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ORIGINAL RESEARCH

Uncovering hidden biodiversity through the role of soil seed banks in conserving arid wadis

Sara Hassanen[1] · Yasmin M. Hassan[1] · Elsayeda Gamal Eldin[1] · Wafaa Kamel[1] · Mohamed Saad Zaghloul[1]

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Abstract
Arid desert ecosystems harbor unique plant communities that are highly adapted to harsh environmental conditions but are increasingly threatened by human activities and climate change. Understanding the composition and dynamics of these ecosystems is crucial for effective conservation. In the Ataqa region, the native flora of four unprotected arid wadis is under threat. These wadis are Wadi Hagul, Wadi El-Bada, Wadi El-Gamil, and Wadi Amlog. The main threats include vegetation over-collection, resort development, quarrying, industrial expansion, road construction, and climate change. This study underscores the vital role of soil seed banks as biodiversity reservoirs that enhance ecosystem resilience and aid in conserving native and rare plant species under such pressures. Between 2023 and 2024, fieldwork was conducted to collect plant specimens and soil samples, enabling a comparative analysis of above-ground vegetation and soil seed banks. A total of 41 species were identified in the soil seed bank, comprising 31 flowering plants and 10 bryophytes. However, only 12 of these species were also found in the above-ground flora. The families Asteraceae, Caryophyllaceae, and Poaceae were the most represented in the seed bank, with therophytes emerging as the dominant life form. TWINSPAN classification revealed five distinct plant assemblages, with *Bryum argenteum*, *Tamarix nilotica*, *Zygophyllum coccineum*, and *Spergularia diandra* as dominant species. Environmental parameters particularly electrical conductivity, pH, and calcium carbonate content were key drivers influencing the distribution patterns of above-ground vegetation. Notably, the seed bank contained several species not recorded in the existing flora of the region, including *Chenopodium vulvaria*, *Juncus fontanesii*, and *Riccia congoana*. This suggests that the seed bank serves as a reservoir for rare and cryptic species. These findings have important implications for ecological restoration and the conservation of biodiversity in arid environments under anthropogenic and climatic pressures.

Keywords Soil seed bank diversity · Arid ecosystem restoration · Vegetation–Soil relationships flowering plants · Bryophytes · New recorded species

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Extended author information available on the last page of the article

Introduction

Biodiversity loss is a growing global crisis, with native plant species facing severe threats from habitat degradation, climate change, and human activities. These pressures contribute to soil degradation, salinization, erosion, and the spread of invasive species, leading to drastic shifts in plant community structures and ecosystem functioning (Reed et al. 2011). In arid and semi-arid regions, where vegetation is already adapted to extreme environmental conditions, these threats pose an even greater risk, reducing plant regeneration potential and accelerating desertification (Bai et al. 2020).

The Egyptian Eastern Desert, characterized by its fragile arid ecosystems, is experiencing increasing anthropogenic pressure, particularly in unprotected Wadis. The expansion of industrial projects, quarries, resort development, road construction, and overharvesting of medicinal plants has led to significant habitat loss and fragmentation (Abd El-Ghani et al. 2014). These impacts not only threaten native and rare plant species but also disrupt the natural regeneration processes that sustain biodiversity in such harsh environments. Conservation strategies tailored to protect and restore these unique plant communities are therefore urgently needed.

Soil seed banks are critical biodiversity reservoirs that contribute to ecosystem resilience in arid environments. They serve as genetic repositories, ensuring species persistence despite unpredictable rainfall, grazing, and other disturbances. By accumulating dormant seeds over time, seed banks act as an ecological buffer, allowing plant communities to recover after extreme events such as droughts, floods, or human-induced disturbances (Chang et al. 2001). This makes them a powerful tool for habitat conservation and ecological restoration, particularly in regions experiencing land degradation and climate variability (Nafea 2016). In addition to flowering plants, bryophyte diaspore banks are important indicators of ecosystem health, reflecting habitat quality through their dependence on specific environmental conditions (Govindapyari et al. 2010). However, diaspore banks are often overlooked in conservation research, leaving a gap in understanding their contribution to biodiversity and ecosystem resilience. By incorporating both seed and diaspore banks in conservation studies, researchers can gain a more comprehensive understanding of ecosystem health, which is crucial for developing more effective strategies to preserve native flora in arid areas.

Despite their recognized importance, soil seed banks in arid regions remain poorly studied, particularly in the context of their relationship with above-ground vegetation. Previous studies have focused on seed bank dynamics in temperate and tropical ecosystems, yet little is known about how arid soil seed banks contribute to plant community regeneration (Kemp 1989; Al-Faraj et al. 1997; Zaghloul 2008; Gomaa 2012, 2014; Al-Huqail et al. 2025). Moreover, most research in Egypt has concentrated on protected areas, leaving unprotected and human-impacted landscapes largely unexplored.

This study represents the first conservation-focused investigation of soil seed banks in the Ataqa region, examining four unprotected wadis: Wadi Hagul, Wadi El-Bada, Wadi El-Gamil, and Wadi Amlog. It is also the first in the region to integrate both seed and diaspore banks, offering a comprehensive and unique perspective on biodiversity resilience in arid ecosystems. By comparing the composition of the soil seed bank with the above-ground flora, the study sheds light on species persistence, seed bank functionality, and the conservation potential of these fragile habitats. We hypothesize that the soil seed bank differs significantly from the above-ground flora in both species diversity and structure. This

research aims to uncover hidden biodiversity, document ecological patterns, and provide critical insights for the conservation of rare and native plant species in these threatened desert ecosystems.

Materials and methods

Study area

The study area is located at the Red Sea coastal land of Egypt characterized by several Wadis that run eastward to flow into the Gulf of Suez and Red Sea. It covers about 3,619 km², represented by 30 collection sites including four Wadis: Wadi Amlog, Wadi Hagul, Wadi El-Bada, and Wadi El-Gamil. Moreover, they include other sites: Ain Shokna, Infront of Gebel Moghra Bahria, and Infront of Gebel Um Rosis (Supplementary Table **S1;** Fig. 1**).**

The four main Wadis selected for this study were chosen for their representativeness of the study area. Wadi Hagul, the largest and most prominent inland Wadi, serves as a key site for inland desert flora. Wadi El-Bada, the second most significant inland Wadi, offers additional ecological diversity that complements Wadi Hagul. On the other hand, Wadi Amlog and Wadi El-Gamil, located along the coast, represent coastal environments, together providing a comprehensive overview of the region's flora.

The general climate of the Suez region can be described as hyper-arid to arid, characterized by high temperatures, scarce rainfall, and large thermal amplitude between day and night. Based on the Köppen–Geiger classification, the region falls within the BWh (hot desert) climate type, while according to the Holdridge life zone system, it is classified as a subtropical desert. The mean annual temperature averages around 23 °C, and the mean annual precipitation is approximately 17 mm, with a rainfall probability of less than 2% throughout most of the year. Using the UNEP Aridity Index (AI = P/PET), the region's value (< 0.05) confirms its extreme aridity, reflecting very limited soil moisture availability. The climate is predominantly influenced by northern winds averaging 12 km/h, contributing to high evapotranspiration and low relative humidity (Climate-Data.Org 2023). These climatic indices collectively indicate an environment of strong desiccation stress, which shapes the xerophytic vegetation composition and plant adaptation strategies in the study area.

The Red Sea's surrounding desert has primarily mountainous geomorphological features with a series of coastal mountains (1,705-2,187 m above sea level) flanking the sea on its western side. The deep plain is a gently sloping plain that lies between the hills and the coastline. The unevenly sized coastal plain is covered in sand and the Wadis or shallow drainage systems meander over it. The water in these Wadis drains as they meander eastward emptying into the Red Sea and the Gulf of Suez (Zahran and Willis 2009).

Wadi Hagul comprises 53.3% of the studied collection sites and covers an area of approximately 375 km². Positioned in the northwestern Gulf of Suez, it lies between Gebel Ataqa to the north and the El-Galala El-Bahariya Plateau to the south. The Wadi's primary drainage system stretches for about 35 km, channeling runoff from both flanks. As it flows, it cuts through Miocene limestone formations and carves its way into ochreous-hued marls, grits, and calcareous layers of the Upper Eocene. Gradually, the channel widens, meandering through deposits of alluvial gravel before reaching the coastal plain and eventually emptying into the Gulf of Suez (Arnous et al. 2023).

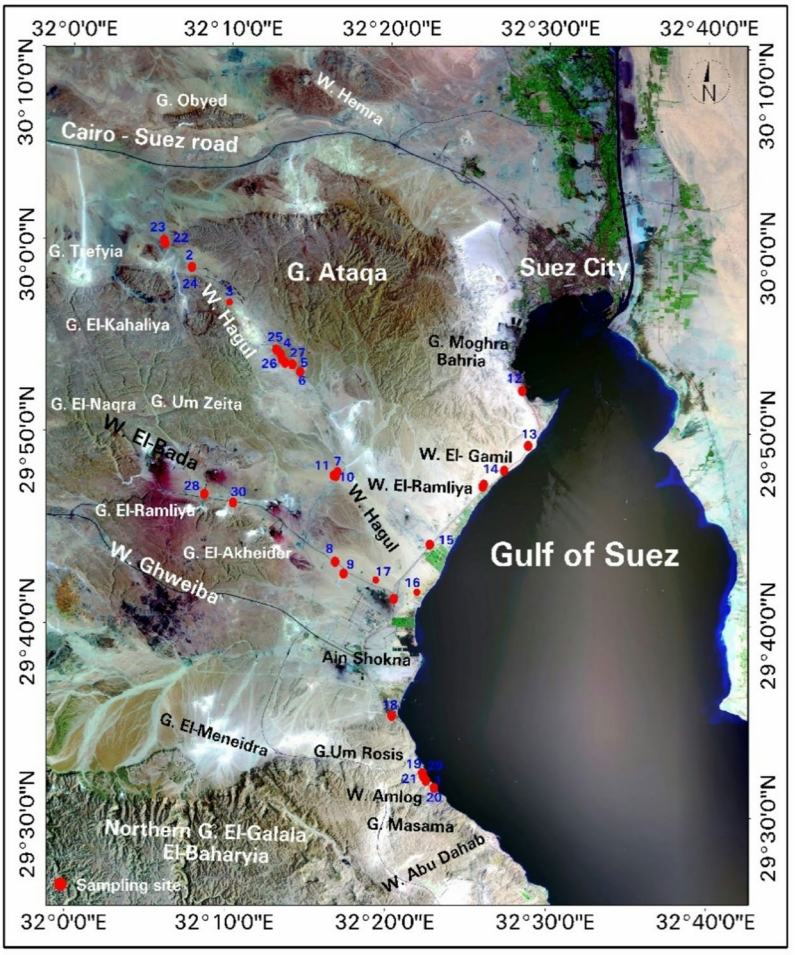


Fig. 1 Map of collection sites created by using ERDAS Imagine 14 and ArcGIS 10.6 (Esri 2024)

