Do aeolian deposits and sand encroachment intensity shape patterns of vegetation diversity and plant functional traits in desert pavements? Postprint

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Abstract

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LLSE to HLSE induced significant changes in plant community variables including decreases in plant density, plant rarity, lifeform composition, morphological type, and aridity adaptation. Desert pavements with HLSE favor the degradation of vegetation and trigger biodiversity erosion.

Full Text

Preamble

Do aeolian deposits and sand encroachment intensity shape patterns of vegetation diversity and plant functional traits in desert pavements?

M'hammed BOUALLALA[1], Souad NEFFAR[2],[3], Lyès BRADAI[4], Haroun CHENCHOUNI[5],[6]*

[1] Laboratory of Saharan Natural Resources, Faculty of Sciences and Technology, University of Ahmed Draia, Adrar 01000, Algeria
[2] Department of Nature and Life Sciences, Faculty of Exact Sciences and Nature and Life Sciences, University of Tebessa, Tebessa 12002, Algeria
[3] Laboratory Water and Environment, University of Tebessa, Tebessa 12002, Algeria
[4] Laboratory of Saharan Bioresources Preservation and Valorization, Faculty of Nature and Life Sciences, University of Kasdi Merbah, Ouargla 30000, Algeria
[5] Department of Forest Management, Higher National School of Forests, Khenchela 40000, Algeria
[6] Laboratory of Natural Resources and Management of Sensitive Environments, University of Oum-El-Bouaghi, Oum-El-Bouaghi 04000, Algeria

Abstract: The effects of sand encroachment on composition, diversity, and functional patterns of vegetation in drylands are rarely studied, yet addressing these aspects is important to deepen our understanding of biodiversity conservation. This study aimed to investigate the effect of sand encroachment on plant functional biodiversity of desert pavements (gravel deserts) in the Sahara Desert of Algeria. Plants were sampled and analyzed in three desert pavements with different levels of sand encroachment (LSE) and quantity of aeolian deposits (low, LLSE; medium, MLSE; and high, HLSE). Within the sample-plot area (100 m^2), density of every plant species was identified and total vegetation cover was determined. Plant taxonomic and functional diversity were analyzed and compared between LSE. Results showed that 19 plant species in desert pavements were classified into 18 genera and 13 families. Asteraceae and Poaceae were the most important families. The species *Anabasis articulata* (Forssk.) Moq. characterized LLSE desert pavements with 11 species, whereas *Thymelaea microphylla* Coss. & Durieu ex Meisn. and *Calobota saharae* (C&D) Boatwr. & van Wyk were dominant species of desert pavements with MLSE (14 species) and HLSE (10 species), respectively. The highest values of species richness and biodiversity were recorded in desert pavements with

MLSE, while low values of these ecological parameters were obtained in desert pavements with HLSE. Desert pavements with LLSE were characterized with the highest values of species abundances. Plant communities were dominated by chamaephytes, anemochorous, arido-active, and competitive stress-tolerant plants. The increase in LSE along the gradient from LLSE to HLSE induced significant changes in plant community variables including decreases in plant density, plant rarity, lifeform composition, morphological type, and aridity adaptation. Desert pavements with HLSE favor the degradation of vegetation and trigger biodiversity erosion.

Keywords: desert pavements; hot and arid rangeland; plant diversity; land degradation; sand encroachment; plant functional trait; Sahara Desert

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*Corresponding author: Haroun CHENCHOUNI (E-mail: chenchouni@gmail.com; chenchouni.haroun@ensf.dz)

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1 Introduction

Drylands, in their different regimes of aridity, account for more than 40% of the global land surface and are extending due to global warming [?, ?, ?]. The Sahara Desert is not only the largest hot desert worldwide but also the most typical desert for its extreme aridity. This ecoregion is characterized by prolonged periods of drought and special flora with remarkable adaptations [?, ?]. According to Bouallala et al. [?, ?], landscapes with different geomorphology exist in the Sahara Desert, including erg and sandy soils, gravel deserts, stony and clayey substrate, rocky lands, mountain range, depressions, nabkhas, wadis with or without saline soil, wetlands, and oases. Among these landscapes, desert pavements are widespread and most common [?, ?]. Parsons and Abrahams [?, ?] define a desert pavement as a flat desert surface covered with closely packed, interlocking angular or rounded rock fragments of pebble and cobble size. A desert pavement is a gravel desert also called "Reg" in the western Sahara region.

