

Plant diversity of the Lut Desert natural world heritage site: the hottest place on earth

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Abstract

Located in southern Iran, the Lut Desert is one of the world's most extreme and unique arid environments. It was inscribed as Iran's first Natural World Heritage Site by UNESCO in 2016. Although often perceived as barren and lifeless due to its harsh conditions, this region exhibits remarkable botanical significance. This study aimed to conduct a comprehensive survey of the floristic composition and life forms in key subregions of the Lut Desert. Extensive fieldwork was carried out across five major sites during the spring and summer of 2021. For all plant species, we documented key traits including life form, cotyledon type, growth form, life span, chorotype, NCBI ID, and IUCN conservation status. Chorological analysis of the 76 recorded plant species (64 genera, 31 families) classified them into monoregional, biregional, and pluriregional groups, with the Irano-Turanian/Saharo-Sindian chorotype being the most dominant (30.3%). Plant distribution is primarily influenced by elevation and geographic location, with the highest species richness observed at mid-high elevations (764–1386 m) and in the northwest quadrant. Key species, such as *Hammada salicornica*, demonstrate wide adaptability across these environmental gradients. The flora is dominated by perennial shrubs and grasses (93% of species), mainly phanerophytes and hemicryptophytes, reflecting adaptations to extreme aridity. In a rare pattern,

both species richness and phylogenetic diversity increase monotonically with elevation, reaching their highest levels at upper elevations (>750 meters) due to milder temperatures, increased precipitation, and improved soil conditions. The discovery of one threatened species, *Haloxylon persicum*, underscores the conservation importance of this desert ecosystem. This study reveals a critical elevation-diversity relationship and underscores the ecosystem's vulnerability to climate change and human impacts, necessitating targeted conservation. Contrary to prior views of it being barren, the Lut Desert hosts significant plant diversity, acting as a biological refuge.

Keywords: Chorological analysis; Threatened species; Cotyledon type; IUCN status

Introduction

Accounting for between 13% and 33% of Earth's terrestrial surface are desert ecosystems, which encompass a range of categories, including warm, semi-arid, coastal, and cold deserts. Although dry environments may be inhospitable, they have enticed explorers and researchers alike for centuries (An, 2013). Among the most fragile, these ecosystems support a great deal of geodiversity and vital ecosystem services, as well as many threatened species. According to species richness, there is significantly less plant variety in hot deserts than in more humid regions. Although desert plants are crucial for preserving ecosystem stability and managing the hydrological and carbon cycles, their low resilience leaves them particularly susceptible to disturbances that could alter community composition and diminish biodiversity (Luo & Gong, 2023; Tu et al., 2024). Furthermore, they house about six percent of the global population, often comprising some of the most impoverished communities (Chen & Costanza, 2024; Han et al., 2025). Understanding their ecological roles and values is imperative for sustainable management practices.

Iran is situated in southwestern Asia within the mid-latitude zone of arid and semiarid regions, with over 60% of its land area (1.75 million km²) classified as such. The definition of “desert” varies among geobotanists. The term “desert” in Iran refers to areas receiving less than 100 mm of annual rainfall, minimally impacted by human activities, and possessing low production potential (Dastorani & Poormohammadi, 2016). In Iran, deserts cover an area of 907,293 km² (Khosroshahi et al., 2009), and sand dune fields are scattered throughout the arid and occasionally semiarid regions of the country. The vegetation in desert regions is dispersed and is predominantly found in low-lying areas, channels, and desiccated riverbeds (Liz et al., 2023). Two extensive endorheic basins in the Persian Plateau give rise to Iran's two main deserts. In the north is Dašt-e Kavīr, a large salt-based desert with sparse vegetation at its center, and in the south is the Lut Desert, an

area known as one of the hottest places on Earth, where summer air temperatures exceed 50 °C. The Lut Desert is encircled by mountain ranges, so the desert encompasses a wide altitude range from the below-sea-level Lut basin to the elevated Sirch-Kashit Mountain plateau, resulting in significant elevation variations. The Lut desert remains dry and extremely hot that only a few plants with special survival features can survive the extreme heat and dry conditions (Raeisi et al., 2022). Many lands in southern Iran are deteriorating moderately to severely owing to inadequate management techniques, resulting in ecosystem degradation and the loss of numerous kinds of flora (Bakhshi et al., 2020).

Desert flora has consistently drawn the interest of ecologists globally (Tu et al., 2024). Despite the fact that over two-thirds of Iran's landmass is composed of deserts, semideserts, and steppes, the country is home to an impressive 8,000 plant species, making it the most botanically diverse nation in the Middle East.

The evaluation of the potential and capacity for vegetation; enhancing species density; and discovering durable and multifunctional species (Sikuzani et al., 2024) fundamentally relies on accurate plant identification and classification within an area. The process of plant identification and classification as an essential part of the ecosystem has the essential ability to provide access to specific plants quickly and easily whenever and wherever they are needed. This study seeks to fill information gaps on desert plant diversity in the Lut Desert Natural World Heritage Site (LDNWHS) as a site with an extreme climate, i.e., low rainfall, high evapotranspiration, and poor soil. This is the first comprehensive floristic inventory on the interior of the Lut Desert Natural World Heritage Site, using the World Heritage nomination and management protocols.

Materials and methods

Study area

The Lut Desert World Heritage Site (LDWHS) in southeastern Iran spans about 51,800 km² across three provinces and is bounded by the Nayband and Nehbandan Faults (Fig. 1). Classified as a tropical hyper-arid hot desert ('BWh'), it experiences annual precipitation below 30 mm, mostly in winter, leading to extended drought periods. Temperature extremes are notable, with satellite measurements reaching 70.7°C (Mildrexler et al., 2006) and ground readings up to 78°C in 2017 (Trescher, 2017). Average annual temperatures at the Shahdad station range from -2.6°C to 50.4°C, with soil surface temperatures often exceeding 66.5°C (Ghorbani et al., 2023).

The desert's morphology includes expansive sand seas, megayardangs (Kaluts), desert pavements, saline flats, and playas (Alavipanah et al., 2007). The semi-permanent Shur River runs northwest to southeast, ending in the Chaleh Markazi depression (Fig. 2). Despite vast vascular plant absence (aphytism), extremophile soil microorganisms thrive, enduring intense heat, radiation, and dryness (Mohseni et al. 2014). Recent fieldwork revealed shallow groundwater in some areas, challenging previous assumptions of complete subsurface dryness (Trescher, 2017).