Methods

Plant samples

Plant specimens were collected using the belt transect method within the study area, encompassing Wadi Hagul, Wadi El-Bada, Wadi El-Gamil, and Wadi Amlog, over the period 2023–2024. At each site, transects were established along the radius of the wadi, with their length determined by the point at which no new species were recorded, indicating stabilization of vegetation composition. This criterion ensured that species richness was adequately captured for each wadi. These transects ranged from approximately 150 m to 200 m in length according to prevailing vegetation status. Similarly, transect widths varied between 30 m and 50 m adjusted based on vegetation structure and composition changes to ensure accurate representation of plant diversity in each habitat. Within each transect, the presence

and absence of all encountered plant species were recorded continuously along and within the transect. It was established in different sites in each wadi to encompass habitat heterogeneity and ensure full coverage of the wadi's vegetation. Plant samples were clipped using sterilized clippers, placed in labeled plastic bags and numbered for reference. The gathered samples underwent drying, pressing, mounting, labeling and identification. Sample locations were recorded using a handheld Magellan GPS 315 device, providing accurate geographic coordinates for each site.

The plant specimens, specifically flowering plants were identified by Prof Elsayeda Gamal Eldin, Prof Wafaa Kamel, and Dr Sara Hassanen based on the works of Täckholm (1974), and Boulos (1999, 2000, 2002, 2005). For precise identification, the plant flora of neighboring countries was also consulted, following the methods demonstrated by Zohary (1966) and Migahid (1978). The most current valid names of the recorded taxa were updated and confirmed using global reference databases (IPNI POWO). Additionally, specimens and herbarium sheets stored at the Suez Canal University Herbarium (SCU-I) were compared. Each specimen is preserved at the SCU-I Herbarium, Suez Canal University, with three to seven voucher specimens per taxon (Supplementary Table S2). The geographical distribution of species was determined according to Boulos (2009).

Bryophytes samples

The specimens of bryophytes (liverworts and mosses) were first cleaned mechanically using a brush or needle to remove soil particles then were gently cleaned under a binocular stereoscopic microscope. They were then soaked in a drop of diluted glycerine and washed with tap water. The specimens were then transferred to glycerine and had left for several hours to fully saturated plant tissues. They were then mounted in glycerine jelly and refrigerated to solidify (Johansen 1940; Abou Salama 1985).

The study also examined the morphological and anatomical criteria of stems and leaves. Free hand sections were prepared from leaves from the sub-apical part of the gametophyte which were considered typical for the species under examination. For studying leaf shape, cells and other characteristics, leaves were carefully removed from the stems ensuring that entire leaves were detached. For leaf and stem sections, free-hand transverse sections were prepared from the gametophyte's leaves and stems. These sections were created by placing the specimens in water on a clean glass slide under a binocular stereoscopic microscope and cutting them with a sharp razor blade and a fine needle (Wilson 1990).

The bryophyte specimens were identified according to the works of Bilewsky (1965), Flowers (1973), Heyn and Hernstadt (2004), Smith (1980, 2004), Magill (1981), and Nyholm (1975). The specimens were matched with pre-identified Egyptian bryophyte specimens stored in the Suez Canal University Herbarium (SCU-I). The geographical distribution of the bryophytes was based on the research of El-Saadawi et al. (2015); El-Saadawi and Taha (2020).

Identifying bryophytes presented significant challenges due to their abnormal growth in the greenhouse and the limited time they took to mature before the final census. Generally, bryophyte identification is a complex procedure. Numerous factors can impede the identification process including polymorphism, the variability of taxonomically significant traits, environmental adaptability reduced individual numbers in certain samples and the rarity of sporophytes as most identification keys are based on sporophytic characteristics.

Additionally, the lack of literature and comparable bryophyte vegetation relevant to Egypt poses a significant challenge. A major issue confronting scientists studying bryophytes is the ambiguous definition of species within certain taxa and the frequent reclassification of multiple species across different genera.

Soil samples

Soil seed bank samples

The soil sampling was carried out in late summer 2023 after seed shedding of most species in the study area. A total of 90 soil samples were taken from 30 sites with three samples collected from each site. Each sample was obtained by marking a 25 × 25 cm quadrate and digging to a depth of 0–3 cm. These samples were labeled, air-dried and stored under laboratory conditions until sowing. To ensure comprehensive representation of the soil seed bank each sample was shown in three separate trays resulting in nine replicates per site and a total of 270 trays in the experiment. This high level of replication allowed for a robust estimation of species diversity effectively capturing both common and less frequent species across the study area.

To control potential airborne contamination in the greenhouse, nine control trays were used, each containing only sterile soil. These control trays were prepared at the beginning of the experiment and maintained under the same environmental conditions as the sample trays from March 2024 to October 2024. The sterile soil in these trays provided a baseline to detect any extraneous seeds or spores that might have entered the greenhouse environment during the study period.

The methodology for seed bank studies was outlined by Roberts (1981) and Hutchings (1986). The most direct method for detecting viable seeds in soil is to observe the emergence of seedlings in situ. However, it is likely that the germination requirements for many seeds present will not be met during the observation period. A more commonly employed technique involves taking a representative soil sample and determining seed numbers either by placing the soil under conditions conducive to germination or by using physical separation methods based on differences in size and/or density (Roberts 1981).In this method of estimating seed numbers soil was placed directly into a shallow container or spread in a thin layer on a suitable medium kept moist and the resulting seedlings are identified and recorded.

The seed bank investigation was conducted in a greenhouse from March 2024 to October 2024. Prior to sowing the bottoms of plastic trays (approximately 25 cm in diameter) were filled with 3 cm of pre-washed and sterilized sand heated in an oven at 200 °C for 24 h to ensure it was nutrient-deficient and free from viable seeds. This substrate allowed only the viable seeds from the investigated soil samples to germinate, promoting quick root development in search of nutrients.

Soil seed bank samples were sieved through a 2 mm mesh to separate and eliminate larger gravel particles ensuring no microhabitat effects that could lead to misleading results during sowing. This sieve size was chosen to prevent the exclusion of any seeds. A volume of 50 cm^3 from each sample was sown with three replicates for each sample to ensure replication. This amount was spread in a 0.25–0.5 cm thick layer over the sterilized sand. In the greenhouse, the temperature for the soil seed bank study was carefully controlled gradually

increasing from 25 to 27 °C during the first two months to 30–32 °C in the following two months and reaching 33–35 °C for the final phase. Humidity was consistently maintained at 65% and natural light conditions were used without any artificial light supplementation (i.e. natural regime). The watering regime was implemented daily with watering starting every morning for a duration of 10 min to ensure the soil remained adequately moist for seed germination. Germinated seedlings and bryophytes were documented with weekly photographs. While some seedlings successfully developed foliage leaves others failed to thrive and died at early stages rendering them unidentified and categorized as unknowns.

Chemical and physical analysis of soil samples

For soil analysis, three soil samples were collected from each collection location. Using a shovel, the samples were taken at a depth of 0–30 cm. To create a single composite soil sample, the samples were combined and allowed to air dry for a week on sheets of paper. To remove pebbles and debris, the composite soil samples were run through a 2 mm sieve. The Pipette technique was used for physical analysis (Tributh 1970). By using the Walkley and Black method the amount of organic matter and carbon was calculated (Jackson 1967).

Chemical soil analysis was performed on soil samples. In which, the Jenway 3310-meter model was used to measure the electrical conductivity (EC) of the saturated soil paste extract (Richards 1954). A bench-type Beckman glass electrode pH meter was used to measure the pH of the soil in 1:2.5 soil water solutions (Page et al. 1982). The saturated soil was subjected to volumetric titration employing ethylene diamine tetra acetic acid (EDTA) to extract calcium and magnesium which used to test potassium and sodium using a flame photometer (Page et al. 1982). Sulfuric acid was used to titrate bicarbonate (Page et al. 1982). and silver nitrate was used to quantify chloride. Total carbonates were computed using Collin's Calcimeter (Piper 1950).

Statistical analysis and diversity indices

The TWINSPAN (Two-way Indicator Species Analysis) technique was used in the PC-ORD computer program version 4.01 for Windows (McCune and Mefford 1999), to classify the phytosociological data set which included 30 sites and 41 species of seed bank, in addition to 30 sites and 72 species of above-ground flora. By classifying individuals and attributes, this multivariate analytic technique puts multivariate data in an ordered two-way table. The DCA (Detrended Correspondence Analysis) was used in the PC-ORD computer program (McCune and Mefford 1999), version 4.01 for Windows to interpret the relationships between species and their environments (seed bank and above- ground flora (.

The one-way Permutational Multivariate Analysis of Variance (PERMANOVA) was used to assess differences in species composition between above-ground flora and soil seed bank communities across 30 sites. Euclidean distance was used, with 9,999 permutations, to evaluate the differences between the two community types. These statistical analyses were performed using PAST version 4.11 (Hammer et al. 2001).

