

# Sixty-five years of change, from annuals to subshrubs: Diachronic vegetation dynamics in the halophytic–steppe ecotone of Chott Chergui, a Mediterranean semi-arid depression, Algeria

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**Abstract.** The current study presents a comprehensive 65-year diachronic analysis of the *Atriplex mauritanica*-*Suaeda fruticosa* subassociation in eastern Chott Chergui, Algeria. By resurveying historical plots from 1954 in 2019, the present study quantifies shifts in taxonomic composition, life-form spectra, biogeographic affinities, and diversity metrics (Shannon-Wiener index, Pielou's evenness, Margalef's richness, Jaccard similarity, Cohen's *d*). Species richness declined by 26.1 %, with therophytes decreasing from 68 % to 51 % and chamaephytes increasing from 19 % to 31 %. A significant decline in Shannon diversity (from 3.97 to 3.70, Welch's  $t = 3.12$ ,  $p < 0.001$ ) and a Jaccard similarity of only 0.46 confirm substantial floristic turnover. Endemic taxa persisted (100 %), while mesic Mediterranean and pluri-regional elements contracted. The emergence of Saharo-Sahelian *Atractylis serratuloides* highlights ongoing xerophytization under accelerating aridification. Conservation of this fragile ecosystem demands a combination of livestock exclusion and soil restoration, along with continuous climate monitoring. These efforts should be underpinned by multivariate and trait-based analyses to pinpoint the drivers of change. Beyond documenting a hallmark of Mediterranean desertification, our study delivers a concise, transferable framework for long-term vegetation-change assessments in other climate-sensitive steppes.

**Keywords:** diachronic vegetation dynamics; xerophytization; halophytic-steppe ecotone; diversity indices; Chott Chergui.

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## 1. Introduction

Anthropogenic pressures frequently arrest successional trajectories or even reverse vegetation to earlier seral stages, ultimately exposing bare or eroded substrates (Ozenda, 1986). This degradation dynamic is acutely manifested in halophytic and steppic communities of arid regions, where synergistic climate-human pressures disrupt ecosystem equilibrium (Benkhetou *et al.*, 2015). In the eastern basin of Chott Chergui (Algeria), a topographically complex saline depression, halophilous and steppe communities have experienced progressive degradation under the dual influence of increasing aridity and intensive grazing (Benkhetou *et al.*, 2014). Historically documented as a botanical hotspot since the 19<sup>th</sup> century

(Warion, 1864, 1872), its vegetation was systematically cataloged by Dubuis and Simonneau (1954). Between 1954 and 1957, Dubuis and Simonneau (1954-1957) conducted the first systematic surveys at Ain Skhoua, delineating the *Artemisia herba-alba-Atriplex mauritanica* association and its two sub-associations (*Artemisia herba-alba-Atriplex mauritanica* and *Atriplex mauritanica-Suaeda fruticosa*). These subassociations occupy clay-silt alluvia-sometimes with sandy lenses-on valley floors and depression margins, where episodic moisture and salinity gradients strongly structure plant composition (Dubuis and Simonneau 1954-1957).

Subsequent Algerian studies have refined our understanding of steppe floristics and dynamics. Bouazza *et al.* (2004) and Benabadji *et al.* (2007, 2009) documented species-environment relationships in South-Western steppes, while Chermat (2012), Bahi *et al.* (2020) and Gourari (2023) traced floristic shifts under fluctuating land use. Adi *et al.* (2016) linked floristic assemblages to soil salinity gradients in Chott Chergui, and Benkhetou *et al.* (2013, 2014, 2022) combined plot-based surveys with GIS mapping to pinpoint diversity hotspots across semi-arid landscapes. Furthermore, remote-sensing studies (Haddouch *et al.*, 2009; Oukil *et al.*, 2020; Khallef *et al.*, 2021; Bouchelouche *et al.*, 2022; Gharbi *et al.*, 2022) have further quantified vegetation cover change. However, aside from these recent studies on land-use change, no prior investigation has directly resampled mid-20th-century plots to quantify long-term community shifts, underscoring the novelty of our 65-year diachronic approach. Existing research in Chott Chergui has focused on salinity gradients (Adi *et al.*, 2016) or regional floristics (Benkhetou *et al.*, 2022), neglecting long-term community-level shifts. This gap is critical given the ecosystem's role as a climate-change sentinel site (Emberger quotient: 24.07; arid upper stage), a refugium for endemic taxa (e.g., *Herniaria mauritanica*, *Thymus algeriensis*), and a benchmark for Mediterranean desertification processes (Meddour, 2010).

To address these gaps, the present study aims to bridge this knowledge break through conducting a direct 65-year diachronic comparison of the *Atriplex mauritanica-Suaeda fruticosa* subassociation between 1954 and 2019. We quantify changes in (1) systematic composition, (2) biological and life-form spectra, (3) biogeographic affinities, and (4) diversity metrics, thus elucidating long-term vegetation dynamics and providing guidance for conservation in Chott Chergui.