Designated as Iran's first natural UNESCO World Heritage Site in 2016 (site no. 1505), the Lut Desert's unique geomorphology and extreme climate have drawn comparisons to Martian landscapes (Ghorbani et al., 2023). This study, part of the AFLDB project, advances understanding of abiotic factors and biological adaptations sustaining life in this extreme desert environment.

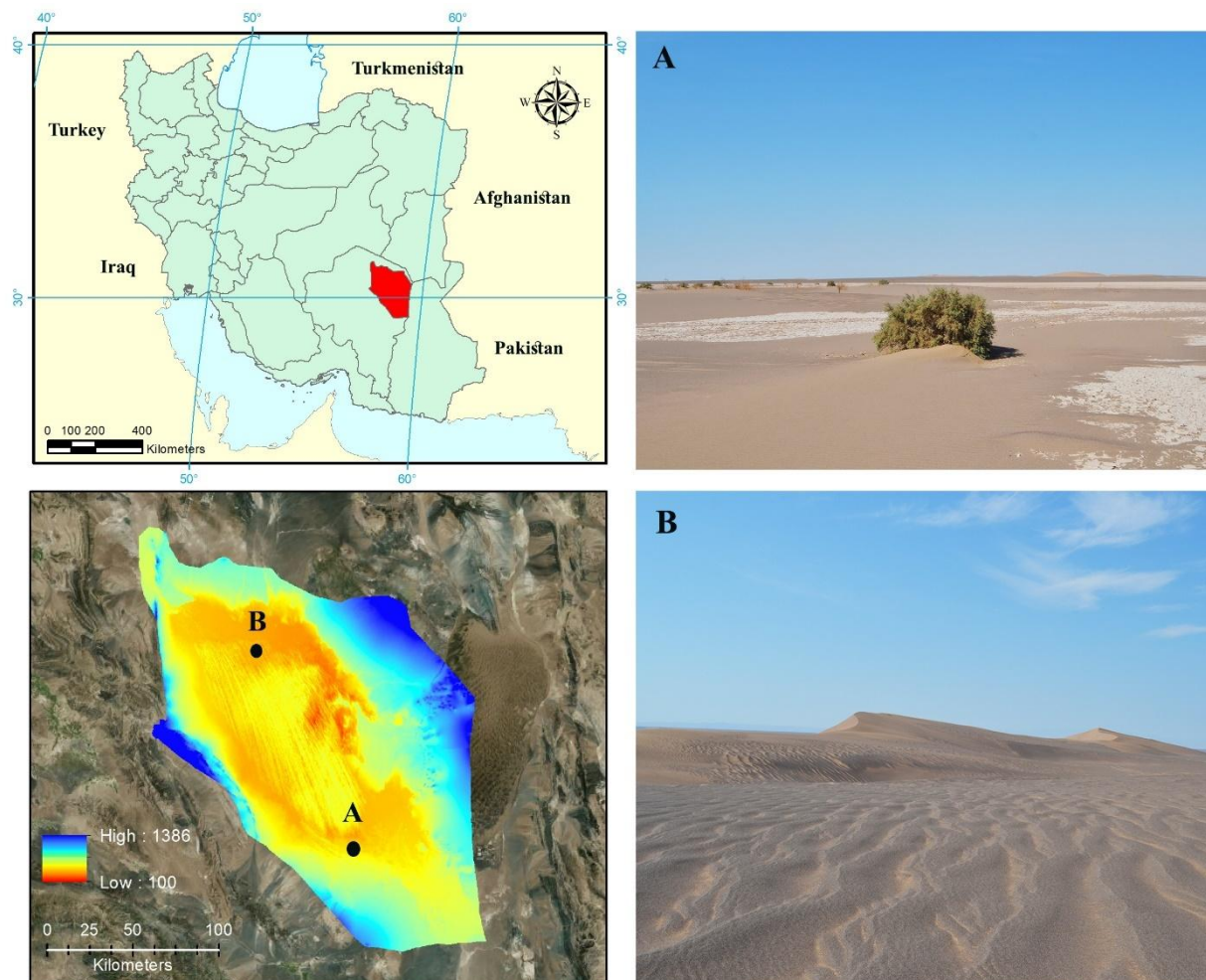


Figure 1. Geographic location and topographic context of the Lut Desert in Iran, with two representative field photographs illustrating local environmental conditions. A: a representative plant species growing in clay pan habitat, B: sand dunes and Ripple marks in northern Lut.

Vegetation Sampling and Species Identification

Initially, using topographic maps and Google Earth, various land areas for field visits were determined and transferred to the map. In order to achieve this objective, plant samples were collected from a variety of locations in the study region based on the presence of various plant species, using a survey approach and field excursions. The sampling locations of these plant species were recorded using a GPS device. Figure 3 shows representative plant species adapted to the harsh conditions of the Lut Desert.



Figure 2. Visual examples of landscape and environmental characteristics of the desert. (a) salt flats and yardangs in the central Lut Desert, (b) the Nabkas with *Tamarix passerinoides* in the southeastern Lut Desert, (c) the community of *Cyperus conglomeratus* in the sandy plains of the Southern Lut, and (d) the Shur River next to the large-magnitude explosive volcanic eruptions of Gandom Beryan in the northwest of the desert (June 2021).

After preparation for identification, the collected plant species were first categorized by family, genus, and species; then they were identified to the level of species and subspecies using available floras. Their scientific names, along with author names and classification by family, were compiled in a prepared list. The regional plant species were dried and pressed after collection. Scientific

resources, such as "Flora of Iran" (Assadi et al., 1988-2016), and "Flora of Yazd" (Mozaffarian, 2000) were utilized for identification purposes. By comparing the collected samples with those identified in these scientific resources, confidence in identifying the collected species was achieved. Fieldwork was undertaken in the spring and summer of 2021. Samples were dried, and voucher specimens were stored in the herbarium of the International Desert Research Center (IDRC), University of Tehran, Iran.