Beta diversity was used to measure the rate at which a region's species composition varies. As a result, it counts the number of unique habitats found in an area as well as the occurrence of species switching between different areas of the same habitat. The indices will be computed using each of the chosen samples present in the current data set. The samples

were thought to be organized in the data grid according to where they appear along the transect. Beta Diversity (ß-Diversity) is calculated by using the PAST 4.11 version (Hammer et al. 2001), including six indices:

1. Whittaker's βw.

$$\beta_W = (S/\alpha) - 1$$

S = the total number of species, α the average species richness of the samples.

2. Cody's βc.

$$\beta_C = \frac{g(H) + l(H)}{2}$$

g(H) is the number of species gained, l(H) the number lost moving along the transect.

3. Routledge.

$$\beta_R = \frac{[S^2]}{2r + s} - 1$$

r the number of species pairs with overlapping distributions.

4. Wilson and Schmida's βT.

$$\beta_T = \frac{[g(H) + l(H)]}{2\alpha}$$

5. Harrison 1.

$$\beta = \left\{ \frac{[(S/\bar{\alpha} - 1)]}{(N - 1)} \right\} \times 100$$

6. Harrison 2.

$$\beta = \left\{ \frac{[(S/\alpha_{max} - 1)]}{(N - 1)} \right\} \times 100$$

α is the maximum species richness in any one sample.

Map processing and analysis

The mosaic map was produced utilizing Landsat 8 satellite imagery (Path 176/Row 39 and 176/Row 40) acquired from the USGS Earth Explorer. To ensure optimal visibility, cloud-free imagery from late summer was selected. The data underwent geo-rectification and projection to the WGS84 datum and UTM N36 coordinate system. Atmospheric correction, employing the Dark-Object subtraction method at a 30-meter spatial resolution, was applied. Subsequent analysis involved standard remote sensing and GIS image processing techniques, executed within ERDAS Imagine 14 and ArcGIS 10.6.

Results

Seed bank composition

The seed bank experiment showed the presence of 41 species in the study area including 31 species of flowering plants and 10 non-flowering plants (Bryophytes). The recorded flowering plants comprised 31 species, including 7 monocotyledons and 24 dicotyledons, distributed among 28 genera and 12 families. Of these species, 13 were perennials and 18 were annuals. The most represented families were Asteraceae (7 species; 22.5%), Caryophyllaceae (6 species; 19.3%), and Poaceae (5 species; 16.1%). These were followed by Brassicaceae (4 species) and Zygophyllaceae (3 species). While the monogeneric families were represented by eight families among them: Amaranthaceae, Fabaceae, Plantaginaceae, Polygonaceae and Tamaricaceae (Table 1; Fig. 2). No germination was observed in the control trays throughout the study period confirming that the observed seedling emergence in the sample trays originated from the soil seed bank and was not affected by external contamination. Moreover, a few individuals failed to thrive and died at early stages, preventing complete identification. These were coded as unknown species. A total of three such unidentified individuals were recorded in sites 9 and 23 (Supplementary Table S3).

The annuals represented most of the recruited species by 58% including *Chenopodium vulvaria*, *Eragrostis barrelieri*, *Ifloga spicata*, *Pteranthus dichotomus* and *Spergularia diandra*. On the other hand, the perennials represented 41.9% of the recruited species including *Pulicaria undulata*, *Gypsophila capillaris*, *Juncus fontanesii* and *Phragmites australis.*

While the Bryophytes (liverworts and mosses) were represented by ten species, 5 genera and 3 families. The three families were Ricciaceae, Pottiaceae and Bryaceae. Moreover, *Trichostomum*, *Barbula*, *Riccia*, *Bryum* and *Ptychostomum* were represented by the five genera. The ten species of the non-flowering plants represented 24.3% of the recorded taxa, among these species were *Barbula convoluta*, *Riccia congoana*, *Bryum argenteum*, and *Ptychostomum imbricatulum*.

Dominant species and abundance patterns

Some of the species that were recorded in seed bank exhibit significant dominance. For example, *Tamarix nilotica* was recorded in 30 sites (206 pots) and represented 100% of the total number of sites, indicating its highest occurrence, followed by *Zygophyllum coccineum* recorded in 27 sites (123 pots, 90%). Moreover, the most abundant non-flowering plant was *Bryum argenteum* which was recorded in 9 sites (26 pots with 30%). But *Matthiola longipetala*, *Pteranthus dichotomus*, *Eragrostis barrelieri*, *Schismus arabicus*, *Halopeplis perfoliate*, and *Riccia congoana* were recorded in only site (one pot, 3.33%) showing the lowest occurrence (Table S3).

Comparison with above-ground flora

Although the soil seed bank samples were collected from the same locations as the above-ground flora, there were noticeable differences between the two (Table 1). The most common plant families in the above-ground flora were Asteraceae (14 species), Zygophyllaceae (7 species), Amaranthaceae (6 species), and Poaceae (7 species) (Fig. 2). However, the

Table 1 Difference between plant species recorded in the soil seed bank and the above-ground flora. Note: lifespan: Ann=Annual, Bi=Biennial, Per = Perennial. Life form: Th=Therophytes, H= Hemicryptophytes, Ph= Phanerophytes, Ch= Chamaephytes, C= Cryptophytes, P=Parasites, asterisk (*) refers to new recorded species to the study regions, (^) meaning this plant wasn't collected by any previous study as Abdelaal (2017) and Bedair et al. (2021)

Family	Species	life span	Life form	Above-ground Flora	Seed bank
Aizoaceae	*Aizoon canariense* L.	Ann	Th	+	-
Amaranthaceae	*Anabasis setifera* Moq.	Per	Ch	+	-
	Arthrocaulon macrostachyum (Moric.) Piirainen & G. Kadereit	Ann	Th	+	-
	Bassia indica (Wight) A.J.Scott	Per	Ch	+	-
	Caroxylon. inerme (Forssk.) Akhani & Roalson	Ann	Th	+	-
	^Chenopodium vulvaria L.	Ann	Th	-	+
	Haloxylon persicum Bunge	Per	Ph	+	-
	H. salicornicum (Moq.) Bunge ex Boiss.	Per	Ch		
Apiaceae	*Deverra tortuosa* (Desf.) DC.	Per	Ch	+	-
Apocynaceae	*Calotropis procera* (Aiton) W.T. Aiton.	Per	Ch	+	-
	Cynanchum acutum L.subsp. *acutum*	Per	H	+	-
	*Leptadenia pyrotechnica (*Forssk.) Decne	Per	Ph	+	-
	Pergularia tomentosa L.	Per	Ch	+	-
Asteraceae	*Achillea fragrantissima* (Forssk.) Sch.Bip.	Per	Ch	+	-
	Brocchia cinerea (Delile) Vis.	Ann	Th	-	+
	Centaurea aegyptiaca L.	Bi	Th	+	-
	C. pallescens Delile.	Ann	Th	+	-
	Echinops spinosus L.	Per	H	+	-
	Erigeron bonariensis L.	Ann	Th	+	-
	Ifloga spicata (Forssk.) Sch.Bip. subsp. *spicata*	Ann	Th	+	+
	Iphiona mucronata (Forssk.) Asch. & Schweinf	Per	Ch	+	-
	Launaea mucronata (Forssk.) Muschl subsp *mucronate*	Per	Ch	+	-
	L. nudicaulis (L.) Hook.f.	Per	Ch	+	-
	L. spinosa (Forsk.) Sch.Bip. ex Kuntze	Per	Ch	+	-
	Pluchea dioscoridis (L.) DC.	Per	Ph	+	+
	Pulicaria incisa (Lam.) DC.	Per	Ch	+	-
	P. undulata (L.*)* C. A. Mey.subsp. *undulata*	Per	Ch	+	+
	Reichardia tingitana (L.) Roth	Ann	Th	+	+
	^Senecio aegyptius L.	Ann	Th	-	+
	Sonchus oleraceus L.	Ann	Th	-	+
Boraginaceae	*Echium humile* Desf	Ann	Th	-	+
	Heliotropium arbainense Fresen.	Per	Ch	+	-
	H. bacciferum Forssk. var *bacciferum*	Per	Ch	+	-
	H. digynum (Forssk.) Christens	Per	Ch	+	-
	Trichodesma africanum (L.) Sm.	Ann	Th	+	-

Table 1 (continued)