Sand encroachment is one of the phenomena of hot and arid environments [?, ?, ?, ?]. It is the consequence of a complex phenomenon resulting from multiple causes and manifests in different ways, including sand tearing, aeolian transportation, deposit, and accumulation to build different forms of dunes [?, ?, ?]. The effect of wind is the major reason in drylands [?, ?]. This natural factor can selectively erode fine particles and remove them, and can accumulate several meters downwind, causing severe sand encroachment problems [?, ?, ?, ?], without neglecting the anthropogenic perturbations that contribute to aggravate the consequence of sand encroachment [?, ?]. One of the repercussions of sand encroachment in drylands is the erosion of both land and phytogenetic resources with multiple uses (medicinal, food, energy, industrial, etc.) [?, ?], knowing that hundreds of hectares of land are lost each year due to desertification [?, ?] and different forms of erosion [?, ?, ?, ?, ?].

Land degradation resulting from sand encroachment in desert habitats represents a serious challenge to the sustainability of ecosystem functioning, especially since these xeric species are known for their vulnerability to climate change combined with the increase in intensity of anthropogenic disturbances, which can lead to a decrease in ecosystem services provided by various natural resources [?, ?, ?, ?]. Moreover, it has been reported by Shameem et al. [?, ?] that the magnitudes of natural and human disturbances can be the drivers of changes in species diversity in plant communities.

The vegetation of different geomorphological formations of the Sahara Desert has been widely surveyed [?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. Some investigations of the Sahara Desert have assessed the carrying capacity of camel in desert rangelands [?, ?, ?]. Previous climatological [?, ?, ?, ?, ?, ?, ?] and vegetation studies of this ecoregion have highlighted the low and irregular precipitation, large thermal ranges, strong evaporation, and frequent and intense winds. These factors act seasonally on the dynamics of sandy formations, and consequently on the dynamics and structure of vegetation under different levels of sand encroachment (LSE), although plant survival in drylands is affected by the combination of high solar radiation, high temperatures, low relative humidity, and scarcity of available water [?, ?].

As the movement of sands is a characteristic phenomenon of hyper-arid environments [?, ?], its effects on the plant component remain little studied and poorly understood. The studies related to this topic have focused on the composition, community structure, and functional traits of plants in the Sahara Desert [?, ?, ?, ?, ?]. However, there is no study about plant community composition and functional diversity in relation with LSE. This work addressed and examined the relationships of vegetation diversity and plant functional attributes with LSE in desert pavements at northern Sahara Desert.

This study aimed to answer the following questions: (1) do the floristic composition and plant diversity parameters vary according to LSE in desert pavements? (2) what are and which functional traits predominate in this xeric environment? and (3) is there a relationship of plant functional traits, composition, and diversity parameters with LSE?

2.1 Study area

The region of El-Guerrara is located 115 km northeast of the Ghardaia Province in the Sahara Desert of Algeria (Fig. 1 [Figure 1: see original paper]). The climate of this region is hot and hyper-arid (de Martonne aridity index=1), where the dry season lasts all year. The annual precipitation totals 40.0 mm with precipitation deficit of 1639.0 mm/a (Table S1). The coldest month is January (annual mean temperature is 4.4°C ($±3.2°*C*))*andthewarmestmonthisJulywiththemaximumtemperatureof*42.7°*C*(±4.6°*C*), *andpotentialevapot* mm (Table S2). The main agricultural activity in the Sahara Desert is date palm cultivation, which is expanding in space and increasing over time [**?**, **?**, **?**]. Recently other vegetables and industrial crops are grown in the understory of date palm and in new exploited lands. Rocky and sandy soils predominate with a very low or even zero organic matter [**?**, **?**]. The dominant soil is lithic leptosol [**?**, **?**].