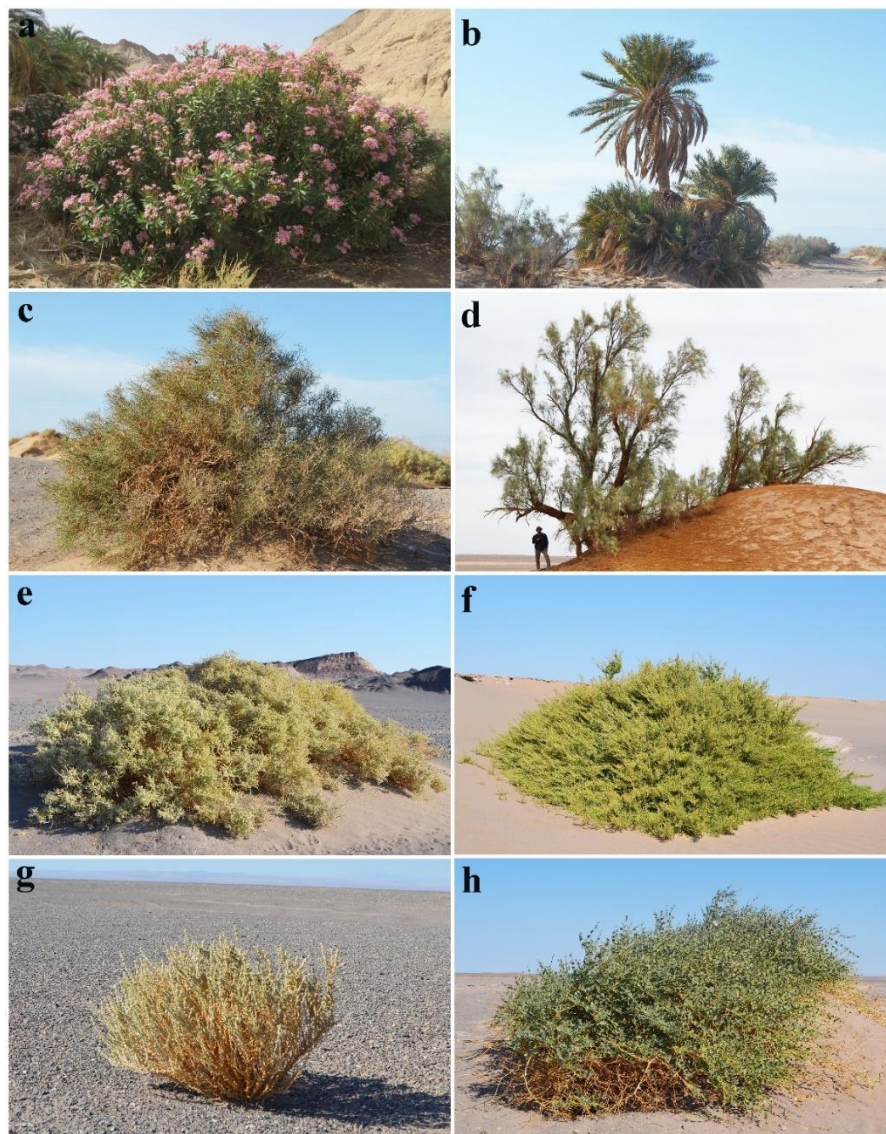


Figure 3. Selected Plant Species of the Lut Desert Flora (photos by Amir Reza Keshtkar). (a) *Nerium oleander* L. (b) *Phoenix dactylifera* L. (c) *Calligonum comosum* L'Her (d) *Tamarix aphylla* L. (e) *Hammada salicornic* (f) *Salsola imbricata*, (g) *Cornulaca monacantha*, (h) *Capparis spinosa* L., (i) *Cyperus conglomeratus* Rottb., (j) *Pycnocycla nodiflora* Decne. ex Boiss., (k) *Iphiona aucheri* Anderb, (l) *Tripidium ravennae* (L.) Scholz., (m) *Hyoscyamus insanus* Stocks., (n) *Cressa cretica* L., (o) *Haloxylon salicornicum* (Moq.) Bunge Boiss., (p) *Fagonia bruguieri* DC.

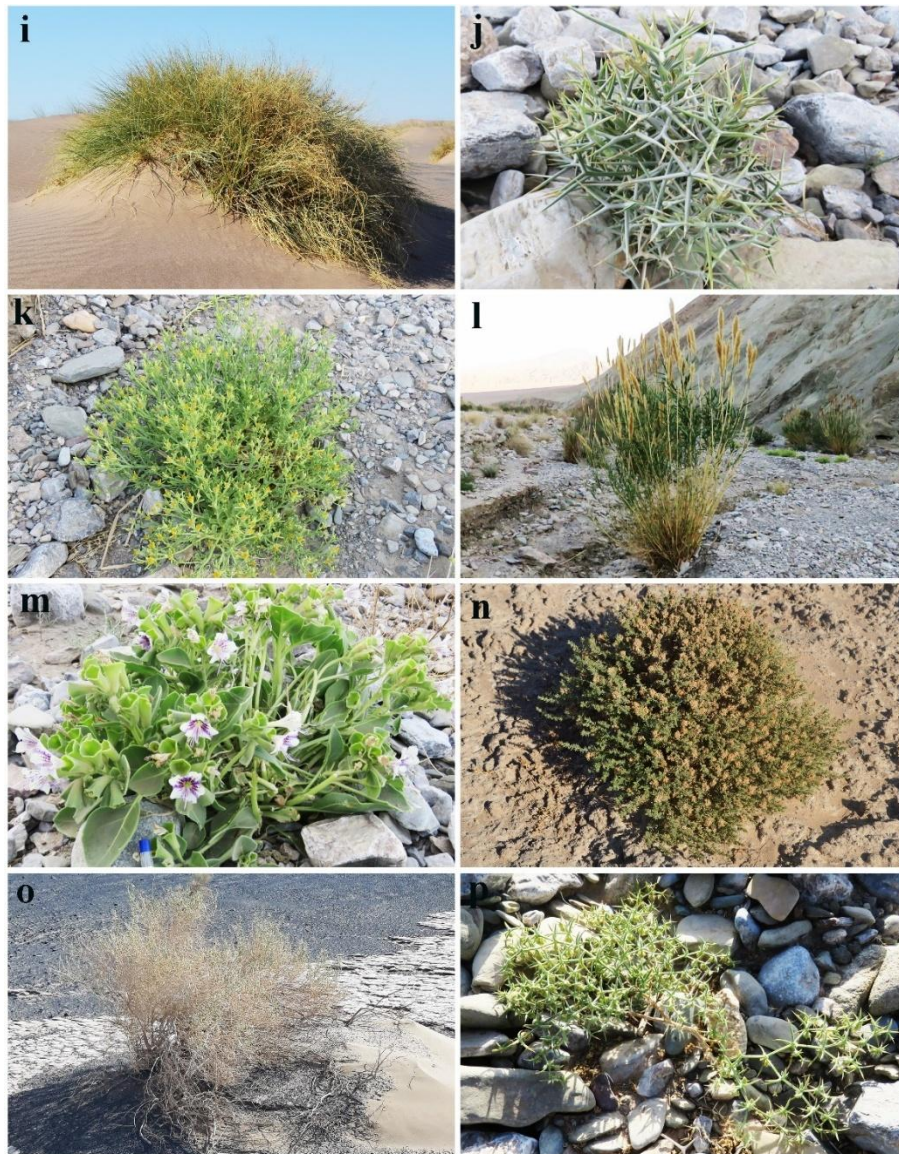


Figure 3. (continued).