Family	Species	life span	Life form	Above-ground Flora	Seed bank
Brassicaceae	*Anastatica hierochuntica* L.	Ann	Th	+	+
	Coincya tournefortii (Gouan) Alcaraz, T.E.Díaz, Rivas Mart. & Sánchez-Gómez	Ann	Th	+	-
	Diplotaxis harra (Forssk.) Boiss.	Ann	Th	-	+
	Eremobium aegyptiacum (Spreng.) Asch. var *aegyptiacum.*	Bi	Th	+	-
	Farsetia aegyptia Turra, Farset.	Per	Ch	+	-
	Matthiola longipetala (Vent.) DC.	Ann	Th	-	+
	Zilla spinosa (L.) Prantl.	Per	Ch	+	-
Capparaceae	*Cleome amblyocarpa* Barratte & Murb.	Ann	Th	+	-
Caryophyllaceae	*Gypsophila capillaris* (Forssk.) C.Chr ^	Per	Ch	+	+
	Herniaria hemistemon J.Gay	Per	H	-	+
	^*Polycarpaea robbairea* (Kuntze) Greuter & Burdet.	Per	Ch	-	+
	^*Pteranthus dichotomus* Forssk.	Ann	Th	-	+
	^*Spergularia diandra* (Guss.) Heldr.	Ann	Th	-	+
Convolvulaceae	*Convolvulus hystrix* Vahl.	Per	Ch	+	-
	C. lanatus Vahl.	Per	Ch	+	-
Cucurbitaceae	*Citrullus colocynthis* (L.) Schrad.	Per	H	+	-
	Cucumis melo L.	Ann	Th	+	-
Euphorbiaceae	*Euphorbia retusa* (L.) Forssk.	Per	Ch	+	-
Fabaceae	*Astragalus sieberi* DC.	Per	Ch	+	-
	Crotalaria aegyptiaca Benth.	Per	Ch	+	-
	Taverniera aegyptiaca Boiss.	Per	Ch	+	-
	Trigonella stellata Forssk	Ann	Th	-	+
	Vachellia tortilis subsp. *raddiana* (Savi) Kyal. & Boatwr.	Per	Ph	+	-
Juncaceae	^*Juncus littoralis* C. A. Mey.	Per	H	-	+
	*^*J. fontanesii* Gay. ex *Laharpe* subsp. *Pyramidatus*	Per	C	-	+
Lamiaceae	*Lavandula coronopifolia* Poir.	Per	Ch	+	-
Neuradaceae	*Neurada procumbens L.*	Ann	Th	+	-
Nitrariaceae	*Nitraria retusa* (Forssk.) Asch.	Per	Ph	+	-
Plantaginaceae	^*Plantag sp*.	Per	Ch	-	+
Poaceae	^*Cenchrus biflorus* Roxb	Ann	Th	-	+
	C. divisus (J.F.Gmel.) Verloove, Govaerts & Buttler	Per	C	+	-
	Cynodon dactylon (L.) Pers.	Per	Ch	+	-
	Diplachne fusca (L.) P.Beauv. ex Roem. & Schult.	Per	C	+	-
	^*Eragrostis barrelieri* Daveau	Ann	Th	-	+
	Imperata cylindrica (L.) Raeusch	Per	H	+	+
	Lasiurus scindicus Henrard.	Per	H	+	-
	Panicum turgidum Forssk.	Per	H	+	-
	Phragmites australis (L.) (Cav.) Trin.ex. Steud.	Per	C	+	+
	^*Schismus arabicus* Nees.	Ann	Th	-	+
Polygonaceae	*Rumex vesicarius* L.	Ann	Th	+	+
Resedaceae	*Ochradenus baccatus* Delile	Per	Ph	+	-

Table 1 (continued)

Family	Species	life span	Life form	Above-ground Flora	Seed bank
Solanaceae	*Lycium shawii* Roem. & Schult.	Per	Ph	+	-
	Hyoscyamus boveanus (Dunal.) Asch. & Schweinf.	Per	Ch	+	-
	H. desertorum (Asch. ex Boiss.) Täckh.	Ann	Th	+	-
	H. muticus L.	Per	Ch	+	-
Tamaricaceae	*Tamarix aphylla* (L.) H. Karst.	Per	Ph	+	-
	T. nilotica (Ehrenb.) Bunge.	Per	Ph	+	+
	T. tetragyna Ehrenb.	Per	Ph	+	-
Urticaceae	*Forsskaolea tenacissima* L.	Per	Ch	+	-
Zygophyllaceae	*Tribulus mollis* Ehrenb. ex Schweinf.	Ann	Th	+	-
	T. terrestris L.	Ann	Th	+	-
	Zygophyllum arabicum (L.) Christenh. & Byng	Per	Ch	+	-
	Z. coccineum L.	Per	Ch	+	+
	Z. decumbens Delile	Per	Ch	+	+
	Z. molle (Delile) Christenh. & Byng	Per	Ch	+	+
	Z. Simplex L.	Ann	Th	+	+
Bryophytes					
Bryaceae	^*Bryum argenteum* Hedw.	-	-	-	+
	^*B. radiculosum* Brid.	-	-	-	+
	^*B. subapiculatum* Hampe.	-	-	-	+
	^*Ptychostomum imbricatulum* (Müll. Hal.) D.T. Holyoak & N.Pedersen	-	-	-	+
Pottiaceae (sub family): Merceyoideae	^*Barbula convoluta* Hedw.	-	-	-	+
	^*B. unguiculata* Hedw.	-	-	-	+
Pottiaceae (sub family): Trichostomoideae	^*Trichostomum brachydontium* Bruch.	-	-	-	+
Ricciaceae	^*Riccia. cavernosa* Hoffm	-	-	-	+
	*^*R. congoana* Stephani.	-	-	-	+
	^*R. frostii* Austin.	-	-		+

composition of annuals and perennials varied significantly. In the seed bank, there were only 18 annual species, 52 perennial species, and two biennials, while the above-ground flora showed a different balance (Fig. 3).

Furthermore, species diversity varies between the two components. The seed bank study recorded 41 species; a lower number compared to the 72 species identified in the above-ground flora. Notably, a substantial proportion (70.7%) of the species recorded in the seed bank were absent from the above-ground survey. These exclusive species included *Chenopodium vulvaria*, *Pteranthus dichotomus*, *Spergularia diandra*, *Trigonella stellata*, *Juncus fontanesii*, *Schismus arabicus*, and all non-flowering plants.

Conversely, the similarity between the seed bank and the above-ground flora was relatively low, with only 12 shared species, accounting for 15.2% of the above-ground flora. These included *Tamarix nilotica*, *Pluchea dioscoridis*, *Pulicaria undulata*, *Reichardia tingitana*, *Gypsophila capillaris*, *Anastatica hierochuntica*, *Zygophyllum coccineum*, *Zygo-*

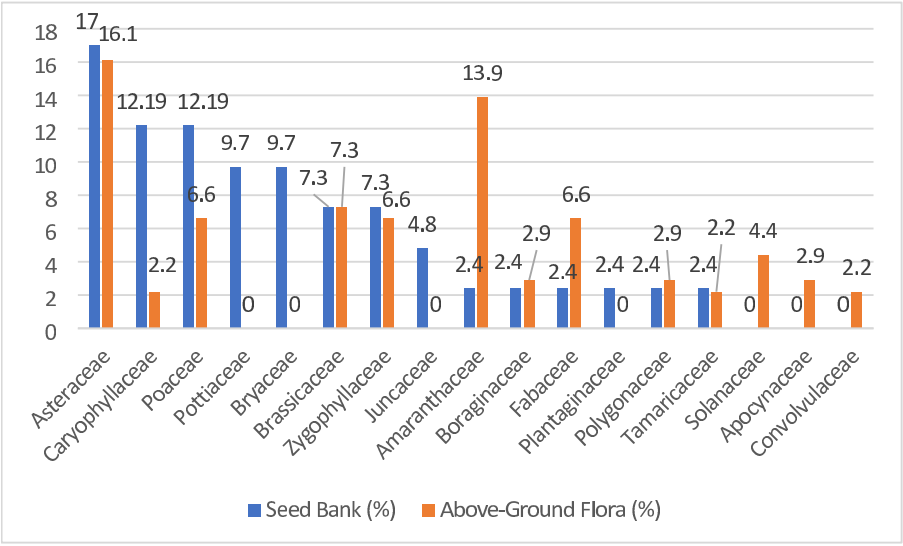


Fig. 2 Comparison of family size between above- ground flora and seed bank flora

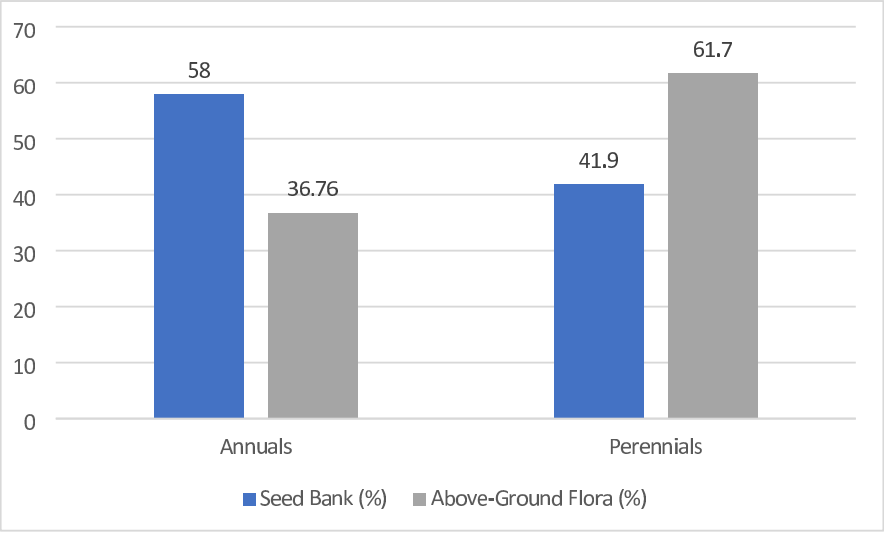


Fig. 3 Difference in lifespan among above- ground flora and seed bank flora

phyllum simplex, and *Zygophyllum decumbens.* This limited overlap suggests differential survival and recruitment strategies between the seed bank and the standing vegetation.

Life form spectrum: seed bank vs. above-ground flora

The life forms spectrum of soil seed bank revealed that Therophytes was the highest one with a percentage 54.8%. Followed by Chamaephytes representing 22.5% followed by Hemicryptophytes and Cryptophytes represented 9.6% and 6.4% (Table 1).

Upon the comparison between the life form spectrum of the soil seed bank and above-ground flora, there were a clear difference between them (Table 1) (Fig. 4). Accordingly, the lifeform spectrum of the collected wild flora revealed that the highest represented lifeform, Chamaephytes was 44.4%, followed by Therophytes, which was 27.7%. Phanerophytes, Hemicryptophytes, and Cryptophytes represented 13.8%, 9.7%, and 6.4%, respectively.

Species composition and dominance within soil seed bank assemblages

The presence and average abundance of species composition of soil seed bank for these assemblages are given in Supplementary Table S4 and Table 2. It is clear that the first assemblage (I) has two dominant species with 100% presence *Bryum argenteum* and *Tamarix nilotica* with average abundance 4.6 and 4.8. While the codominant species is *Zygophyllum coccineum* whose presence and average abundance represent 80%, 4.75. Moreover, *Pluchea dioscoridis* and *Zygophyllum simplex* represent the associated species whose presence and average abundance is 60%, 1.00 and 3.33.