This is the first study in the Maghreb to directly compare mid-20<sup>th</sup>-century and contemporary field plots for a halophytic-steppe ecotone, offering novel insights into long-term xerophytization trajectories. Based on xerophytization theory, we hypothesize that intensifying summer drought and grazing pressure have driven a decline of mesic annuals (therophytes) alongside a proliferation of drought-tolerant subshrubs (chamaephytes), reflecting a directional shift toward more xerophilous communities. By delivering empirical evidence of xerophytization under accelerating aridification, our study informs adaptive conservation strategies for Maghrebian wetland-steppe ecotones and establishes a methodological template for similar assessments elsewhere.

## 2. Material and methods

### 2.1. Study area

The eastern sector of Chott Ech Chergui (34.350-34.633° N, 0.850-1.117° E) lies at the southwestern margin of the Tiaret region, on the high steppic plains of north-central Algeria. Geomorphologically, it forms a broad NE-SW oriented depression immediately south of the Saïda Mountains, with rim elevations at ~1,000 m asl and a floor at 985-990 m asl (Larnaude, 1948). Stratigraphically, Pliocene fluvial conglomerates and continental limestones underlie Quaternary alluvio-colluvial gypsum deposits and Holocene dunes, which support psammophilous vegetation (ITGC & IAO 1995). Phytogeographically, the site belongs to the Maghreb-Steppe domain, High Steppic Plains sector [H1] (Meddour, 2010; Benkhetou *et al.*, 2022).

### 2.2. Climatic context

Climatic normals were obtained from the El-Kheïter meteorological station (34.250° N, 0.060° E; 1,001 m asl) for 2002-2016 record. Mean annual precipitation is 252 mm, placing the area between the 200-300 mm isohyets of Mediterranean semi-arid climates (Chaumont & Paquin, 1971; Le Houérou *et al.*, 1977). The Bagnouls-Gausson ombrothermic diagram (1953) defines a nine-month summer drought

from mid-January to October. Mean July maximum temperature (M) is 37.3 °C; mean January minimum (m) is 1.5 °C, yielding a continentality index ( $CI = M - m$ ) of 35.8 (Rivas-Martínez 1981, 1999, 2002, 2011), and an Emberger pluviothermic quotient ( $Q2 = 2000 P/(M^2 - m^2)$ ) of 24.1, corresponding to an upper arid climate with cool winter (Emberger, 1955; Daget & Godron, 1995). Moreover, recent climatological analyses indicate that northern Algeria has experienced persistent drought conditions since the 1970s, with decreasing rainfall and rising temperatures. For example, precipitation in parts of the country may have declined by up to ~40% over the late 20th century, aligning with broader Mediterranean trends of increased drought frequency and reduced rainfall under warming climates (Ceppi *et al.*, 2025). Interannual precipitation anomalies (1940–2020) were also correlated with species turnover rates to disentangle climatic versus grazing drivers.