The National Center for Biotechnology Information (NCBI) taxonomy database was used to verify and update the list of scientific names and their family affiliations for the recorded species so that it could contain names that were current, as all known plants are identified and categorized by naming conventions or nomenclature. The spreadsheet was developed with the approach of arranging the data we collected methodically and we ensured that we included multiple variables for each plant, e.g., family name, scientific name, NCBI Taxonomy ID and accepted scientific name. Additional ecological and morphological variables were also collected, e.g., type of cotyledon (monocotyledonous or dicotyledonous), growth form (e.g., forb, shrub, tree, grass),

duration or life span (annual or perennial), Raunkiaer life form classification, and chorotype or geographic distribution. Finally, the IUCN Red List was evaluated to report on the conservation status of each plant species to provide an international overview of potential threat levels of the species.

The type of cotyledon was determined using NCBI taxonomy and additional botanical literature, which allowed the authors to answer the question of whether the species is a monocot or eudicot. Fieldwork in conjunction with literature study provided a means of categorizing shape of growth/form and duration of life. Raunkiaer's (1934) life form classification was applied to the classes looking at perennating organ location and how the organisms adapted. Raunkiaer classified life forms based on where the buds or organs are located from which they repeat after a dormant season into five forms: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes (geophytes), and therophytes (Raunkiaer, 1934). Chorotypes were assigned to represent the phytogeographical affinities of the species in the regional flora. The geographical distribution and chorology of plant elements were also recognized according to geographic classification divisions and floristic regions by academic resources Zohary (1973) in addition to Gholami et al. (2021). To assess the conservation status of the plant species, present in Lut Desert flora, the IUCN Red List of Threatened Species was consulted. The scientific names of the recorded plant species were systematically searched on the official IUCN Red List website (<https://www.iucnredlist.org>) to determine their current global conservation status. IUCN Red List is the leading global source for information on species extinction risk and conservation needs, providing comprehensive data on the status, threats, and distribution of plant species worldwide.

The distribution of plant species in Lut Desert is intricately linked to both elevation and geographic coordinates, which together shape the environmental gradients influencing vegetation patterns. Thus, to simplify the analysis of recorded data, elevation data were categorized into five quantiles to represent distinct ecological zones: Low (100–315 m), Low-Mid (315–434 m), Mid (434–562 m), Mid-High (562–764 m), and High (764–1386 m). This classification was conducted using the Quantile method applied to the study area's spatial extent, aiming to create elevation classes with roughly equal area distribution. Furthermore, spatial coordinates were divided into four quadrants based on median longitude and latitude values: Southwest (SW: Low longitude, Low latitude), Southeast (SE: High longitude, Low latitude), Northwest (NW: Low longitude, High latitude), and

Northeast (NE: High longitude, High latitude). This quadrant-based approach can facilitate the identification of spatial patterns in species distribution.

In this study, no fixed-size plots or standardized sampling efforts were employed. The rationale for this approach is that the vegetation in the Lut Desert is extremely sparse and patchy, often being limited to wadis, runoff channels, and isolated microhabitats. This distribution makes traditional plot-based designs both unfeasible and unrepresentative. Instead, we adopted a flexible, presence-oriented floristic inventory approach aimed at maximizing species detection across the full environmental gradient. Consequently, sampling intensity was adapted to local vegetation density, with more time and effort invested in areas where preliminary reconnaissance using satellite imagery had identified visible plant presence. This methodology is widely accepted for comprehensive floristic surveys in hyper-arid environments, where standardized plot sampling would severely underestimate regional species richness.

Results

Floristic Composition

The study identified 76 flowering plant taxa across 31 families and 64 genera. Dicots comprised the majority, with 64 taxa (85.8%) from 29 families, while monocots included only 12 taxa from four families (14.2%). The most species-rich families were Poaceae and Chenopodiaceae each (11.8%), followed by Asteraceae and Tamaricaceae each (9.2%) (Fig. 4). Poaceae and Chenopodiaceae each contributed nine taxa, while Tamaricaceae and Asteraceae had seven species, Polygonaceae and Fabaceae had five taxa; three additional families contained three species each, and three families had two species each. Conversely, another 19 families were represented by a single species each (1.3%). The Asteraceae family had the highest number of genera, with five. Poaceae and Chenopodiaceae followed with four genera, and Fabaceae and Lamiaceae had three genera. Tamarix, with seven species (9.2%), and Calligonum, with three species (4.0%), were the most prevalent taxa. Furthermore, Populus, Prosopis, Salsola, and Stipagrostis; each represented by two species (2.6%), while fifty-eight other genera were monotypic with one species apiece (1.3%). The plant species identified in the study area, along with their growth forms and life spans, are listed in Table 1. Thus, a summary table providing the families, NCBI Accepted Names, and NCBI IDs of the examined species is available in supplementary A.