Fig. 1 Geographic location and elevation (a1 and a2) of the El-Guerrara region (Ghardaia Province, Algeria), and monthly meteorological data for mean temperature, precipitation, and potential evapotranspiration (PET; b). Bars are standard errors.

2.2 Plant sampling, data collection, and analysis

At the El-Guerrara region (Fig. 1), plants were sampled within three desert pavements, representing different LSE and quantities of aeolian deposits: (1) low LSE (LLSE): presence of aeolian sand ripples less than 5 cm tall; (2) moderate LSE (MLSE): presence of sand ripples and small nabkhas less than 50 cm tall; and (3) high LSE (HLSE): presence of aeolian sand ripples (<5 cm tall), small dunes (<50 cm tall), and bushy nabkhas less than 2 m tall. Plants were sampled during the period of plant growth (February–April) of 2015, with five replicates per site. In each sample plot, plant density was determined within an area of 100 m^2 [**?**, **?**, **?**]. Vegetation cover was also estimated inside the same sampling plots by computing the proportion of horizontal vegetated area occupied by the vertical projection of plant canopy. Species identification was referenced from Quézel and Santa [**?**, **?**, **?**] and Ozenda [**?**, **?**].

2.3.1 Composition and classification of plant diversity

For the entire study area and for each LSE, plant traits and taxonomic diversity were assessed by calculating the following parameters: vegetation cover (VC) as mean of samples of LSE, density (N′) was determined as sum of species abundances per LSE, relative abundance (RA) computed as the proportion of species abundance to the total abundances of all species per LSE, species richness (S) consisted of the total number of species identified in each sampling plot and LSE, average of species abundance (N′:S ratio) defined as the average number of individuals per species, average of species cover (VC:S ratio) established as the average vegetation cover per species, average of individual cover (VC:N′ ratio) defined as the average vegetation cover per individual, occurrence (Occ) was calculated for each species by the number of samples in which the species occurred/total number of samples. Four classes of Occ were distinguished: very accidental species (Vac) with occurrence <10% in samples, accidental species (Acc) having occurrences ranging from 10% to 25%, common species (Cmt) are present in 25%–50% of samples, and constant species (Cst) with occurrence equals to 50% or more [?, ?].

Two diversity indices (Shannon's diversity index and Simpson's diversity index), and one evenness index (Pielou's evenness) were computed in this study. Shannon's diversity index (H′) was the most frequently used index compared with other diversity indices; its values range between 0.0 and 5.0, and in most cases, results vary between 1.5 and 3.5, and rarely exceed 4.5 [?, ?]. It was computed using the formula:

$$H' = -\sum_{i=1}^{S} p_i \log_2 p_i, \text{ with } p_i = n_i/n$$

where p_i is the proportion of individuals of species i (n_i) on the total number of individuals (n) of all species. Simpson's reciprocal index (SRI) was computed by:

$$\mathrm{SRI} = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

The ratio of observed value of Shannon's index to its maximum value gives the Pielou's evenness (E) index: $E = H'/H'_{\max}$, with $H'_{\max} = \log_2 S$, where S is the species richness. Values of E range between 0 and 1. When the value is getting closer to 1, it means that the plant community is equally distributed [?, ?].

2.3.2 Species richness estimation

The estimation of species richness of plants (S_{est}) was performed using the EstimateS program [?, ?]: (1) S_{est} that provided the expected number of plants for a given number of samples; (2) first $S(\text{Jack1})$ and second $S(\text{Jack2})$ order Jackknife's estimator:

$$S(\text{Jack1}) = S + Q_1\left(\frac{m-1}{m}\right)$$

$$S(\text{Jack2}) = S + \left(\frac{Q_1(2m-3)}{m}\right) - \left(\frac{Q_2(m-2)^2}{m(m-1)}\right)$$

(3) first $S(\text{Chao1})$ and second $S(\text{Chao2})$ order Chao's estimator:

$$S(\text{Chao1}) = S + \left(\frac{n-1}{n} \times \frac{F_1(F_1-1)}{2(F_2+1)}\right)$$

$$S(\text{Chao2}) = S + \left(\frac{m-1}{m}\right)\left(\frac{Q_1^2}{2Q_2}\right)$$

where S is the observed species richness; m is the total number of samples; Q_1 and Q_2 are the frequency of unique (species that occur in only one sample) and duplicate (species that occur in only two samples), respectively; F_1 is the singletons; and F_2 is the doubletons. Values of species richness estimators were given as mean (±standard deviation) following a 100-randomization runs.