In the second assemblage (II), *Tamarix nilotica* is the dominant species with 100% presence and average abundance of 3.9. The codominant species is *Zygophyllum coccineum*, whose presence and average abundance are 89.4% and 4.11. Moreover, *Sonchus oleraceus*

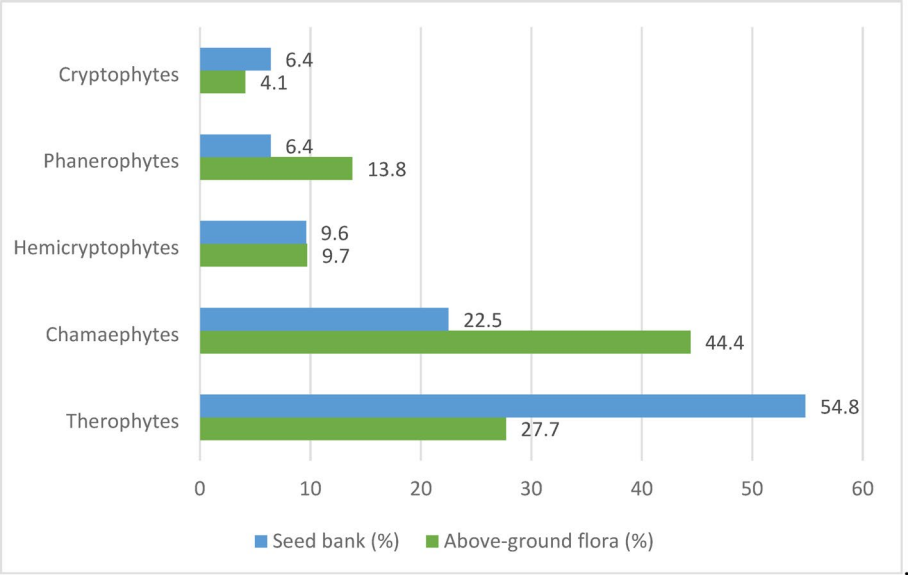


Fig. 4 Difference in life forms percentages among above ground flora and seed bank flora

Table 2 Phytosociological table showing presence percentage and average abundance for main assemblages of seed bank resulted from TWINSPAN classification. Avg = Average abundance, P = Presence

Group	I		II		III		IV		V		Abbreviations
Species/No. of sites	5		19		3		2		1		
	P	Avg	*P*	Avg	*P*	Avg	*P*	Avg	*P*	Avg	
Anastatica hierochuntica			5.26	3.00							***Ana hie***
Barbula convoluta	20	4.00	10.52	3.00	33.3	3.00					***Bar con***
Barbula unguiculata			5.26	3.00							***Bar ung***
Brocchia cinerea	20	1.00									***Bro cin***
Bryum argenteum	100	4.6	10.52	1.5					100	3.00	***Bry arg***
Bryum radiculosum	20	4.00	5.26	3.00							***Bry rad***
Bryum subapiculatum	20	3.00									***Bry sub***
Cenchrus biflorus			5.26	1.00							***Cen bif***
Chenopodium vulvaria			5.26	2.00							***Che vul***
Diplotaxis harra	20	5.00	5.26	1.00			50	2.00			***Dip har***
Echium humile			5.26	1.00							***Ech hum***
Eragrostis barrelieri			5.26	1.00							***Era bar***
Gypsophila capillaris					66.6	1.5					***Gyp cap***
Herniaria hemistemon			5.26	1.00							***Her hem***
Ifloga spicata	20	1.00									***Ifl spi***
Imperata cylindrica			5.26	1.00							***Imp cyl***
Juncus fontanesii							50	1.00	100	5.00	***Jun fon***
Juncus littoralis	20	4.00	5.26	1.00	66.6	1.00					***Jun lit***
Matthiola longipetala	20	1.00									***Mat lon***
Phragmites australis			10.52	2.5					100	5.00	***Phr aus***
Plantago sp.			5.26	4.00							***Pla sp***
Pluchea dioscoridis	60	1.00					50	2.00			***Plu dio***
Polycarpaea robbairea	10	2.00	10.52	2.00			50	1.00			***Pol rob***
Pteranthus dichotomus			5.26	1.00							***Pte dic***
Ptychostomum imbricatulum							100	2.5			***Pty imb***
Pulicaria undulata	20	5.00	10.52	3.5							***Pul und***
Reichardia tingitana					33.3	1.00					***Rei tin***
Riccia. cavernosa			5.26	1.00							***Ric cav***
Riccia congoana	20	1.00									***Ric con***
Riccia frostii	40	1.5	5.26	1.00	33.3	1.00					***Ric fro***
Rumex vesicarius	20	1.00									***Rum ves***
Schismus arabicus			5.26	1.00							***Sch ara***
Senecio aegyptius	20	1.00									***Sen aeg***
Sonchus oleraceus	20	1.00	36.82	1.42	66.6	1.5	50	2.00			***Son ole***
Spergularia diandra	20	1.00	15.78	1.00	100	1.3					***Spe dia***
Tamarix nilotica	10	4.8	100	4.7	100	4.00	100	4.00	100	2.00	***Tam nil***
Trichostomum -brachydontium							50	1.00			***Tri bra***
Trigonella stellata					33.3	3.00					***Tri ste***
Zygophyllum coccineum	80	4.75	89.42	4.11	100	5.00	100	3.5			***Zyg coc***
Zygophyllum decumbens			5.26	1.00							***Zyg dec***
Zygophyllum Simplex	60	3.33	47.34	2.1	33.3	1.00					***Zyg Sim***

and *Zygophyllum simplex* represents the associated species, with 36.8% and 47.3% respectively, with an average abundance of 1.42 and 1.00.

In the third assemblage (III), the species with the 100% presence are *Zygophyllum coccineum*, *Tamarix nilotica* and *Spergularia diandra* with average abundances 5,4,1.3. Followed by *Bryum radiculosum*, *Juncus littoralis*, *Sonchus oleraceus* and *Gypsophila capillaris* that are the codominant species, with a presence 66.6% and average abundance of 3,1.5.

The fourth assemblage (IV) has four dominant species with 100% presence, which are *Bryum radiculosum*, *Tamarix nilotica* and *Zygophyllum coccineum* and *Ptychostomum imbricatulum* with average abundances of 4, 3.5, 2.5.

While the fifth assemblage (V) is represented by *Juncus fontanesii*, *Bryum argenteum*, *Tamarix nilotica* and *Phragmites australis* with 100% presence and an average abundance of 3.25. Followed by two codominant species, which are *Nitraria retusa* and *Haloxylon salicornicum*, with a presence of 75% and an average abundance of 5, 3, 2, 1.

Species composition and dominance within above-ground flora assemblages

The presence and average abundance of species composition for these assemblages are given in Supplementary Table S5 and Table 3. The first Assemblage (I) is represented *by Zygophyllum coccineum* and *Zilla spinosa* as dominant species with 100% presence and average abundances of 3.5 and 3.25. While *Calotropis procera* and *Ochradenus baccatus* are the codominant species with 75% presence and average abundance. They represent 3.3 and 2.6. Moreover, *Tamarix nilotica*, *Bassia indica*, and *Leptadenia pyrotechnica* represent the associated species whose presence and average abundance represent 50% and 3.5, 2.5.

In the second assemblage (II), *Zygophyllum coccineum* is the dominant species with 100% presence, and average abundance represents 3.4. The codominant species are *Zilla spinosa* and *Haloxylon salicornicum*, whose presence and average abundance are 77.7% and 3.5, 2.2. Moreover, *Crotalaria aegyptiaca* and *Ochradenus baccatus* represent the associated species, with 55.5% respectively, with an average abundance of 2.6 and 1.8.

Zilla spinosa, *Zygophyllum coccineum*, *Iphiona scabra*, and *Launaea spinosa* represent dominant species in the third assemblage (III) with 80% presence and their average abundances represent 3.25, 2.9, and 2.75. Followed by three codominant species which are *Ochradenus baccatus*, *Lycium shawii*, and *Zygophyllum decumbens*, with a presence of 70%, 40%, and 50% and an average abundance of 3.14, 2.25, and 1.8. While the associated species are *Panicum turgidum*, whose presence and average abundance represent 40%, 2.25.

The fourth assemblage (IV) has two dominant species with 100% presence, which are *Zygophyllum coccineum* and *Ochradenus baccatus* with average abundances of 4, 1.6. Moreover, *Trichodesma africanum* and *Zygophyllum simplex* are the codominant species whose presence and average abundance represent 66.6%, 3, 2.

While the last assemblage (V) is represented by *Tamarix nilotica* with 100% presence and an average abundance of 3.25. Followed by two codominant species, which are *Nitraria retusa* and *Haloxylon salicornicum*, with a presence of 75% and an average abundance of 2.33, 2. While the associated species is represented by *Zygophyllum coccineum*, *Trichodesma africanum*, and *Arthrocaulon macrostachyum*, whose presence and average abundance represent 50%, 3.5, and 2.5.