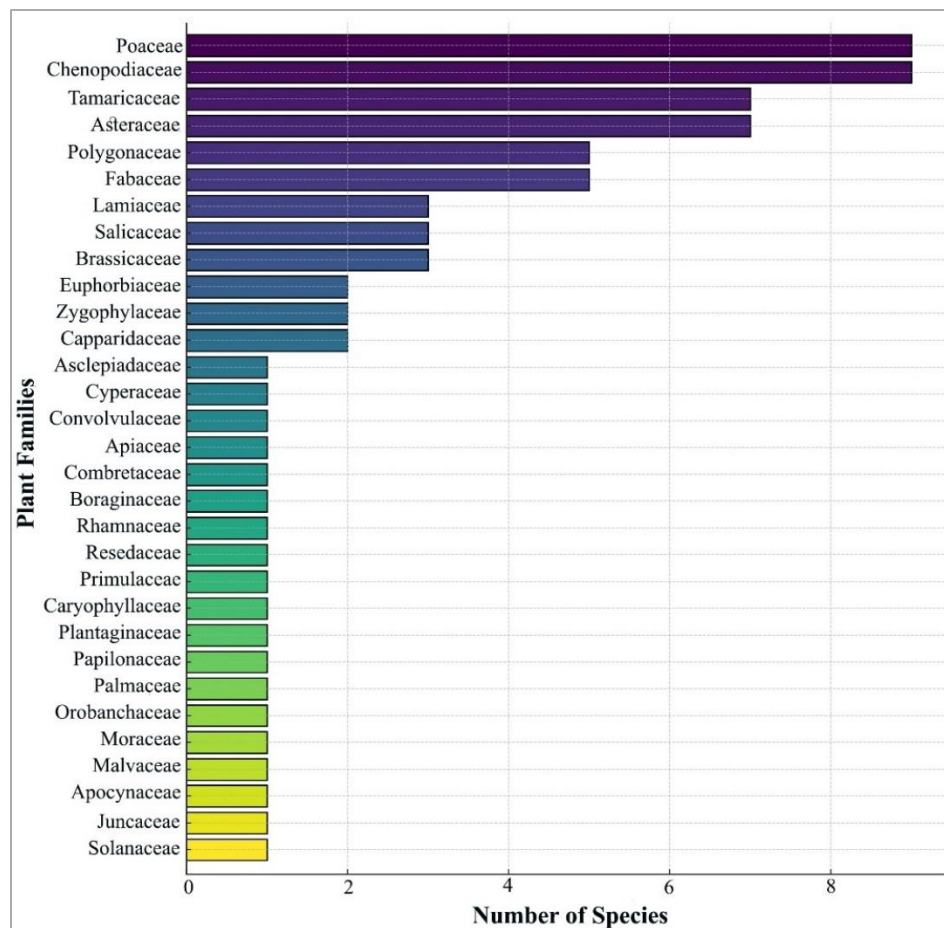


Figure 4. Family distribution of plant species of the Lut desert.

Life-Form Spectra

The study identified five life-form classes. Hemicryptophytes were the most prevalent, comprising 27 taxa, followed by Phanerophytes with 24 taxa, Chomophytes with 11 taxa, Geophytes with eight taxa, and Therophytes with six taxa (Fig. 5, Table 1).

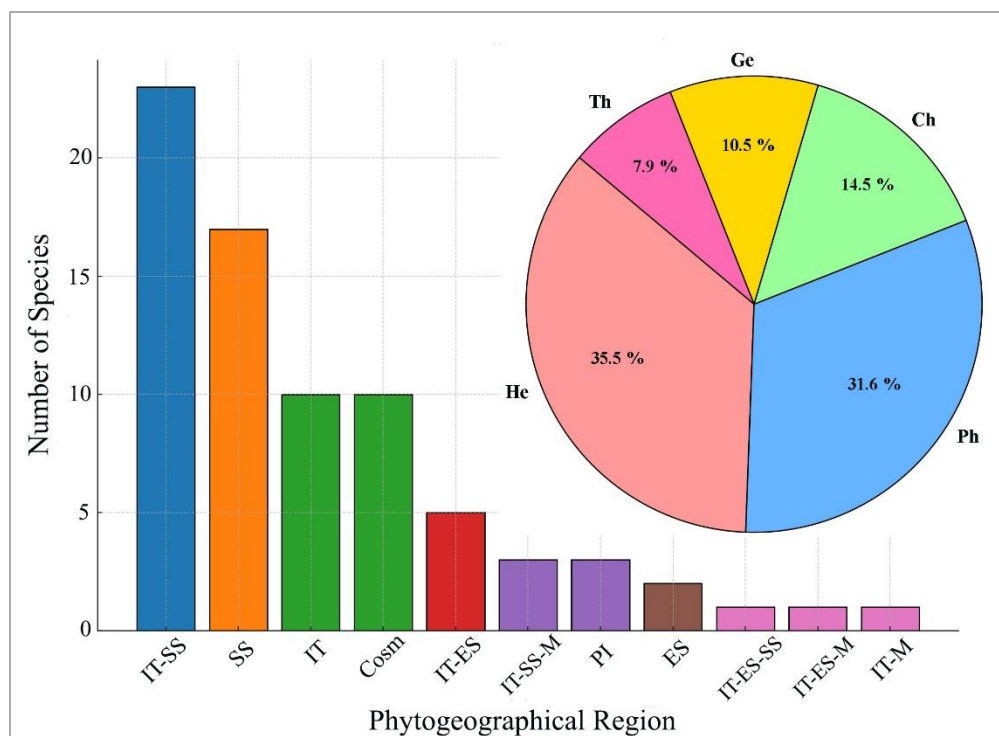


Figure 5. Life form distribution (%) and phytogeographical analysis of plant species in the Lut Desert. For the abbreviations, see Table 1.

The chorological analysis

Using chorological methods to study the flora within the borders of the explored area allowed us to identify 76 taxa of plants which can be grouped into single-region (monoregional), two-region (biregional), and multi-region (pluriregional) phytogeographical units. Out of these, five taxa (6.6% of the total) were recognized as pluriregional elements of various affinities distributed over three main chorotypes. Specifically, 23 species were part of Irano-Turanian/Saharo-Sindian types, making up 30.3% of all the plants, while five species belonged to the Irano-Turanian/Euro-Siberian types (6.6%), and one taxon represented the Irano-Turanian/Mediterranean chorotypes (1.3%).

Pluriregional elements comprised three main chorotypes with a total of five taxa (6.6%). In contrast, 32 species represented the monoregional group, 17 taxa belonged to the pure Saharo-Sindian, 10 taxa represented the Irano-Turanian chorotype, and two taxa belonged to the Euro-Siberian. Additionally, 10 species (13.2%) were classified under the Cosmopolitan chorotype (Fig. 5, Table 1).

Table 1. List of plant species along with their life form, cotyledon type, growth form, life span, chorotype, and IUCN status. Life forms abbreviations: Ch: Chamaephyte; Ge: Geophyte; He: Hemicryptophyte; Ph: Phanerophyte; Th: Therophyte. Chorotype abbreviations: Cosm: Cosmopolitan; ES: Euro-Siberian; IT: Irano-Turanian; Me: Mediterranean; Pl: Pluriregional; SS: Saharo-Sindian. IUCN abbreviations: NE: Not Evaluated; LC: Least Concern; NT: Near Threatened.