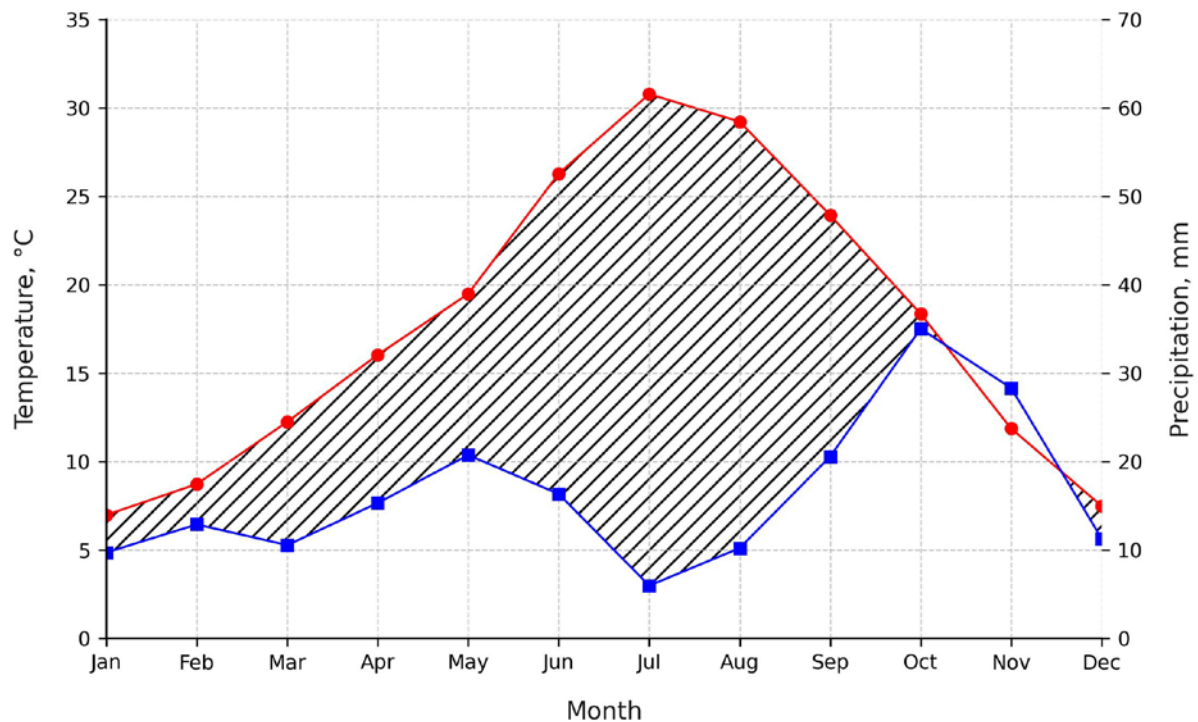


Figure 1. Bagnouls–Gaussen ombrothermic diagram of the study region, illustrating the prolonged dry season (approximately ten months and half, mid-November through October) characteristic of the local climate.

### 2.3. Diachronic vegetation survey

We adopted the direct diachronic approach of Dutoit (1996), comparing historical surveys of Dubius and Simonneau (1954) with contemporary resampling (2019) across the same stations. Historical plot coordinates, originally in Lambert projection, were converted to UTM and georeferenced by overlaying the 1:50,000 topographic map used in 1954 onto high-resolution imagery from Google Earth Pro (Venard *et al.*, 2010). Contemporary plot centers were validated in the field using a GPS during peak vegetation (mid-April to May).

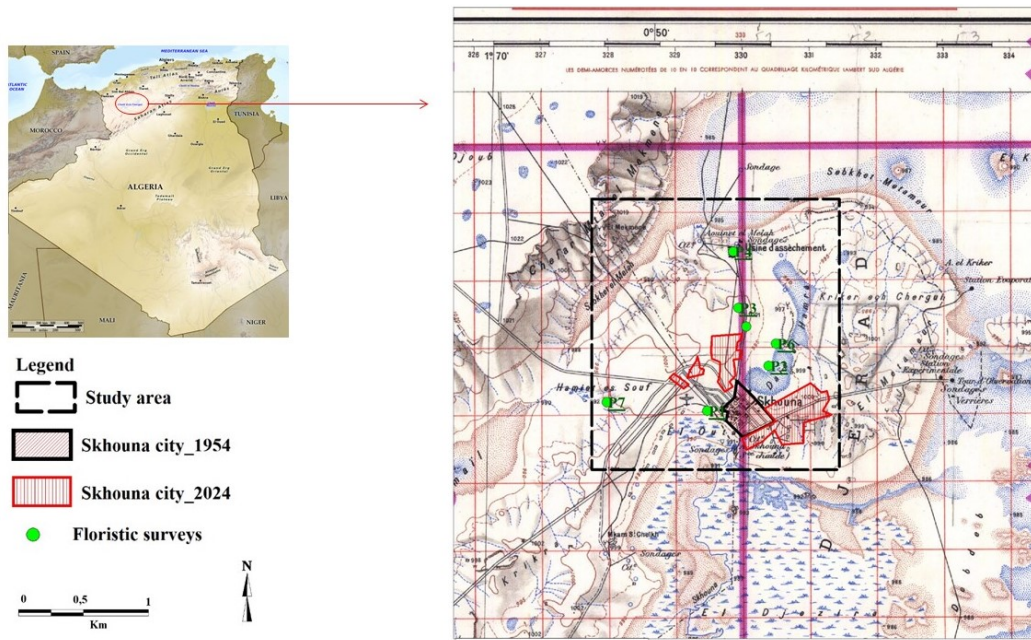


Figure 2. Geographic location of the study area. The map shows Chott Chergui in north-central Algeria, with an inset indicating the study site's position within the country.

## 2.4. Minimum area determination

Following the nested-plot method of Mueller-Dombois and Ellenberg (1974), sequential subplots were established in logarithmic series (25, 50, 100, 200, 400 m<sup>2</sup>) until species accumulation reached an asymptote. In Chott Ech Chergui, plateauing of species counts between 100 and 400 m<sup>2</sup> indicated a minimal sampling area of 100 m<sup>2</sup> for robust species inventories, consistent with Le Floch (2008) protocols for arid ecosystems.

## 2.5. Species identification and data recording

Within each 100 m<sup>2</sup> plot, all vascular plants were recorded for presence–absence and Braun-Blanquet abundance–dominance scores (1964). Taxa were determined using Quézel and Santa's *Nouvelle Flore de l'Algérie* (1962–1963), Le Floch et al. (2010), and El Oualidi et al. (2012), with nomenclature updated to APG IV (2016) and validated via IPNI (2019). Biological life-forms were classified per Raunkiaer (1905).