Table 3 Phytosociological table showing presence percentage and average abundance for main assemblages of above-ground flora resulted from TWINSPAN classification. Avg = Average abundance, P = Presence

Group	I		II		III		IV		V		Abbreviations
Species/No. of sites	4		9		10		3		4		
	P	Avg	*P*	Avg	*P*	Avg	*P*	Avg	*P*	Avg	
Achillea fragrantissima					20	1.5					***Achi fra***
Aizoon canariense			11.11	1.00							***Aizo can***
Anabasis setifera			11.11	3.00							***Anab seti***
Anastatica hierochuntica					10	1.00					***Anas hie***
Arthrocaulon macrostachyum			11.11	1.00	10	1.00			50	2.5	***Arth mac***
Astragalus sieberi					10	2.00					***Ast sie***
Bassia indica	50	2.5					33.3	4.00	25	4.00	***Bass ind***
Calotropis procera	75	3.3					33.3	1.00			***Calo pro***
Caroxylon inerme									25	3.00	***Caro ine***
Cenchrus divisus							33.3	2.00			***Cenc div***
Centaurea aegyptiaca					10	1.00					***Cent aeg***
Centaurea pallescens			11.11	1.5							***Cent pal***
Citrullus colocynthis	25	2.00	22.22	1.5							***Citr col***
Cleome amblyocarpa	25	4.00									***Cleo amb***
Coincya tournefortii							33.3	2.00			***Coin tou***
Convolvulus hystrix	25	2.00	11.11	2.00							***Conv hys***
Convolvulus lanatus			11.11	1.00	30	3.00					***Conv lan***
Crotalaria aegyptiaca			55.5	2.6	30	2.3					***Crot aeg***
Cucumis melo	25	1.00									***Cucu mel***
Cynanchum acutum	25	3.00	11.11								***Cyna acu***
Cynodon dactylon							33.3	3.00			***Cyno dac***
Deverra tortuosa					10	4.00			25	1.00	***Deve tor***
Diplachne fusca.							33.3	1.00			***Dipl acr***
Echinops spinosus			33.33	2.6	40	2.75					***Echi spi***
Eremobium aegyptiacum.			11.11	2.00							***Erem aeg***
Erigeron bonariensis			11.11	3.00							***Erig bon***
Euphorbia retusa			11.11	2.00							***Euph ret***
Farsetia aegyptia			22.22	3.5							***Fars aeg***
Forsskaolea tenacissima	25	3.00					33.33	4.00			***Fors ten***
Gypsophila capillaris			11.11	2.00							***Gyps cap***
Haloxylon persicum					10	1.00					***Halo sal***
Haloxylon salicornicum			77.7	2.2	20	2.00			75	2.00	***Halo sco***
Heliotropium arbainense			11.11	1.00	30	1.66					***Heli arb***
Heliotropium bacciferum	25	2.00									***Heli bac***
Heliotropium digynum							33.3	2.00			***Heli dig***
Hyoscyamus boveanus	25	3.00									***Hyos bov***
Hyoscyamus desertorum	25	3.00									***Hyos des***
Hyoscyamus muticus	25	3.00									***Hyos mut***
Ifloga spicata			11.11	2.00	10	2.00					***Iflo spi***
Iphiona mucronata			11.11	3.00	80	2.75					***Iphi muc***
Lasiurus scindicus	25	2.00	33.33	1.5							***Lasi sci***

Table 3 (continued)

Group	I		II		III		IV		V		Abbreviations
Species/No. of sites	4		9		10		3		4		
	P	Avg	*P*	Avg	*P*	Avg	*P*	Avg	*P*	Avg	
Launaea nudicaulis							33.3	1.00			***Laun muc***
Launaea spinosa			11.11	2.00	80	2.27					***Laun pro***
Launaea mucronata							33.3	1.00			***Laun spi***
Lavandula coronopifolia					10	2.00					***Lava cor***
Leptadenia pyrotechnica	50	2.5	22.22	2.00	10	3.00					***Lept pyr***
Lycium shawii			22.22	2.5	40	2.25					***Lyci sha***
Neurada procumbens			11.11	1.00							***Neur pro***
Nitraria retusa			11.11	1.00					75	2.33	***Nitr ret***
Ochradenus baccatus	75	3.3	55.5	1.8	70	3.14	100	1.6			***Ochr bac***
Panicum turgidum			11.11	2.00	40	2.25	33.3	2.00			***Pani tur***
Pergularia tomentosa	25	3.00	11.11	2.00	10	3.00					***Perg tom***
Phragmites australis			11.11	2.00	10	2.00			50	3.00	***Phra aus***
Pluchea dioscoridis					10	1.00	33.3	2.00			***Pluc dio***
Pulicaria incisa									25	2.00	***Puli inc***
Pulicaria undulata					10	4.00					***Puli und***
Reichardia tingitana							33.3	1.00			***Reic tin***
Rumex vesicarius							33.3	2.00			***Rume ves***
Tamarix aphylla					10	4.00					***Tam aph***
Tamarix nilotica	50	3.5	44.4	2.5	20	2.00	33.3	3.00	100	3.25	***Tam nil***
Tamarix tetragyna					10	4.00					***Tam tet***
Taverniera aegyptiaca	25	1.00					33.3	2.00	25	2.00	***Tave aeg***
Tribulus mollis					10	1.00					***Trib mol***
Tribulus terrestris							33.3	1.00			***Trib ter***
Trichodesma africanum							66.6	3.00	50	2.5	***Tric afr***
Vachellia tortilis subsp. raddiana			22.2	2.5	30	1.66	33.33	1.00			***Vac t rad***
Zilla spinosa	100	3.25	77.7	3.5	80	3.25			25	2.00	***Zill spi***
Zygophyllum coccineum	100	3.5	100	3.4	80	2.9	100	4.00	50	3.5	***Zyg ara***
Zygophyllum arabicum	25	1.00			10	1.00					***Zyg coc***
Zygophyllum decumbens					50	1.8					***Zyg dec***
Zygophyllum molle			11.11	1.00	10	1.00					***Zyg mol***
Zygophyllum Simplex					10	1.00	66.6	2.00	25	2.00	***Zyg Sim***

Edaphic characteristics and ordination of vegetation assemblages

This study examined sixteen environmental elements, both chemical and physical. The ranges and means of environmental variables of the seed bank sites supporting each assemblage are tabulated in Table 4. Obviously, the highest values of silt, clay, soil moisture content, organic matter, organic carbon, pH, EC, Na^{+}, Mg^{2+}, K^{+}, Ca^{2+}, HCO_3^{-}, SO_4^{2-}, and Cl^{-} were restricted to the 2nd assemblage, which corresponded to 27.3%, 15.9%, 7.7%, 1.18%, 0.68%, 9.24, 151 dsm^{-1}, 858 mEq/L, 180 mEq/L, 2 mEq/L, 470 mEq/L, 81 mEq/L, 233 mEq/L and 1196 mEq/L. Conversely, the first and third assemblage represent the maximum value of sand and $CaCO_3$ which are 82.2% and 27.5%.

Table 4 Minimum, maximum, mean, and standard deviation of environmental variables for the main assemblages of seed bank resulted from TWINSPAN

Assemblage	I				II				III				IV				V			
NO. of sites	11				30				27				9				2			
	Min	Max	Mean	Std Dev	Min	Max	Mean	Std Dev	Min	Max	Mean	Std Dev	Min	Max	Mean	Std Dev	Min	Max	Mean	Std Dev
Physical properties																				
Soil texture (pipette)																				
Sand%	64.3	82.2	71.52	6.92	34.1	81.4	62.02	13.24	64.3	82.2	6.14	6.92	59.5	79.6	68.3	10.28	71.4	71.4	71.4	-
Silt%	2.2	7.8	6.14	2.24	4.3	27.3	10.2	6.59	2.2	7.8	6.14	2.24	4.1	9	6.1	2.55	4.8	4.8	4.8	-
Caly%	6.7	11.9	8.64	2.01	3.1	15.9	10.51	3.59	6.7	11.9	8.64	2.01	1	7.9	5	3.57	7.1	7.1	7.1	-
Organic matter%	0.14	0.41	0.54	0.17	0.19	1.18	0.54	0.28	0.17	0.54	0.41	0.14	0.37	0.74	0.51	0.19	0.49	0.49	0.49	-
Organic carbon %	0.10	0.31	0.24	0.08	0.11	0.68	0.31	0.16	0.10	0.31	0.24	0.08	0.21	0.43	0.30	0.11	0.28	0.28	0.28	-
Moisture content %	0.26	1.4	0.66	0.44	0.5	7.7	2.23	1.92	0.26	1.4	0.66	0.44	0.6	2.4	16	0.916	1.7	1.7	1.7	-
Chemical properties																				
pH	7.53	8.37	7.90	0.34	7.11	9.24	7.98	0.53	7.53	8.37	7.90	0.34	7.89	8.34	8.04	0.25	8.11	8.11	8.11	-
EC (dsm^{-1})	3.8	43.2	12.8	17.17	1.94	151	21.55	38.4	3.8	43.2	12.56	17.17	1.71	5.24	3.45	1.76	1.4	1.4	1.4	-
Cations (mEq/L)																				
Ca^{2+}	20	151	51.2	56.37	10	470	77	116	20	151	51.2	56.37	9.5	25	17.5	7.76	7	7	7	-
Mg^{2+}	11	99	30.76	38.19	4.4	180	38.22	53.81	11	99	30.76	38.19	7.5	16	13.16	4.90	5	5	5	-
Na^{+}	7.2	181	45.04	76.04	3.1	858	100.96	215.6	7.2	181	45	76	3.8	11.1	6.4	4	4.8	4.8	4.8	-
K^{+}	0.3	1	0.44	0.31	0.2	2	0.57	0.64	0.3	1	15.72	17.92	0.2	0.3	0.23	0.05	0.2	0.2	0.2	-
Anions (mEq/L)	-																			
HCO_3^{-}	3	45	15.72	17.92	1.4	81	14.42	24.6	3	45	15.72	17.92	4.4	7	5.33	1.44	3.8	3.8	3.8	-
Cl^{-}	21	240	68.8	95.77	10	1196	148.14	291.4	21	240	68.8	95.77	7	30	18	11.53	5.5	5.5	5.5	-
$SO4^{2-}$	9.4	147	41.12	59.31	6.3	233	53	74.8	9.4	147	41.12	59.31	5.5	15.4	11.16	5.10	1.7	1.7	1.7	-
$CaCO_3$%	13.7	27.5	5.69	21.34	7.5	26.2	18.82	6.24	13.7	27.5	21.34	5.69	11.2	14.9	13.3	1.9	19.5	19.5	19.5	-

While in the case of the above- ground flora, the highest values of soil moisture content, organic matter, organic carbon, EC, Na^{+}, Mg^{2+}, K^{+}, Ca^{2+}, HCO_3^{-}, $CaCO_3$ and SO_4^{2-} were restricted to the fifth assemblage, which corresponded to 7.7%, 1.18%, 0.28%, 151 dsm^{-1}, 180 mEq/L, 180 mEq/L, 2 mEq/L, 470 mEq/L, and 233%, 81 mEq/L, and 1196 mEq/L. Conversely, the second assemblage represents the maximum values of pH, sand, and silt, which are 9.24, 81.4%, and 27.3%. Clay contributed to the fourth assemblage, which represented 15.9%, while Cl^{-}contributed to the first assemblage, which made up 240 mEq/L.