Life form (Raunkiaer)	Taxa	Cotyledon Type	Growth form	Life span	Chorotype	IUCN status
Ch	<i>Artemisia sieberi</i>	eudicots	Scrub	Perennial	IT	NE
	<i>Grantia aucheri</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Farsetia heliophila</i>	eudicots	Scrub	Perennial	IT-SS	NE
	<i>Fortuynia gracinii</i>	eudicots	Scrub	Perennial	IT-SS	NE
	<i>Gymnocarpos decander</i>	eudicots	Scrub	Perennial	SS	NE
	<i>Atriplex leucoclada</i>	eudicots	Scrub	Perennial	IT-SS	NE
	<i>Cornulaca monacantha</i>	eudicots	Scrub	Perennial	IT-SS	NE
	<i>Hammada salicornic</i>	eudicots	Shrub	Perennial	IT-SS	NE
	<i>Krascheninnikovia ceratoides</i>	eudicots	Scrub	Perennial	IT	NE
	<i>Salsola drummondii</i>	eudicots	Scrub	Perennial	SS	NE
	<i>Salsola imbricata</i>	eudicots	Shrub	Perennial	SS	NE
Ge	<i>Cyperus aucheri</i>	monocots	Graminoid	Perennial	IT-SS	NE
	<i>Mentha longifolia</i>	eudicots	Forb	Perennial	ES	LC
	<i>Cistanche tubulosa</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Aeluropus lagopoides</i>	monocots	Grass	Perennial	IT-SS-Me	NE
	<i>Saccharum ravennae</i>	monocots	Grass	Perennial	IT-SS	LC
	<i>Cynodon dactylon</i>	monocots	Grass	Perennial	Cosm	LC
	<i>Phragmites australis</i>	monocots	Grass	Perennial	Cosm	LC
	<i>Stipagrostis pennata</i>	monocots	Grass	Perennial	IT-ES	NE
	<i>Stipagrostis plumosa</i>	monocots	Grass	Perennial	IT-SS	NE
He	<i>Centaurea sp.</i>	eudicots	Forb	Perennial	IT	NE
	<i>Pulicaria gnaphalodes</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Taraxacum sp.</i>	eudicots	Forb	Perennial	Cosm	NE
	<i>Trichodesma africanum</i>	eudicots	Forb	Perennial	SS	NE
	<i>Cardaria draba</i>	eudicots	Forb	Perennial	IT-SS-Me	LC
	<i>Capparis spinosa</i>	eudicots	Scrub	Perennial	Cosm	LC
	<i>Cleome dolichostyla</i>	eudicots	Forb	Perennial	SS	NE
	<i>Cressa cretica</i>	eudicots	Forb	Perennial	IT-SS	LC
	<i>Merremia dissecta</i>	eudicots	Forb	Perennial	SS	NE
	<i>Andrachne telephioides</i>	eudicots	Forb	Perennial	IT-ES-SS	NE
	<i>Chrozophora hierosolymitana</i>	eudicots	Forb	Perennial	SS	NE
	<i>Alhagi camelorum</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Glycyrrhiza glabra</i>	eudicots	Forb	Perennial	IT-ES	LC
	<i>Medicago sativa</i>	eudicots	Forb	Perennial	ES	LC
	<i>Juncus inflexus</i>	monocots	Graminoid	Perennial	Cosm	LC
	<i>Salvia macrosiphon</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Teucrium polium</i>	eudicots	Forb	Perennial	IT-ES	LC
	<i>Sophora alopecuroides</i>	eudicots	Forb	Perennial	IT	NE

	<i>Plantago lanceolata</i>	eudicots	Forb	Perennial	IT-ES-Me	LC
	<i>Chloris virgata</i>	monocots	Grass	Perennial	Cosm	LC
	<i>Lolium perenne</i>	monocots	Grass	Perennial	PI	LC
	<i>Rumex sp.</i>	eudicots	Forb	Perennial	PI	NE
	<i>Reseda lutea</i>	eudicots	Forb	Perennial	IT-Me	LC
	<i>Hyoscyamus insanus</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Fagonia bruguieri</i>	eudicots	Forb	Perennial	IT-SS	NE
	<i>Peganum harmala</i>	eudicots	Forb	Perennial	IT-ES	LC
Ph	<i>Nerium indicum</i>	eudicots	Scrub	Perennial	SS	LC
	<i>Calotropis procera</i>	eudicots	Tree	Perennial	SS	LC
	<i>Haloxylon persicum</i>	eudicots	Tree	Perennial	IT-SS	NT
	<i>Seidlitzia rosmarinus</i>	eudicots	Scrub	Perennial	IT	NE
	<i>Conocarpus erectus</i>	eudicots	Tree	Perennial	SS	LC
	<i>Prosopis koelziana Burkil</i>	eudicots	Tree	Perennial	SS	LC
	<i>Prosopis juliflora</i>	eudicots	Tree	Perennial	SS	LC
	<i>Ficus johannis</i>	eudicots	Tree	Perennial	IT-SS	NE
	<i>Phoenix dactylifera</i>	monocots	Tree	Perennial	IT-SS	NE
	<i>Calligonum amoenum</i>	eudicots	Shrub	Perennial	IT-SS	NE
	<i>Calligonum bungei</i>	eudicots	Shrub	Perennial	IT	NE
	<i>Calligonum comosum</i>	eudicots	Shrub	Perennial	IT-SS	NE
	<i>Pteropryum aucheri</i>	eudicots	Shrub	Perennial	IT	NE
	<i>Ziziphus spina-christi</i>	eudicots	Tree	Perennial	SS	LC
	<i>Populus euphratica</i>	eudicots	Tree	Perennial	IT-SS	LC
	<i>Populus nigra</i>	eudicots	Tree	Perennial	IT-ES	LC
	<i>Salix sp.</i>	eudicots	Tree	Perennial	IT	NE
	<i>Tamarix aphylla</i>	eudicots	Tree	Perennial	SS	LC
	<i>Tamarix indica</i>	eudicots	Scrub	Perennial	SS	LC
	<i>Tamarix karakalensis</i>	eudicots	Scrub	Perennial	IT	NE
	<i>Tamarix kermanensis</i>	eudicots	Scrub	Perennial	SS	NE
	<i>Tamarix kotschyi</i>	eudicots	Scrub	Perennial	IT	NE
	<i>Tamarix mascatensis</i>	eudicots	Scrub	Perennial	IT-SS	NE
	<i>Tamarix passerinoides</i>	eudicots	Scrub	Perennial	IT-SS	NE
Th	<i>Pycnocycla nodiflora</i>	eudicots	Forb	Perennial	SS	NE
	<i>Senecio glaucus</i>	eudicots	Forb	Annual	IT-SS-Me	NE
	<i>Sonchus oleraceus</i>	eudicots	Forb	Annual	Cosm	LC
	<i>Malva sp.</i>	eudicots	Forb	Annual	Cosm	NE
	<i>Avena fatua</i>	monocots	Grass	Annual	Cosm	LC
	<i>Anagallis arvensis</i>	eudicots	Forb	Annual	Cosm	LC