## 2.6. Diversity and similarity metrics

Floristic diversity was quantified using Shannon's diversity index ( $H'$ ) and Pielou's evenness ( $J'$ ), while species-richness was assessed via Margalef's index ( $DMg$ ). Temporal turnover was measured by the Jaccard similarity coefficient ( $J$ ). Species richness ( $S$ ) and individual counts ( $N$ ) per plot were used to calculate:

### 2.6.1. Shannon's diversity

Species diversity in each plot was quantified using the Shannon–Wiener index ( $H'$ ), which accounts for both species' richness and relative abundance.  $H'$  is defined as:

$$H' = - \sum_{i=1}^S p_i \ln(p_i)$$

where  $p_i$  is the proportion of individuals in species  $i$ . Values of  $H'$  range from 0 (monoculture) to  $\ln S$  (maximum diversity).

### 2.6.2. Evenness (Pielou's J')

Evenness was quantified using Pielou's index, which expresses how uniformly individuals are distributed among species. It is defined as:

$$J' = \frac{H'}{\ln S}$$

reflects how evenly individuals are distributed among species (0 = uneven; 1 = completely even).

### 2.6.3. Margalef's richness (D<sub>Mg</sub>)

Species-richness was also quantified using Margalef's index (D<sub>Mg</sub>), which standardizes raw species counts by sample size. It is defined as:

$$D_{Mg} = \frac{S - 1}{\ln S}$$

where  $S$  is species number and  $N$  the total number of individuals; higher values indicate greater richness.

### 2.6.4. Jaccard similarity (J)

To quantify floristic turnover between the two survey dates, we calculated the Jaccard similarity coefficient (J), defined as the ratio of shared species to the total species pool across both periods. Specifically:

$$J = \frac{c}{a + b - c} \times 100$$

with  $a$  and  $b$  the species counts in 1954 and 2019, respectively, and  $c$  the number of species common to both.

### 2.6.5. Cohen's (d) index

Cohen's (d) index is an effect-size statistic that quantifies the magnitude of a difference between two means in standardized units. In our context, it translates the raw difference in Shannon–Wiener diversity ( $H'$ ) between 1954 and 2019 into a dimensionless measure, making it easier to judge how large the change is, beyond mere statistical significance.

$$d = \frac{\overline{H'}_{1954} - \overline{H'}_{2019}}{\sqrt{\frac{S_{1954}^2 + S_{2019}^2}{2}}}$$

## 2.7. Statistical analysis

Shannon indices from individual surveys were compared between 1954 and 2019 using Welch's  $t$ -test (unequal variances) in R, with effect size (Cohen's  $d$ ) and 95 % confidence intervals estimated via bootstrapping (Efron & Tibshirani, 1993). Normality and homoscedasticity assumptions were checked by Shapiro–Wilk and Levene's tests; where violated, non-parametric (Mann–Whitney) tests were applied.

## 3. Results

### 3.1. Systematic composition and floristic diversity

Floristic surveys conducted by Dubuis and Simonneau in 1954 on 8 plots documented 69 vascular plant species spanning 62 genera and 19 botanical families. The most speciose families were Poaceae (16

species; 23.5 % of the total number of species), Asteraceae (9 species; 11.8%), Brassicaceae (8 species; 11.8%), Caryophyllaceae (6 species; 8.8 %) and Amaranthaceae (5 species; 7.4 %). Together, these five families accounted for 56.5 % of the species richness (39 species) and 66.7 % of the genera (38 genera) in the sub-association *Atriplex mauritanica*–*Suaeda fruticosa*. Six additional families were represented by 2–4 species each, while the remaining eight families were monospecific.

Surveys across analogous plots (7 plots) in 2019 documented only 51 species belonging to 44 genera and the same 19 families previously identified. Poaceae remained the dominant family (9 species; 18 %), followed by Amaranthaceae (8 species; 16 %) and Asteraceae (7 species; 14 %), which showed an increase in rank. Overall, these three plant families, along with Caryophyllaceae (5 species; 10 %), together contributing 56 % of the species richness (28 species) and 53.5 % of the genera (23 genera). All the other families were represented by between one and four species. Three novel families were identified in 2019; Nitrariaceae (*Peganum harmala* L.), Aizoaceae (*Aizoon hispanicum* L.), and Convolvulaceae (*Convolvulus cantabrica* L.) (Table 1).

### 3.2. Floristic turnover and diversity metrics

Comparing the two surveys, notable floristic shifts include the local extirpation of 31 species of the original 69 species historically associated with the sub-association *Atriplex mauritanica*–*Suaeda fruticosa*, indicating the loss of 44.9 % of the 1954 flora.

Extirpated taxa spanned many families (e.g., several Brassicaceae and Poaceae) and include *Astragalus geniculatus* Desf., *Aegilops ventricose* Tausch, *Alyssum linifolium* Willd., *A. scutigerum* Durieu, *Arnebia decumbens* Kuntze, *Eremopyrum orientale* subsp. *orientale*, *Filago germanica* subsp. *spatulata*, *Koeleria pubescens* subsp. *villosa* Trab., *K. linearis*, *Lamium amplexicaule* L., *Lappula redowskii* (Lehm.) Gürke, *Lepidium subulatum* L., *Limonium echioides* Mill., *Linaria follax* Coss. ex Batt. & Trab., *L. simplex* DC., *Lolium rigidum* Gaudin, among others.