2.3.3 Rarefaction and extrapolation

To make a comparison between the values of species richness between different communities observed in LSE, we established rarefaction and extrapolation curves for the entire area and for each LSE. This helped to evaluate the sampling effort and compared it with predicted richness. Using the observed data (the whole samples and samples at each LSE), the accumulation curve allowed to obtain an estimate of cumulative species richness. On the other hand, an extrapolation of species richness was made for a total number of 150 samples, i.e., 10 times higher than the reference sample for the whole area, and 30 times higher than the reference sample of each LSE.

2.3.4 Beta diversity

Using the software EstimateS [?, ?], the analysis of species richness similarity between LSE was performed by computing several similarity indices. These include qualitative (Jaccard and Sørensen) and quantitative indices, namely raw and estimated Chao's Jaccard indices, raw and estimated Chao's Sørensen indices, Morisita-Horn index, and Bray-Curtis index [?, ?].

2.4 Plant functional traits (PFT)

According to Lavorel et al. [?, ?] and Violle et al. [?, ?], PFT are observable characteristics of plants, widely used to represent the responses of vegetation to environmental conditions, and also the effects of vegetation on environment and climate, at scales from individuals to biomes. We attributed several PFT to each species. We determined these PFT based on previous studies [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?] and from the Tela-Botanica eflora database in North Africa (https://www.tela-botanica.org/flore/afrique-du-nord).

2.4.1 Raunkiaer's lifeform spectrum

Depending on the location and level of protection of buds or other renewing organs (seeds, tubers, and rhizomes) in relation to protection from unfavorable seasons [?, ?], we categorized plant species of this study into five main groups, namely therophytes, geophytes, hemicryptophytes, chamaephytes, and phanerophytes, which are ligneous single-stem plants with perennating buds above the soil surface by at least 25 cm [?, ?]. These biological types were a combination of morphological characteristics resulting from the adaptations of species to environmental conditions [?, ?].

2.4.2 Dispersal spectrum

The dispersal spectrum is the frequency distribution of dispersal modes in a particular vegetation type, here in different LSE [?, ?]. Depending on the agent involved in the dissemination of diaspores, we used a term to name the dispersal unit or mode of the plant [?, ?]. van der Pijl [?, ?] distinguished five main categories that are anemochory, autochory, barochory, hydrochory, and zoochory. We made the determination of these types on the basis of literatures [?, ?, ?, ?, ?, ?, ?, ?].

2.4.3 Morphological spectrum

We determined the morphological types based on Quézel and Santa [?, ?, ?] and Ozenda [?, ?]. Depending on the persistence of aerial vegetative part during unfavorable season, we classified the plants as perennial, biennial, or annual [?, ?].

2.4.4 Grime's strategy

According to this model, species present in similar environments (i.e., stressed, disturbed, or productive environments) should have similar functional traits. The CSR (competition-stress-ruderality) model classified plants in respect to their responses to stress and disturbance into three main groups [?, ?], which results in competitors (low stress and disturbance), stress-tolerators (high stress and low disturbance), and ruderals (low stress and high disturbance), and plants that have mixed and multiple responses to stress and disturbance types, i.e., CS, CR, and SR for two responses, and CSR for three responses combined [?, ?].

2.4.5 Noy-Meir's strategy

Based on plant photosynthetic activity during dry season, Noy-Meir [?, ?] classified plants into two categories (arido-passive and arido-active species) according to their drought adaptation strategy. The identification of Noy-Meir's strategy of adaptation in this study was based on the following works of Quézel and Santa [?, ?, ?], Ozenda [?, ?], Jauffret [?, ?] and Bradai et al. [?, ?].

2.4.6 Chorological spectrum

According to Quézel [?, ?], the study area belongs to the Holarctic region, particularly to the Saharo-Arabian region (Saharan sub-region), and to the northern Sahara domain. The determination of chorological (or biogeographical) types of studied plants was referenced from the works of Quézel and Santa [?, ?, ?] and Quézel [?, ?].