Species richness of the Lut Desert plant communities

The distribution of plant species in the Lut Desert is intricately linked to elevation and geographic coordinates, which together shape the environmental gradients influencing vegetation patterns. The distribution of plant species across various elevation ranges in the Lut Desert is summarized

in Table 2, which includes the number of data points, the unique species richness, and the most dominant species within each elevation class. The analysis reveals distinct patterns in plant species distribution across elevation gradients. As shown in Table 2, the number of unique plant species varies across elevation zones, with the highest species richness observed in High elevation range (764–1386 m). Lower elevations host species like *Tamarix passerinoides* and *Seidlitzia rosmarinus*, while higher elevations feature *Calligonum comosum* and *Hammada salicornica*. The species *Hammada salicornica* appears frequently across multiple elevation ranges, particularly dominating in the mid to high elevation categories. This implies that the species is highly adaptable to a variety of environmental conditions, rendering it a critical component of the ecosystem under investigation. The findings indicate that the greatest diversity of species is frequently observed in mid-elevation ranges. By identifying elevation-specific species habitats, this information can serve as a guide for conservation efforts.

Table 3 presents the distribution of plant species diversity and dominance across four quadrants of the Lut Desert. The data include the number of sampling points, unique species richness, dominant species with their respective abundances, and the average elevation for each quadrant. As shown, the northwest quadrant shows the highest species richness with 26 unique taxa, while dominant species vary among quadrants.

Table 2. Plant species distribution and dominant species across elevation ranges in the Lut Desert. The numbers in parentheses indicate the presence of this species in the total number of surveyed sites.

Elevation Range	Data Points	Unique Species	Top Species
Low (100-315 m)	85	10	<i>Tamarix passerinoides</i> (25), <i>Tamarix mascatensis</i> (10), <i>Salsola drummondii</i> (8)
Low-Mid (315-434 m)	81	7	<i>Seidlitzia rosmarinus</i> (39), <i>Tamarix passerinoides</i> (32)
Mid (434-562 m)	82	13	<i>Hammada salicornica</i> (48), <i>Seidlitzia rosmarinus</i> (17), <i>Tamarix passerinoides</i> (11)
Mid-High (562-764 m)	82	9	<i>Hammada salicornica</i> (36), <i>Calligonum comosum</i> (23), <i>Haloxylon persicum</i> (10), <i>Stipagrostis plumosa</i> (10)
High (764-1386 m)	83	16	<i>Calligonum comosum</i> (52), <i>Haloxylon persicum</i> (39), <i>Stipagrostis plumosa</i> (16)

To recognize spatial patterns, the study area was split into four quadrants according to median longitude and latitude values. The species *Calligonum comosum* shows a remarkable spatial

concentration in the Northeast quadrant, where it dominates with high frequency. This implies that the region is characterized by a particular environmental niche, which may be associated with sandy or dune habitats. This is also supported by the high average elevation of approximately 700–800 meters. The Southwest quadrant is dominated by *Tamarix passerinoides* and *Tamarix mascatensis*, often associated with lower elevations (around 300–400 m), indicating saline habitats. The Northeast quadrant is characterized by *Calligonum comosum* and *Hammada salicornica*, thriving at higher elevations (700–800 m), likely in xeric dune environments. The results show species like *Seidlitzia rosmarinus* widely distributed across quadrants, suggesting high adaptability.

Table 3. Plant Species Diversity and Dominance by Quadrant in the Lut Desert. X: Longitude; Y: Latitude. The numbers in parentheses indicate the presence of this species in the total number of surveyed sites.

Quadrant	Data Points	Unique Species	Top Species	Avg Elevation (m)
SW (Low X, Low Y)	87	7	<i>Hammada salicornica</i> (56) <i>Tamarix passerinoides</i> (18) <i>Tamarix karakalensis</i> (6)	469
SE (High X, Low Y)	120	7	<i>Tamarix passerinoides</i> (46) <i>Hammada salicornica</i> (32) <i>Seidlitzia rosmarinus</i> (20)	432
NW (Low X, High Y)	120	26	<i>Hammada salicornica</i> (22) <i>Tamarix passerinoides</i> (20) <i>Tamarix mascatensis</i> (16)	532
NE (High X, High Y)	86	6	<i>Calligonum comosum</i> (74) <i>Seidlitzia rosmarinus</i> (6) <i>Tamarix mascatensis</i> (3)	677

Discussion

Floristic Composition and life form of Lut Desert plant communities

Desert vegetation in arid regions tends to be uniform over larger areas but exhibits heterogeneity on smaller scales (Perelman et al., 2001; Zheng et al., 2022). Research on plant composition generally focused on these more limited spatial dimensions. In the present study area, plant growth is focused in small environments where runoff water accumulates, supplying essential moisture. Like other extremely dry desert areas, plants mainly grow in wadis, small channels, and low-lying areas that have rich fine soil and receive enough water. Because of the low rainfall and frequent droughts in arid areas, water availability is a significant factor in determining species distribution.

Regarding severe environmental circumstances, the Lut Desert has a rather simple plant structure. A total of 76 species from 30 families were surveyed, with Poaceae, Chenopodiaceae, Tamaricaceae, Asteraceae, Polygonaceae, and Fabaceae being the most diverse families (42 species or 55.3%).

Lut Desert is mostly covered by shrubs and perennial herbs. This survey noted a total of 71 species of perennials and five species of annuals, which indicates that most of the species recorded, per around 93%, were in terms of habitat features affecting perennation and ecological adaptation. Shrubs of the Chenopodiaceae and Asteraceae families are some of the best representatives of arid regions because they possess deep roots, small or reduced leaves, and other water storing features (Gurjazkaite et al., 2018). Other contributors to the vegetation of the desert include perennial grasses of Poaceae family which increase vegetation cover, aid in the retention of eroded soil, and help in the creation of little homes for other plants (Azizi et al., 2021; Zhong et al., 2024). The presence of annual forbs, though limited, highlights the ability of certain species to take advantage of short-term favorable conditions following rare precipitation events (Raymundo et al., 2021). The low abundance of annual species suggests that surface moisture conditions in this region are harsh.

Life-form analysis based on Raunkiaer classification indicates that the greatest portion of the plant species are phanerophytes and hemicryptophytes. Hemicryptophytes, which have perennating buds at or near the soil surface, are well adapted to the extreme conditions by utilizing protective soil cover against desiccation and temperature fluctuations (Raunkiaer, 1934; Akhani, 2006). The other group, Phanerophytes, is remarkable for tall growing habit and they have the benefit of accessing deeper soil moisture which is vital for sustenance in arid areas. Such pattern of life form dominance is in line with several studies conducted on the flora of desert regions, for example in the Iranian central highland (Akhani et al., 2010) which in some regions of North Africa (Le Hou  rou 1996). In what concerns the therophytes, despite being conspicuous, they are less present compared to other hyper-arid deserts, such as Sahara (Wickens et al. 1985) and Thar Desert (Charan & Sharma, 2016), indicating that Lut Desert has a relatively stable community of perennial plants.