In contrast, 13 species not previously recorded appeared by 2019, mostly halophytes or disturbance-tolerant plants. The persistent core (38 species) indicates moderate turnover over 65 years.

Table 1. Comparative taxonomic composition of the *Atriplex mauritanica*–*Suaeda fruticosa* sub-association (1954 vs. 2019), showing family-level species counts and percent contribution in each period.

Botanical family	1954 Genera	1954 Species	1954	2019 Genera	2019 Species	2019
Poaceae	14	16	23.5	9	9	18
Asteraceae	9	9	11.8	6	7	14
Brassicaceae	5	8	11.8	1	1	2
Caryophyllaceae	5	6	8.8	3	5	10
Amaranthaceae	3	5	7.4	5	8	16
Boraginaceae	4	4	5.9	2	2	4
Cistaceae	1	3	4.4	1	2	4
Fabaceae	2	3	4.4	2	2	4
Plantaginaceae	2	3	4.4	1	2	4
Lamiaceae	2	2	2.9	4	4	8
Ranunculaceae	2	2	2.9	1	1	2
Apiaceae	1	1	1.5	1	1	2
Cynomoriaceae	1	1	1.5	1	1	2
Frankeniaceae	1	1	1.5	1	0	0
Geraniaceae	1	1	1.5	1	2	4
Liliaceae	1	1	1.5	–	0	0
Malvaceae	1	1	1.5	–	0	0
Orobanchaceae	1	1	1.5	1	1	2
Plumbaginaceae	1	1	1.5	–	0	0

Nitrariaceae	–	0	0	1	1	2
Aizoaceae	–	0	0	1	1	2
Convolvulaceae	–	0	0	1	1	2
<b>Total</b>	<b>57</b>	<b>69</b>	<b>100</b>	<b>43</b>	<b>51</b>	<b>100</b>

### 3.3. Biological life-form spectra and functional shifts

The Raunkiaer life-form spectrum of the Chott Chergui sub-association (Table 2) reveals significant structural changes in the vegetation between study periods.

In 1954 therophytes (annual, seed-propagated plants) markedly dominated (47 of 69 species, 68%), but by 2019 they comprised only 26 of 51 species (51%), a drop of 17 percentage points. However, their reduction over time, although substantial (-17%), did not reach statistical significance ( $\chi^2 = 2.93$ ,  $p = 0.087$ ), suggesting a trend rather than an abrupt shift in the annual-herbaceous component.

Table 2. Temporal shifts in Raunkiaer life-form spectra between 1954 and 2019, highlighting the decline of therophytes (annuals) and the increase of chamaephytes (perennial subshrubs).

Life-form	1954 Count	1954 %	2019 Count	2019 %	$\Delta\%$ (1954–2019)
Therophytes	47	68	26	51	↓17%
Chamaephytes	13	19	16	31	↑12%
Hemicryptophytes	6	9	6	12	↑3%
Geophytes	3	4	3	6	↑2%
<b>Total species</b>	<b>69</b>	<b>100</b>	<b>51</b>	<b>100</b>	<b>↓18 species</b>

Concurrently, chamaephytes, low-growing perennial shrubs and subshrubs with perennating buds close to the ground, increased from 13 species (19 %) in 1954 to 16 species (31%) in 2019, reflecting a +12 % increase.

Hemicryptophytes (perennial herbs with buds at or just below the soil surface) remained low (9% in 1954 vs. 12% in 2019). Geophytes (plants with underground storage organs) held steady at 4-6 %, reflecting the limited niche for bulbous or rhizomatous species in highly drained, saline substrates.

### 3.4. Syngenetic and anthropogenic drivers

Historical records of Dubuis and Simonneau (1954) describe degraded remnants and residual elements of a former wooded community of *Pinetum halepensis* (Maire 1925) forest associations (*Quercus ilex*, *Juniperus oxycedrus*, *Pistacia lentiscus*, *Jasminum fruticans*, *Rosmarinus tournefortii*). Our surveys confirm the complete extirpation of these arboreal relics' woody species that have entirely vanished from the region. Instead, small woody taxa of several chamaephytic persist as relict indicators of former forest assemblages (*Teucrium polium* L., *Thymus algeriensis* Boiss. & Reut., *Globularia alypum* L.), hinting at long-term degradation of the holm-oak–juniper woodlands.

Notably, the proliferation of disturbance-tolerant species indicative of prolonged overgrazing, *Sisymbrium irio* L. (ruderal therophyte), *Peganum harmala* L. (nitrophilous chamaephyte), and *Atractylis serratuloides* Sieber ex Cass. (spiny hemicryptophyte), provides strong evidence of chronic overgrazing. Indeed, selective grazing tends to eliminate palatable perennials, opening niches for both annual therophytes and grazing-tolerant chamaephytes. This functional shift underscores a transition toward arid-adapted, grazing-resistant communities.