2.4.7 Analysis of plant ecological groups

Ecological group of each species was defined following Quézel [?, ?]. Ecological groups retained in this study were psammophiles, gypsophiles, saxicoles, and ruderals.

2.4.8 Analysis of rarity/abundance status of flora

We determined rarity/abundance status of flora based on abundance appraisal retrieved from Quézel and Santa [?, ?, ?]. Each species was assigned to one of the following statuses: widespread (CCC), very common (CC), common (C), fairly common (AC), quite rare (AR), rare (R), and very rare (RR).

2.5 Statistical analysis

The data observed and/or computed at the level of sampling plots were exploited using free statistical software R [?, ?]. To compare beta diversity between and within LSE, we carried out nested Venn diagrams using the Venn package v.1.11 by displaying similarities of species richness intra and inter LSE. The variation in values of composition and taxonomic diversity parameters among LSE was tested using generalized linear model (GLM). Variables with count data (N and S) were fitted to GLM with Poisson distribution error and log link function, whereas the GLMs of other variables (VC, N′:S, VC:N′, VC:S, H′, H′max, E, SRI, SRI:S, and H′:SRI) were implemented using Gaussian distribution and identity function. For each LSE, relationships between the above-mentioned composition and taxonomic diversity parameters were analyzed using Pearson's correlations. The resulting correlation matrices were visualized in interactive plots using the R-corrplot package v.0.92. The relationships between these matrices were tested using two-tailed mantel test for a significance level of 0.05. Finally, because vegetation was investigated and characterized using multiple variables of different natures and aspects, a multiple factor analysis (MFA) was implemented to include all these studied variables into a single analysis. The MFA studied multiple tables of plant characteristics for different LSE, then highlighted patterns and distinguished between LSE based on plant variables. In our case, each table (i.e., different measured parameters, such as PFT) gathered a group of individuals (i.e., different plant traits). We implemented the MFA based on ten plant variables, i.e., lifeforms (chamaephytes, hemicryptophytes, and phanerophytes), morphological types (annuals and perennials), dispersal types (anemochore, barochore, and zoochore), Noy-Meir's strategy (arido-active and arido-passive), Grime's strategy (CSR, CS, SR, and S), chorological categories (NA, M-SA, Sah, and SA), rarity/abundance status (CCC, CC, C, AC, AR, R, and RR), density parameters (VC, N′, VC:N′, VC:S, and N′:S), diversity indices (S, H′, H′max, E, SRI, and SRI:S), and the characteristic and common species of all LSE (*A. articulata*, *Centropodia forsskaolii* (Vahl) Cope, *Mecomischus halimifolius* (Munby) Hochr., and *T. microphylla*).

3.1 Flora composition and abundance

Overall, 19 plant species were identified, belonging to 18 genera and 13 families (Table 1). The variation in floristic composition and abundance was notable and dependent on LSE. The plant species that recorded the highest values density, number of individuals, and occurrence frequency was *A. articulata.* While the lowest values were recorded in the following species: *Deverra scoparia* subsp. *scoparia* Coss. & Durieu, *Retama raetam* (Forssk.) Webb, and *Stipagrostis pungens* (Desf.) De Winter. Depending on LSE, *A. articulata* predominated in LLSE, while its highest values were recorded in MLSE. *C. saharae* was dominant in HLSE.

3.2 Importance of botanical families for different LSE

For different LSE, a variation in the distribution of different families was reported (Table 2). Poaceae and Asteraceae were the most represented families in the study area, followed by Amaranthaceae and Thymelaeaceae, and then Apiaceae. Depending on the type sampled LSE, the variation was notable. In LLSE, the families that recorded the highest values of relative frequencies of species richness were Asteraceae, Poaceae, and Scrophulariaceae. But the relative frequencies of abundances showed that the highest value was detained by Amaranthaceae. In MLSE, the highest value of species richness was recorded in Asteraceae, but the highest value of abundance-based relative frequency was reported in Thymelaeaceae. In HLSE, Asteraceae and Poaceae had the highest values of species composition, whereas Fabaceae was dominant in terms of number of individuals.