By evaluating the variations in the means and ranges of environmental variables between seed banks and above-ground plants. The highest values of most edaphic parameters are clearly represented by the seed bank's second assemblage and the above-ground flora's fifth assemblage.

The DCA ordination showed that the ninety plants could be classified into four groups (Fig. 5). All applied edaphic factors had a positive effect on the third group (III) of plants; but pH and $CaCO_3$ had a detrimental effect on this section. The third group included the following plants: *Cucumis melo*, *Aizoon canariense*, *Heliotropium bacciferum*, *Phragmites australis*, *Tamarix nilotica*, *Zygophyllum arabicum* affected. On the other hand, pH and $CaCO_3$ has a positive impact on the second group (II) included *Leptadenia pyrotechnica*, *Zilla spinosa*, *Ochradenus baccatus*, *Tribulus mollis*, *Lycium shawii*, and *Eremobium aegyptiacum*. While the first and the fourth groups are affected by the physical and chemical factors but less than the first and the fourth groups. The first groups (I) are represented by *Zygophyllum coccineum*, *Calotropis procera*, *Pluchea dioscoridis*, and *Farsetia aegyptia* and the fourth one is represented by *Centaurea pallescens*, *Iphiona scabra*, *Ifloga spicata* and *Deverra tortuosa*.

A one-way Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted across 30 sites to assess differences in species composition between above-ground flora and soil seed bank communities. Using Euclidean distance and 9,999 permutations, the test revealed a highly significant difference between the two groups ($F = 385.9$, $p = 0.0001$). The within-group sum of squares (298.5) was markedly lower than the total sum of squares (1.036×10^4), indicating a strong grouping effect and low variation within replicates.

The Global Beta diversity indices showed a high difference between seed bank and above- ground flora (Table 5). Where all indices showed higher number in above-ground flora than those of seed bank except for Harrison that were slightly higher in seed bank.

Discussion

The remarkable species diversity observed in the soil seed bank reflects the contrasting reproductive strategies of different life forms. Perennial species, which dominate the above-ground vegetation, typically produce fewer but larger seeds with limited longevity, making them less represented in the seed bank. In contrast, annuals generate numerous small and long-lived seeds, enhancing their persistence below the soil surface (Chang et al. 2001). Similarly, Zhao et al. (2021) noted that herbaceous species generally prevail in seed banks, while woody plants remain scarce due to their distinct dispersal and germination traits.

In the present study, annuals and perennials constituted 58% and 41.9% of the recorded seed bank species, respectively. However, in the above-ground flora, annuals represented only 25%, perennials 72.2%, and biennials 2.7%. This clear dominance of annuals within

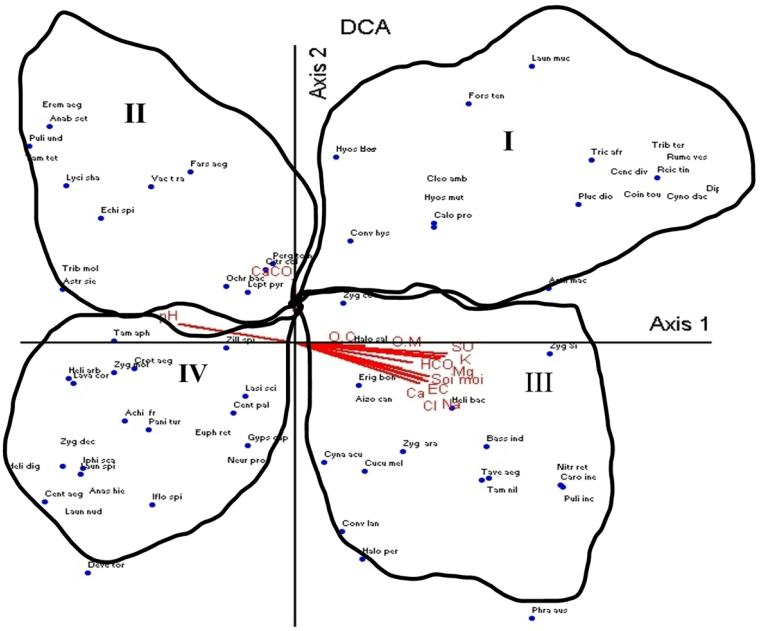


Fig. 5 Detrended Correspondence Analysis (DCA) ordination diagram showing the distribution of above-ground plant species (abbreviated species names) in relation to selected environmental variables (physical and chemical soil parameters)

Table 5 Comparison of Global Beta diversity between seed bank and above ground flora

Global Beta diversity indices	Seed bank	Above- ground flora
Whittaker	6.40	7.53
Harrison	0.16	0.10
Cody	121.50	215.50
Routledge	0.52	0.67
Wilson-Shmida	30.00	61.32
Mourelle	0.75	0.86
Harrison 2	0	0.002
Williams	0	0.13

the seed bank agrees with previous findings from desert ecosystems (Marone et al. 1998; Guo et al. 1999; Zhao et al. 2021), which reported that short-lived species are more frequent than perennials. As suggested by Bertiller (1998) and Gomaa (2012), the larger seeds of long-lived perennials are more vulnerable to predation, whereas the smaller, more persistent seeds of annuals contribute to their higher representation in the soil seed bank a pattern consistent with our observations.

The comparison of the seed bank results with the above-ground data from this study reveals that 70.7% of the recorded species are restricted to the seed bank. These include *Polycarpaea robbairea*, *Pteranthus dichotomus*, *Spergularia diandra*, *Juncus littoralis*, *Cenchrus biflorus*, *Eragrostis barrelieri*, and *Schismus arabicus*, as well as all non-flowering plants. These results agreed with Thompson (1992), Dupuy and Chazdon (1998) and

Vandvik et al. (2016) which reported a weak relationship between species in the above-ground flora and those in the soil seed bank. Several factors may explain this difference, including the season of sampling (Daling et al. 1997), which affects the presence of certain species (e.g., ephemerals), germination conditions, seed viability, dormancy, and disturbances such as fires, droughts, or predation.

These results emphasize the critical role of the soil seed bank in preserving rare species, supporting conservation efforts, and restoring vegetation. It also serves as a historical record of past plant communities in the study area.

The seed bank analysis uncovered two species newly recorded in the flora of the Eastern Desert: *Chenopodium vulvaria* and *Juncus fontanesii*. According to Boulos (2009), the known distribution of *C. vulvaria* is restricted to Sinai, whereas *J. fontanesii* has been reported from the Nile region, oases, and Sinai. Their unexpected appearance in the Eastern Desert indicates that their seeds may have persisted in the soil seed bank for a prolonged period, escaping detection during previous above-ground surveys. To verify these as genuine new records for the region, we carefully reviewed the collections of the Suez Canal University Herbarium (SCU-I), which contains all documented specimens from the Suez Governorate, encompassing our study sites. The herbarium records confirmed that neither species had been previously vouchered or reported from this area, and no published studies have mentioned their occurrence within the Eastern Desert.

Beyond their role in biodiversity conservation, soil seed banks are vital for ecological restoration, serving as natural reservoirs of viable seeds that enable ecosystems to recover after disturbances. This study highlights their importance in the restoration potential of arid ecosystems, demonstrating how seed banks contribute to vegetation recovery and sustain plant diversity even under extreme conditions. Globally, similar patterns have been observed: in Ethiopia, soil seed banks facilitate woody species regeneration and enhance biodiversity in exclosure-based restoration (Megersa and Hailu 2021); in the European Alps, they support the recovery of eroded alpine grasslands (Wellstein et al. 2023); and in Nigeria's Akure Forest Reserve, they inform the management of native and invasive species (Akinkuolie et al. 2021). Likewise, studies from Australia's Lake Kasumigaura revealed that sediment seed banks can re-establish diverse lakeshore vegetation (Dawson et al. 2017), while in Beijing's Yeyahu Wetland and South Korea's Gwangyang Bay they have been successfully applied in wetland and salt marsh restoration (Hong et al. 2012; Lee et al. 2012). In Nicaragua, seed banks have also driven secondary succession on abandoned farmland, aiding the recovery of both pioneer and late-successional species (Uasuf et al. 2009). Collectively, these examples emphasize the universal role of soil seed banks in promoting natural regeneration, enhancing biodiversity, and supporting ecosystem resilience across diverse habitats.

In this study, therophytes emerged as the dominant life form in the soil seed bank, while chamaephytes prevailed in the above-ground flora, a pattern consistent with Figueroa et al. (2004). The dominance of annuals can be attributed to the region's arid conditions, where these species have adapted to survive harsh environments by swiftly completing their life cycles after rainfall. This strategy not only ensures their persistence but also enriches the soil seed bank, securing their presence for future growth (Venable and Lawlor 1980; Abd-ElGawad et al. 2021).

The assemblages of seed banks differ markedly from those of the above-ground flora. This variation agrees with the findings of Thompson and Grime (1979), who demonstrated that numerous plant communities may have seed banks that differ from their standing veg-

etation. Physical stress and disturbance have interacting effects on the above-ground flora, resulting in a decrease in soil seed bank density (Grime 1979; Shiferaw et al. 2018).