### 3.5. Biogeographic affinities



The vascular flora of Chott Chergui exhibits a complex chorological structure, encompassing four main chorological groups; (i) endemic, (ii) Mediterranean, (iii) northern (Euro-temperate), and (iv) pluriregional elements, with notable shifts between 1954 and 2019.

A comparative analysis between 1954 and 2019 (Table 3) reveals both persistence and turnover among these biogeographic groups.

### 3.5.1. Endemics

Endemic elements remained remarkably stable; seven Maghreb-Tunisian and Algerian endemics persisted unchanged (accounted for 10.1% of species in 1954 and 13.7% in 2019), including *Helianthemum apertum* var. *en-apertum*, *H. virgatum*, *Herniaria mauritanica*, and *Thymus algeriensis*. The slight percentage increase reflects the overall decline in total species richness rather than actual recruitment.

### 3.5.2. Mediterranean element

True Mediterranean-affiliated taxa decreased from 27 species (39.1%) to 19 (37.3%), notably with the losses of several Ibero-Mauritanian species (*e.g.*, *Aizoon hispanicum*) and one circum-Mediterranean species. This contraction suggests a reduction in mesic-adapted taxa, possibly driven by increased summer aridity and soil salinization.

### 3.5.3. Northern species

The Northern Euro-temperate element, cold-adapted relicts remained a minor yet persistent component (from 5 to 4 species; representing 7% to 8%), indicating that cooler-climate relicts have neither expanded nor new ones colonized, consistent with the region's persistent semi-arid Mediterranean climate.

### 3.5.4. Pluriregional (widespread) elements

Pluriregional (widespread) taxa decreased from 29 (42 %) to 21 species (41.2 %), reflecting losses among subtropical and Irano-Turanian elements. Notably, a new strictly Saharo-Sahelian newcomer component (*Atractylis serratuloides*) appeared in 2019.

The decline of cosmopolitan/subcosmopolitan taxa (from 6 to 4) indicates a relative increase in arid-adapted and endemic elements at the expense of mesic Mediterranean and cosmopolitan ones.

Table 3: Chorotype (phytogeographic affinity) shifts between 1954 and 2019, illustrating the complete persistence of endemic species and the contraction of mesic Mediterranean and pluri-regional elements over time.

Chorotype	1954 Count	1954%	2019 Count	2019%
Endemic species	7	10.1	7	13.7
– North-African endemics	5	–	3	–
– Moroccan–Algeria–Spain endemics	1	–	1	–
– Ibero-Maghreb endemics	1	–	2	–
Mediterranean species	27	39.1	19	37.3
– True Mediterranean	17	–	13	–
– West Mediterranean	3	–	3	–
– Ibero-Mauritanian	5	–	1	–
– Circum-Mediterranean	2	–	2	–
Northern (Euro-temperate) species	5	7.2	4	7.8
– Euro-Asia	4	–	3	–
– Paleo-temperate	1	–	1	–
Pluriregional species	29	42.0	21	41.2
– Mediterranean–European–American	1	–	1	–



– Paleo-Subtropical	3	–	2	–
– Mediterranean–Irano-Turanian	4	–	1	–
– Mediterranean–Saharan	3	–	3	–
– Saharan	–	–	1	–
– Cosmopolitan/subcosmopolitan	6	–	4	–
– Saharo-Sindian	2	–	1	–
– Atlantic–Mediterranean	3	–	3	–
– Mediterranean–Saharan–Irano-Turanian	1	–	–	–
– Sub-Mediterranean–Siberian	1	–	1	–
– Steppe	1	–	–	–
– Euro-Mediterranean	2	–	2	–
– Eurasia-North African-Tripolitan	1	–	1	–
– South Mediterranean	–	–	1	–
– North Tropical	1	–	1	–
Total species	69	100.0	51	100.0

### 3.6. Floristic diversity and similarity

Floristic diversity was quantified using Shannon’s diversity index ( $H'$ ) and Pielou’s evenness ( $J'$ ), while species-richness was assessed via Margalef’s index ( $DMg$ ). Temporal turnover was measured by the Jaccard similarity coefficient ( $J$ ). Results are summarized in Table 4.

Overall, species richness and diversity declined between 1954 and 2019 by 26.1 % (from 69 to 51 species), mirrored by a decrease in Margalef’s index from 12.8 to 10.19, indicating a significant drop in the effective number of species per individual sample. These species were primarily chamaephytes (low-growing perennials), indicating a structural shift in vegetation.

Regarding Shannon’s diversity, although both surveys exhibit moderate to high diversity ( $H' > 3.5$ ), the slight reduction (from 3.97 to 3.7) suggests a contraction in both species number and abundance distribution.

Furthermore, Evenness stability measured by Pielou’s evenness remained essentially unchanged (from 0.79 to 0.8), implying that the relative abundance distribution among the remaining species has not become more skewed despite species loss.

Ecological analysis revealed that extirpated taxa were predominantly therophytes (annuals) classified as rare (Braun-Blanquet abundance-dominance scale;  $\leq 20\%$  plot frequency).