It's apparent from the species phytogeographic distributions that Irano-Turanian components were clearly prevalent, as the Lut Desert is definitely positioned in that area. The presence of a few Saharo-Sindian species also indicates a biological connection between these desert environments,

suggesting that the plant communities that exist have gradual transitions over arid landscapes (Gurjazkaite et al., 2018). Such a trend has been observed in previous research related to Central Iran (Akhani et al., 2010) and the Arabian Peninsula (Ghazanfar & Fisher, 1998). The species recorded assessment indicates that both monocots and dicots exist, with dicots being the dominant group. This was an expected outcome since dicots generally exhibit a higher number of morphological adaptations (e.g., drought resistant leaf adaption and extensive root adaptations) that facilitate their growth in extreme environments (Akhani, 2006). However, monocots, including Poaceae, are significant in stabilizing dune sand and providing forage for herbivores.

Patterns of plant community diversity in Lut Desert

Over the last few decades, there has been a considerable amount of research done on the trends in biodiversity with respect to latitude, longitude, and elevation regionally and globally (Guo et al., 2013; Gaston, 2000). It is quite well known that, in general, the variety of species tend to decline in longitudinal and latitudinal gradients across different regions of the world. At more regional levels, however, the elevation gradients play an important role in determining species richness and community structure (Rowe & Lidgard, 2009; Tu et al., 2024). Most studies in arid and semi-arid regions report unimodal or bimodal diversity patterns along with elevation (He et al., 2024); however, our findings from the Lut Desert reveal a monotonically increasing trend in both species' richness and phylogenetic diversity with increasing elevation, a pattern rarely documented in desert ecosystems.

Lut Desert encompasses a broad elevation range, from the below-sea-level Lut Basin to the heights of the Sirch-Kashit Mountains, creating a diverse array of habitats. At lower elevations (200–350 m), particularly in the southwest quadrant, halophytic species, such as *Tamarix mascatensis*, *Seidlitzia rosmarinus*, and *Salsola drummondii* dominate. These species are well-adapted to saline, arid lowlands, with some microhabitats supporting wetland-associated taxa like *Phragmites australis* and *Tamarix karakalensis*. Well-established species like *Peganum harmala* and *Alhagi camelorum* continue to thrive by accessing groundwater, enabling survival under extreme heat and drought.

By increasing elevation (350–500 m) in the southeast quadrant, plant communities transition to semi-arid assemblages dominated by *Tamarix passerinoides*, *Seidlitzia rosmarinus*, and *Tamarix aphylla*, often accompanied by *Stipagrostis pennata* in more stable, sandy substrates. This region

represents a transitional zone where species show broader environmental tolerances, reflecting moderate salinity and improved substrate stability.

In the northwest, mid-high elevation (500–650 m) shrub-dominant vegetation communities exist with *Salsoza imbricata*, *Tamarix passerinoides*, *Prosopis cineraria*, and *Capparis spinosa*. These areas have lower salinity, greater topographic variability, and stony soils, which result in more species diversity. Xerophytic species, including *Calligonum comosum*, *Hammada salicornica*, *Haloxylon persicum*, and *Stipagrostis plumosa*, predominate in dune-dominated habitats at the greatest elevations (650–1200 m), particularly in the northeast quadrant. Community types, such as *Cornulaca monacantha* and *Gymnocarpos decander* have greater species richness and phylogenetic diversity at elevations greater than 800m, suggesting more favorable edaphic and climatic conditions. The Sirch-Kashit Mountains, where both arid and montane ecosystems meet, are likely the most species-rich and phylogenetically diverse due to the further reduced temperatures, increased precipitation, and better soil fertility. In summary, the combined effects of specialized plant adaptations, substrate diversity, and climatic amelioration drive the monotonically increasing species richness of the Lut Desert with elevation. Consequently, this region provides a distinct natural experiment that enables us to investigate the biodiversity responses to extreme environmental gradients.

The observed monotonic increase in phylogenetic diversity with elevation also carries important ecological and functional implications for ecosystem stability and resilience in this hyper-arid environment. Higher-elevation assemblages contain a broader range of evolutionary lineages (e.g., Poaceae, Chenopodiaceae, Tamaricaceae, Polygonaceae, and Zygophyllaceae), which typically exhibit divergent functional traits related to water acquisition, salt tolerance, root morphology, and dune stabilization (Díaz & Cabido, 2001; Cavender-Bares et al., 2009). This greater functional complementarity and redundancy reduce niche overlap and provide an insurance effect (Yachi & Loreau, 1999; Pillar et al., 2013), enabling the community to better withstand and recover from extreme droughts, heat waves, wind erosion, and anthropogenic disturbances. Consequently, mid- and high-elevation zones likely serve as critical refugia that maintain higher ecosystem multifunctionality (soil stabilization, nutrient cycling, forage provision, and microhabitat creation) under current and projected climatic extremes. This pattern underscores the particular conservation importance of higher-elevation habitats within the Lut Desert.

Conclusion

This study analyzes the evolutionary structure and diversity of plant communities in the Lut Desert, a hyperarid World Heritage Site in Iran. Despite extreme conditions, the area hosts significant species richness, dominated by drought-tolerant families like Poaceae, Chenopodiaceae, Tamaricaceae, and Asteraceae. These halophytic and xerophytic species are crucial for maintaining the fragile ecosystem equilibrium, providing forage for native herbivores and promoting soil stability.

The research highlights the flora's acute sensitivity to climate change and human activities, particularly increased aridity and overgrazing, which threaten even resilient species. A key finding is the strong relationship between plant distribution and environmental gradients. Species composition varies markedly with elevation: low-elevation areas host specialists for harsh, dry environments, mid-elevations form a transitional zone with diverse niches, and higher elevations are dominated by shrub communities adapted to more complex terrain.

This distribution pattern gives important insights into managing and conserving arid habitats globally. The study serves as a vital baseline, advocating for conservation efforts focused on habitat protection and sustainable land-use practices. Future research on seed banks, ecological interactions, and plant adaptation processes is recommended. Furthermore, the positive correlation between phylogenetic diversity and geographic variables (elevation, latitude, longitude) offers a valuable framework for informing conservation strategies in a changing climate.

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