3.3 Species richness partitioning

Overall, the sampled LSE studied encompassed 19 species, of which 14 species colonized MLSE, whereas LLSE and HLSE had 10 and 11 species, respectively (Fig. 2 [Figure 2: see original paper]). The species *A. articulata*, *C. forsskaolii*, *M. halimifolius* and *T. microphylla* turn out to be common, even omnipresent among the three LSE. Other species were exclusive, the case of *S. acutiflora* in LLSE, *Euphorbia guyoniana* Boiss. & Reut. and *R. raetam* in MLSE, and *D. scoparia*, *Ephedra alata* ssp. *alenda*, *C. saharae* and *S. pungens* in HLSE. Six species were exclusively shared between LLSE and MLSE (*Pulicaria undulata* subsp. *undulata* (L.) C.A. Mey., *Moricandia nitens* (Viv.) E.A. Durand & Barratte, *Polycarpaea repens* (Forssk.) Asch. & Schweinf., *Moltkiopsis ciliate* (Forssk.) I.M. Johnst., *Scrophularia syriaca* Benth. in A. DC., and *Kickxia aegyptiaca* (L.) Nábelek). And 2 species were exclusive in MLSE and HLSE (*Helianthemum lippii* (L.) Dum. Cours. and *Rhanterium suaveolens* Desf.). Finally, no exclusive species occurred between LLSE and HLSE. It is noteworthy to mention that 4 common species above reported and shared species exclusively among LSE were also the common species among sampling sites within each LSE.

Fig. 2 Partitioning of plant species richness (S) recorded at desert pavements in the Sahara Desert of Algeria using nested Venn diagrams. Values of S reported between round brackets represent the total number of species recorded at each level of sand encroachment. Number of species shared exclusively between habitats with different levels of sand encroachment (LSE) and sampling sites are designated between square brackets and within the five-set diagrams, respectively.

3.4 Species richness estimation

The estimation of species richness through the nonparametric estimators S_{Chao1}, S_{Chao2}, S_{Jack1}, and S_{Jack2} revealed variable predictions from one estimator to another (Fig. 3 [Figure 3: see original paper]). In the study area as a whole, the application of S_{Chao1} and S_{Chao2} estimators allowed to predict an increase in species richness of 7% (inventory completeness=93%) for S_{Chao1} and 23% (completeness=77%) for S_{Chao2} to reach 20.5 ($±2.6)*and*24.6(±$6.8) species, respectively. This increase was expected to be 16% (completeness=84%) by S_{Jack1} ($S_{\text{Jack1}} = 22.7$ ($±$1.6)) and 27% (inventory completeness=73%) for S_{Jack2} with $S_{\text{Jack2}} = 26.2$ ($±0.0)*species.WithrespecttoLSE,byapplyingChao1andChao2insampledLSEwithLLSE*(S=11.0$ species), the predicted increases were 0% and 7% with 100% and 93% of completeness, respectively, that is equivalent to 11.0 and 11.8 species; whereas it was 18% (S_{Jack1}) and 23% (S_{Jack2}) corresponding to 13.4 and 14.0 species. In MLSE, 14.0 observed species would experience an increase by 30% with S_{Chao1} ($S_{\text{Chao1}} = 20.0$ species, completeness of 70%) and 10% with S_{Chao2} with 15.6 species (completeness of 90%). As for S_{Jack1} and S_{Jack2}, the increase was expected to be 19% (81% completeness) and 25% (75% completeness), respectively, corresponding to 17.2 and 18.7 species. Finally, in the case of HLSE, the increase by S_{Chao1} was 9%, corresponding to 11.0 species, 2% ($S_{\text{Chao2}} = 10.2$ species), 14% ($S_{\text{Jack1}} = 11.6$ species) and 13% ($S_{\text{Jack2}} = 11.5$ species).

Fig. 3 Observed and estimated plant species richness at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria. Species richness was estimated using first- and second-order Jackknife's (S_{Jack1} and S_{Jack2}) and Chao (S_{Chao1} and S_{Chao2}) estimators. Vertical bars represent standard deviations. S_{est}, estimated species richness.