The Jaccard similarity index between 1954 and 2019 was low. (In our data,  $J \approx 0.46$ , meaning only about half of the species present in 1954 persisted to 2019.) This moderate floristic overlap ( $\approx 55\%$  persistence) underscores substantial community reassembly over 65 years.

### 3.7. Floristic turnover, persistence and replacement

A Jaccard index of 24 % indicates that only 38 of the original 69 taxa reported in 1954 ( $\sim 55\%$ ) reoccurred in 2019, revealing moderate floristic turnover, whereas 31 species were extirpated and 13 newly recorded. Such low similarity underscores substantial community re-assembly over 65 years. Endemics displayed high persistence (100 %), whereas pluriregional and Mediterranean-Ibero-Mauritanian species showed the greatest attrition. The resilience of endemics suggests that microhabitats safeguarding these narrow-range species remain functional, whereas the retreat of mesic Mediterranean and widespread taxa highlights the combined impacts of climate warming, reduced precipitation, overgrazing, and salinization. The combination of declining richness (Margalef), stable evenness (Pielou), and low community similarity (Jaccard) characterizes an ecosystem undergoing taxonomic reorganization without dominance by opportunistic species.

Table 4: Temporal changes in diversity indices (1954 vs. 2019), showing declines in species richness and diversity metrics, stable evenness, and low floristic similarity between the two periods.

Metric	1954	2019	$\Delta\%$
Taxa (S)	69	51	↓26.1%
Individuals	203	135	↓33.5%
Shannon-Wiener (H')	3.97	3.7	↓6.8%
Pielou's Evenness (J')	0.79	0.8	↑1.3%
Margalef Richness (D)	12.8	10.2	↓20.3%
Jaccard Similarity		24%	

Statistical analysis confirms a significant reduction in floristic heterogeneity over the 65-year interval between 1954 (mean = 3.97, variance = 0.00303) and 2019 (mean = 3.7, variance = 0.00444) surveys (Welch's *t*-test on Shannon diversity (H') :  $t = 3.12$ ,  $df = 291.6$ ,  $p = 1.99 \times 10^{-5}$ ).

This highly significant shift ( $p < 0.001$ ) integrates three key ecological trends represented by (i) a 6.8% decline in Shannon diversity, (ii) a 26.1% reduction in species richness, and (iii) exceptionally low community similarity (Jaccard index = 24%) (Table 5).

Table 5. Shannon diversity *t*-test results (1954 vs. 2019), showing Welch's test statistics comparing H' between the two surveys and confirming a significant diversity decline ( $p < 0.001$ ).

Parameter	1954	2019
Shannon (H')	3.97	3.70
Variance	0.00303	0.00444
t-statistic	3.12	
Df	291.6	
p-value	$1.99 \times 10^{-5}$	

Concurrently, this result confirms that the reduction in species heterogeneity accompanied by the increased variance in diversity metrics is not due to random variation but reflects a real fundamental structural reorganization of the Chott Chergui community beyond simple species loss.

#### 4. Discussion

Our 65-year comparison of Chott Chergui's vegetation reveals a profound compositional and functional reorganization driven by convergent climatic and anthropogenic pressures. Nearly half of the original species, predominantly annual herbs, have disappeared, while drought-tolerant perennial shrubs (chamaephytes) have become considerably more prevalent. This transition from an annual-dominated assemblage to a more woody, perennial community suggests the establishment of an alternative ecological state with substantial implications for ecosystem functioning and resilience. Nevertheless, our study is constrained by its reliance on only two temporal snapshots (1954 and 2019), precluding detection of intermediate community dynamics. Additionally, differences in sampling protocols, observer bias, and taxonomic revisions over six decades may have influenced the species inventories. The limited number of surveyed plots ( $n = 7-8$ ) may not capture the full spatial heterogeneity of Chott Chergui's vegetation. Moreover, the absence of direct measurements of historical precipitation regimes, soil salinity profiles, and grazing intensity limits our ability to disentangle climatic from anthropogenic drivers of change.

Comparable long-term research in Mediterranean drylands (Xofis *et al.*, 2024; Arroyo *et al.*, 2024) have confirmed that intensified grazing and aridity drive richness declines. As Arroyo *et al.* (2024) observed, heavy grazing "removes the most palatable species...favoring those that are grazing-tolerant or avoidant," a pattern mirrored here by the loss of perennial herbs and expansion of unpalatable chamaephytes.

We propose that four principal ecological mechanisms underline the observed floristic turnover. First, climate-induced recruitment failure, whereby increasingly severe summer droughts and elevated temperature extremes exceed the physiological thresholds required for germination and establishment of many annuals (therophytes), thereby constraining their regeneration potential (Houti *et al.*, 2016; Xofis *et al.*, 2024). Intensifying summer drought under a Mediterranean semi-arid regime has favored short-lived therophytes, yet their partial decline suggests that extreme aridity may now exceed thresholds for successful annual recruitment (Benkhettou *et al.*, 2022). Concurrently, low-growing chamaephytes have expanded, indicating a successional move toward more persistent woody elements—even if these remain relictual, low-stature survivors rather than a return to pre-degradation woodlands.