Moreover, the PERMANOVA results revealed a clear and highly significant difference in species composition between the above-ground vegetation and the soil seed bank ($F = 385.9$, $p = 0.0001$), emphasizing their distinct community structures. While the above-ground flora is highly susceptible to environmental stressors such as human disturbance, climate change, and habitat loss, the soil seed bank functions as a resilient biological archive. In arid habitats like Gebel Ataqa, where ecological degradation is accelerating, this hidden reservoir safeguards dormant seeds that can drive natural regeneration. Thus, the soil seed bank not only preserves the genetic memory of the ecosystem but also represents a vital mechanism for biodiversity conservation and ecological restoration. Its capacity to maintain species diversity under harsh conditions offers a source of renewal and resilience for degraded desert environments.

On the other hand, the assemblages of seed banks and above-ground flora agreed in having high numbers of *Tamarix nilotica* and *Zygophyllum coccineum*. This result proved that these species have relatively large persistent soil seed banks which improve their chances of survival if they were harmfully affected by the biotic or abiotic hazards.

Despite the high presence of *Haloxylon salicornicum*, *Ochradenus baccatus*, *Iphiona scabra*, and *Launaea spinosa* in the above-ground flora, these species were not recorded in the soil seed bank, which may be attributed to their high seed dormancy. Consequently, they are susceptible to local extinction from the remaining vegetation and are unlikely to be replaced by members of their own species (Fenner 1985; O'Connor 1991; Gomaa 2012). Therefore, such species require greater attention to ensure their conservation, as their restoration would be very difficult.

Although the following four species: *Diplotaxis harra*, *Matthiola longipetala*, *Echium humile* and *Trigonella stellata* were not collected with the study's above-ground flora in Wadi Hagul, they were recorded in seed bank. Nonetheless, Abdelaal (2017) and Bedair et al. (2021) gathered them from the above-ground flora. Hence, this could reflect the bad impact of scare rainfall and high aridity resulted from climate change during the years of collection.

The high levels of pH, $CaCO_3$, and sand accumulation observed in both the seed bank and above-ground flora align with findings by Nafea (2016). DCA ordination of the above-ground flora revealed that pH and $CaCO_3$ are key factors influencing species distribution. These conditions contribute to a larger seed reservoir in the soil, leading to greater species diversity in the seed bank compared to the above-ground flora.

According to Magurran (2004), low beta diversity values (close to 0) indicate high similarity in species composition between sites, whereas higher values (approaching 1 or beyond) reflect greater species turnover and distinct community structures. In this study, the high beta diversity indices highlight strong ecological differentiation and complexity across the region. Whittaker's index (6.4096 for SSB, 7.5375 for AGF) and Cody's index (121.5 for SSB, 215.5 for AGF) reveal substantial variation in biodiversity between sites, suggesting that plant communities are shaped by local environmental factors such as soil properties, water availability, and microclimatic conditions. Similarly, Wilson-Schmida's index confirms that species composition varies considerably due to environmental heterogeneity within the study area.

The high values observed in diversity indices highlight the region's impressive ecological resilience, especially in areas with significant beta diversity, which are better equipped to withstand environmental stressors and disturbances. These areas maintain ecosystem functionality through species turnover and adaptation, ensuring the persistence of diverse plant communities. This resilience is notably evident in the above-ground flora (AGF), which exhibits a dynamic, responsive community structure influenced by environmental factors like salinity, temperature, and moisture levels. Meanwhile, the soil seed bank (SSB), though also diverse, acts as a long-term buffer, preserving species through mechanisms such as bet-hedging (Venable 2007; Al-Huqail et al. 2025). By keeping a portion of their seeds dormant, desert plants particularly annuals enhance their survival prospects, ensuring species persistence even under harsh conditions. The high beta diversity observed may also reflect ecological processes such as habitat fragmentation or differential seed dispersal, as beta diversity often correlates with pronounced environmental gradients and heterogeneous habitats that support diverse species.

The variation among diversity indices underscores the importance of using multiple metrics to understand biodiversity patterns. While Whittaker, Cody, and Wilson-Schmida highlight significant species turnover, indices such as Harrison, Routledge, Mourelle, and Williams indicate moderate to low variation. Collectively, these findings emphasize that habitat heterogeneity plays a key role in shaping plant community structure, maintaining ecological balance, and enhancing adaptive capacity. Beta diversity metrics therefore provide valuable insights into the resilience and functional stability of arid and semi-arid ecosystems (Venable 2007).

This study recorded the presence of ten Bryophytes (liverworts and mosses) in soil seed bank representing 24.39% of the recorded species. The reason for this high presence refers to bryophyte diaspores stored in the soil. These diaspores contribute to biodiversity supporting the species resilience to environmental pressures (climate change and habitat destruction) which greatly resemble that threaten the study area. Moreover, they preserve genetic diversity enabling long-term adaptability and survival of bryophyte populations (During 2001; Govindapyari et al. 2010).

Three hepatic (liverworts) species were identified in the study's seed bank: *Riccia congoana*, *Riccia frostii* and *Riccia cavernosa. Riccia congoana* is classified by the Red List as an endangered species. The critical status of this species wasn't only in Egypt but in many other countries worldwide as North and Central Africa and Southwest Australia (El-Saadawi and Taha 2020). This species is at risk of extinction. Because of the detrimental effects of climate change and human activity on its natural habitats (El-Saadawi and Taha 2020).

Moreover, *Riccia congoana* is a new record to the flora of the Eastern desert which is related to Gebel Elba according to El-Saadawi and Taha (2020). This result may be due to the long-term presence of its diaspore in the soil of the study area and its inability to grow in unfavorable conditions.

Bryum argenteum is a dominate Bryophyte species in the first assemblage in seed bank. The reason for its high presence is that it is well known for its high endurance and capacity to withstand a wide range of harsh conditions, such as elevated pollution levels and high salinity (Proctor and Tuba 2002; Ares et al. 2012). This means that its vegetative diaspores are stored in the soil for a long time. While *Bryum radiculosum* is a co-dominated species in the third assemblage. It prefers calcareous habitats which agree with high $CaCO_3$ levels in the 3rd assemblage. Furthermore, it possesses reproductive strategies that enable it to

withstand any unfavorable circumstances. This strategy is regeneration from small fragments which enables the plant to regrow from damaged or separated portions into a whole plant. These support the effective persistence and expansion of *Bryum radiculosum* in its preferred environments which are humidity and nutrient-rich soil (Smith 2004; Glime and Bisang 2017). These favorable conditions are achieved by seed bank method, so it has a good presence.

Although the current study underscores the importance of soil seed banks in habitat conservation, it has certain limitations. In particular, it does not provide a comprehensive understanding of the long-term dynamics of soil seed banks in maintaining biodiversity. Future research should therefore explore temporal changes in seed bank composition, especially in relation to environmental factors such as climate change and land-use practices. Moreover, further studies could examine the role of seed bank persistence in promoting ecosystem resilience and recovery following disturbances. Experimental approaches combined with long-term monitoring would offer valuable insights into these processes and support the development of more effective conservation strategies.

Conclusion

The soil seed bank in the Gebel Ataqa region serves as a vital reservoir for botanical conservation in an area heavily impacted by human activity and climatic shifts. This study confirms that the composition of the soil seed bank significantly differs from the above-ground flora, both in species diversity and structure, supporting our initial hypothesis. By analyzing the seed bank, we documented several previously unrecorded species in the region, including rare and threatened taxa such as *Polycarpaea robbairea*, *Spergularia diandra*, *Juncus littoralis*, *Cenchrus biflorus*, and *Eragrostis barrelieri*. Notably, we also identified three new species records for the Eastern Desert: *Chenopodium vulvaria*, *Juncus fontanesii*, and the critically endangered bryophyte *Riccia congoana*.

The observed dissimilarity between the seed bank and standing vegetation reveals that many species persist primarily as dormant seeds, highlighting the seed bank's vital role as a source for natural regeneration and ecological restoration. These findings emphasize its importance in preserving genetic diversity, supporting ecosystem recovery, and enhancing species resilience against habitat loss and climate change. As a natural repository, the soil seed bank represents an essential component of long-term conservation strategies, particularly in arid environments like Gebel Ataqa. Integrating seed bank data into restoration and management plans will therefore be key to ensuring the persistence and recovery of plant communities under increasing environmental and anthropogenic pressures.

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Author contributions Mohamed Saad Zaghloul contributed to Conceptualization, Methodology, and Study Design; Sara Hassanen and Yasmin M. Hassan collected plants and soil samples; Elsayeda Gamal Eldin, Wafaa Kamel, and Sara Hassanen identified flowering plants (above-ground flora and seed bank); Yasmin M.

Hassan identified bryophytes; Mohamed Saad Zaghloul and Sara Hassanen conducted Vegetation Analysis; and Sara Hassanen wrote the original draft. All authors reviewed and approved the final manuscript.

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Data availability Data is provided within the supplementary information files.

Declarations

Ethics approval and consent to participate The plant samples collected in this study are wild plants. Experimental research and field studies, including the collection of plant material, were conducted in full compliance with relevant institutional, national, and international guidelines and legislation. This study adheres to the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora. All necessary permits, permissions, and licenses were obtained from the relevant authorities before sample collection.

Competing interests The authors declare no competing interests.

Supplementary Information This study has accompanying supplementary data.

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Authors and Affiliations

Sara Hassanen[1] · Yasmin M. Hassan[1] · Elsayeda Gamal Eldin[1] · Wafaa Kamel[1] · Mohamed Saad Zaghloul[1]

✉ Sara Hassanen
sara_hassanin@science.suez.edu.eg

✉ Yasmin M. Hassan
yasmin_ibrahim@science.suez.edu.eg

✉ Elsayeda Gamal Eldin
elsayeda_gamaleldeen@science.suez.edu

✉ Wafaa Kamel
wafaamoustafa@yahoo.com

Mohamed Saad Zaghloul
zaghloul_mohamed@yahoo.com

[1] Botany & Microbiology Department, Faculty of Science, Suez Canal University, Ismailia, Egypt