) or creosote bush. This remarkably successful, evergreen shrub is believed to have arrived in North America about 20 000 years ago from the Monte Desert in Argentina. This very long-lived shrub reaches 2-3 m in height .

As in the ANR, daisies dominate the MNP shrub component. The most abundant companion of creosote bush is *Ambrosia dumosa,* low-growing species found in all three warm deserts of North America. The next most abundant species is *Encelia farinosa,* also widespread in the California chaparral biome. *Ericameria* is a genus of about 35 species endemic to western North America. *E. linearifolia,* which grows up to 1.5 m, superficially resembles a species of *Euryops* from the Succulent Karoo while the monotypic *Peucaphyllum schottii,* a very large shrub, looks remarkably like a species of *Pteronia,* and like that genus, has resiniferous leaves.

Lycium (Solanaceae) is a cosmopolitan genus largely associated with arid environments. Plants are drought-deciduous, spiny and produce fruits that are dispersed by birds. The MNP has two species and ANR has four. *Salvia* is another genus shared by both deserts. Four shrubby species are found in the MNP and two in the ANR.

Justicia californica (Acanthaceae) barely extends into the Mojave Desert from its stronghold further south in the Sonoran Desert. This tropical family is represented in the ANR by six genera (including *Justicia*) and 14 species. Shrubby legumes are not especially diverse in both desert regions. *Psorothamnus,* a strikingly beautiful genus, is represented by two shrubby species in the MNP, *P. arborescens* and *P. fremontii.*

The MNP is home to five species of shrubby gymnosperms in the genus *Ephedra*, including *E. nevadensis* shown here. No gymnosperms grow in the Succulent Karoo. Another distinctive feature of the MNP is the presence of two species of *Prunus* (Rosaceae), a north-temperate genus from which peach and apricot trees are derived. Loasaceae, a largely neotropical family absent from the ANR, is represented in the MNP by many species of annuals (*Mentzelia* spp.) as well as the shrub *Eucnide urens.*


Schotia afra


Vachellia karroo


Euclea undulata

Anysberg trees

There are seven tree species in the ANR, and all are members of tropical lineages associated with outliers of the Subtropical Thicket biome. Most appear as multi-stemmed, hedge-like plants although they can adopt a tree-like form where conditions permit. They are also mostly evergreen and many have spines.

Schotia (Fabaceae) is a southern African genus of four species of which only *S. afra* penetrates the Klein Karoo. *Vachellia karroo* (Fabaceae), a member of a tropical genus that includes many iconic savanna trees, *and* is widespread in most biomes of southern Africa; it is the only deciduous tree in the ANR. *Euclea undulata* is widespread in the Klein Karoo as well as the drier regions of tropical southern Africa.


Populus fremontii


Celtis reticulata


Salix lasiolepis

Mojave trees

At just four species, the MNP has an even poorer tree flora than the ANR, and one that is less phylogenetically diverse, comprising two species of *Salix*, *Populus fremontii* (Salicaceae), and *Celtis reticulata* (Cannabaceae). All are winter deciduous and require access to summer moisture for their survival. Therefore, it is no surprise that all grow in washes, arroyos, wetlands and stream sides.

While the MNP and ANR deserts, sharing as they do similar climates and physiographies, show clear patterns of convergence in biotic form and function, both deserts have their own individuality, and it is these *differences,* if contemplated, that enrich us about the pathways and patterns of evolution in desert environments.

Let's first look at the differences between the two deserts in the selective regimes that have shaped their evolutionary outcomes. Firstly, the MNP experiences colder temperatures than the ANR, including a significantly higher frequency of hard frosts. Secondly, winter rainfall is considerably less reliable in the MNP than ANR: several years may go by in the MNP without sufficient winter to initiate the greening of this desert. Thirdly, soils are on average much deeper in the MNP than the ANR, where shallow, rocky soils limit the volume of soil that can be foraged for moisture by plant roots. Fourthly, Pleistocene climates have been much wetter and colder than at present in the MNP, displacing desert vegetation to arid refugia; in the ANR, Pleistocene climate change has been much more muted.

Frequent biome shifts in the Mojave Desert over the past million years would have disrupted evolutionary processes in the desert biota, leading to wide-scale extinctions of lineages. This would not have occurred in the ANR where speciation rates likely exceeded extinction rates, resulting in the accumulation of species. As predicted by this hypothesis, area-adjusted species diversity of Succulent Karoo floras are up to four times higher than Mojave Desert floras.

Colder winter temperatures mean that plant growth in the MNP is deferred until the warmer spring months. Higher winter temperatures in the ANR enable growth and flowering throughout the wet season. The deeper soils of the MNP, which are able to store more moisture than the shallow ANR soils, enable the deeper-rooted MNP shrubs to access water well into the warmer months, as the water table recedes. Larger rooting volumes can support larger aboveground volumes: perhaps this is why MNP shrubs are, on average, bigger than ANR shrubs.

Desert differences


Chylismia brevipes


Ornithogalum maculatum


Cylindropuntia bigelovii


Gibbaeum nuciforme


Peucaphyllum schottii


Hermannia althaeifolia


Ambrosia dumosa


Gorteria integrifolia

The higher rainfall reliability of the ANR than the MNP has profound implications for plant form and function. Firstly, it means that plants do not require large storage organs to survive, since the relatively short intervals between rainfall events enables regular replenishment. Hence, ANR succulents can be much smaller than MNP succulents. Similarly, geophytes, whose underground storage organs can be thought of as subterranean succulent organs, are predicted to be more abundant in the ANR than the MNP, as is borne out by this essay.

Secondly, low rainfall reliability would have selected among herbaceous growth forms for annuals over geophytes. This is because seeds, especially if small, hard-walled and with complex dormancy patterns, are a better hedge against rainfall uncertainty than, for example fleshy storage organs such as bulbs, corms and rhizomes, which incur far greater maintenance costs than seeds. Could this be the explanation for the dominance of annual species in the MNP herb flora?

Finally high rainfall reliability is likely to select for longer leaf duration amongst perennial plants. Combining this higher reliability with the lower overall seasonality of the ANR, where the rainy season is longer than the MNP, would predict a lower incidence of summer leaf-shedding among ANR shrubs. And, indeed, this is the case.

There is so much more to be discussed about the differences between these two deserts. Why do so many plants allocate so much energy to attracting pollinators, to the point extravagant flower displays may compromise photosynthetic efficiency? Why are there so many shrubs in the Mojave that capture their carbon primarily via green, photosynthetic stems? Given hotter summer temperatures, would Mojave evergreens have stronger adaptations to maintaining leaf energy budgets than Klein Karoo evergreens? And so on.

And what about the evolution questions? Which growth forms and lineages have radiated in these deserts, and how old are these radiations?