Second, grazing-mediated selection pressures, in which prolonged and intense livestock grazing eliminates palatable perennial herbs and opens niches subsequently occupied by disturbance-tolerant taxa such as *Peganum harmala* and *Atractylis serratuloides* (Arroyo *et al.*, 2024). This dual pressure, climatic and pastoral, has eroded both taxonomic richness and functional resilience, prompting the local extirpation of tree and tall-shrub relics once common on valley margins (Tadj *et al.*, 2022).

Third, soil degradation processes, including trampling, compaction, and vegetation loss, likely accelerate secondary salinization and decrease organic matter, creating edaphic conditions unfavorable to mesic and non-halophytic taxa and promoting salt-tolerant families such as Aizoaceae and Nitrariaceae (Akkacha *et al.*, 2025). Fourth, a successional transition to an alternative stable state, where the former dominance of perennial herbs and woodland relics has been supplanted by a low-stature matrix of shrubs and annuals, which may persist in the absence of active ecological restoration.

These mechanisms align closely with patterns documented in other Mediterranean and semi-arid ecosystems. Laorden-Camacho *et al.* (2025) demonstrated that the interaction of increasing aridity and chronic grazing amplifies shrub encroachment and biodiversity decline in semi-arid steppes, while Di Biase *et al.* (2021) reported that although therophytes often increase under moderate disturbance, their dominance collapses under prolonged extreme drought. The biogeographic fingerprint of “thermophilization”, a decline in mesic Mediterranean and Irano-Turanian taxa offset by a rise in Saharo-Sahelian elements, parallels regional observations in other Mediterranean islands and peninsulas (Xofis *et al.*, 2024; Arroyo *et al.*, 2024). The persistence of narrow-range Maghreb endemics suggests that microrefugia or edaphic niches continue to buffer these taxa even as widespread generalists recede.

Diversity metrics corroborate a fundamental community reassembly: species richness and Shannon diversity declined significantly ( $t = 3.12$ ,  $p < .001$ ), yet evenness remained stable, indicating that species losses were broadly distributed across functional groups. The low Jaccard similarity ( $\sim 0.46$ ) underscores that only half of the 1954 flora persists, a turnover comparable to other Mediterranean rangelands under combined climatic and grazing stressors (Arroyo *et al.*, 2024).

Biologically, the proliferation of chamaephytes likely reflects multiple adaptive strategies—deep root systems accessing subsurface moisture, spines or secondary metabolites deterring herbivory, and perennial lifespan buffering against interannual variability in recruitment. Conversely, the decline of annuals may reflect a mismatch between seed-bank dormancy strategies and increasingly unpredictable precipitation patterns (Di Biase *et al.*, 2021). The emergence of halophytic newcomers highlights the increasing role of soil salinity as an environmental filter, potentially exacerbated by land-use practices such as salt extraction or groundwater withdrawal.

To advance ecological understanding and inform management, future research should integrate high-resolution palaeoclimate reconstructions, detailed soil physicochemical analyses (salinity, organic carbon, bulk density), and quantification of grazing histories. Multivariate approaches (e.g., redundancy analysis, generalized dissimilarity modeling) will enable partitioning of climate versus land-use effects. Additionally, experimental exclosures could evaluate the potential for perennial herb recovery and woodland relic regeneration.

From a conservation perspective, establishing livestock exclusion zones, enhancing soil structure through organic amendments, and monitoring microhabitat refugia are urgent priorities to halt further degradation and promote biodiversity recovery.

## 5. Conclusion

This study provides compelling evidence that over the past six decades, Chott Chergui’s vegetation has undergone extensive taxonomic and functional reconfiguration, reflecting the combined impacts of

climate change and anthropogenic disturbance. Species richness and Shannon diversity have declined significantly, while life-form composition has shifted from annual herbs toward more drought-tolerant chamaephytes (a change that could alter ecosystem processes such as primary productivity, soil stability, and nutrient cycling), indicating a shift toward a more perennial-dominated community. Endemics have endured, suggesting that microrefugia still function, but the loss of mesic and pluriregional taxa, and the first appearance of a Saharo-Sahelian species, signals a biogeographic reorganization under combined climatic and grazing pressures. A low Jaccard similarity (~0.46) indicates that only about half of the 1954 flora persists, underscoring the magnitude of community turnover beyond random expectation. Conservation strategies should focus on mitigating grazing pressure, restoring soil health, and protecting microrefugia to preserve endemic diversity. Future research combining palaeoclimate and edaphic data with advanced multivariate analyses is needed to disentangle the drivers of change and guide adaptive management, ensuring the long-term resilience of Mediterranean semi-arid ecosystems and other climate-sensitive steppe systems.

## Authorship

**M.B., G.B.:** Writing original draft, Methodology, Investigation, Formal analysis. **A.B.:** Writing original draft, Methodology, Investigation, Resources. **K.T.:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

## Declaration of interest

None.

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## Data availability

Data will be made available on request.

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