3.5 Species richness interpolation

Species extrapolation curves revealed that the estimated values of specific richness (S_{est}) increased slowly with the increase in the number of samples (Fig. 4 [Figure 4: see original paper]). At 150 samples, i.e., 10 times more than the reference sample (m=15 with S=19 and n=591), and independently of LSE, the richness would increase by 29.4% for a number of individuals of 5910, reaching 24.6 ($±5.9)*species.Ontheotherhand,withLSE,at150samples(30timesmorethereferencesample)anincreaseof*16.

224)$.WithMLSE($S_{obs}=14$, n = 217), thisincreasewouldbe22.9\pm4.1)speciesforatotalof6510individuals.F$
n=150). In all cases, the plateau in curves was quickly reached even before reaching the 20th sample and a little more, regardless of LSE (Fig. 4).

Fig. 4 Sample-based rarefaction (solid line) and extrapolation (dashed line) curves of estimated plant species richness at desert pavements under different levels of sand encroachment (LSE) in the Sahara Desert of Algeria. Black solid circles indicate species richness estimated based on reference samples, whereas white solid circles refer to extrapolation to 150 samples. Dark colored areas indicate standard deviations, and light colored areas represent lower and upper bounds of 95% confidence intervals for the estimated values. (a), low LSE (LLSE); (b), moderate LSE (MLSE); (c), high LSE (HLSE); (d), overall.

3.6 Plant diversity patterns

The variation of different diversity parameters in sandy desert pavements of Algeria (Fig. 5 [Figure 5: see original paper]) revealed low values regardless of LSE. Indeed, the vegetation cover per sampling plot (100 m^2) varied between 14% and 16% with the increase in intensity of LSE. Plant density scored 44.80 (\$±5.17$)individualsinLLSE, whileitaveraged43.40(\pm19.17)and30.00(\pm8.22)individualsinMLSEandHLSE,$
(\$±\$1.87) species, $H' = 2.24$ (\$±\$0.45), $E = 0.76$ (\$±\$0.14), SRI = 4.34 (\$±2.07$))comparedwithHLSE($S=6.00\$ (\$±\$1.41) species, $H' = 2.04$ (\$±\$0.16), $E = 0.81$ (\$±\$0.09), SRI = 3.62 (\$±0.50$))andLLSE($S=5.80\$ (\$±\$2.17) species, $H' = 1.51$ (\$±\$0.75), $E = 0.59$ (+0.20), SRI = 2.35 (\$±1.06$)).ApartfromVC : N'$\$ ratio that displayed higher value in HLSE, VC:S and N′:S ratios were higher in LLSE. Finally, SRI:S and H′:SRI ratios varied slightly between LSE. GLMs testing the statistical variations of above-mentioned parameters among the studied LSE demonstrated that significant differences were observed in plant density ($F = 17.70$, $P < 0.001$), VC:N′ ratio ($F = 5.90$, $P = 0.016$), and N′:S ratio ($F = 5.00$, $P = 0.026$).

Fig. 5 Variation of diversity parameters at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria. Boxes indicate the IQR (interquartile range, 75th to 25th of the data). The median value is shown as a line within the box. White circle is shown as mean. Outlier is shown as black circle. Whiskers extend to the most extreme value within 1.5×IQR. (a), vegetation cover (VC); (b), plant abundance; (c), species richness (S); (d), individual cover (VC:N′ ratio), N′, density; (e), species cover (VC:S ratio); (f), species abundance (N′:S ratio); (g), Shannon's diversity index; (h), maximum Shannon's diversity index (H′max); (i), Evenness index; (j), Simpson's reciprocal index (SRI); (j), SRI:S ratio; (k), H′:SRI ratio. The abbreviations are the same in the following figures and tables.

3.7 Analysis of similarity

With all the indices of similarity, the greatest affinity was recorded between communities linked to LLSE and MLSE, explained by the values of 66.7% and 80.0%

for indices of Jaccard and Sorenson, 93.2% (raw Chao-Jaccard index), 97.2% (estimated Chao-Jaccard index), 96.5% (raw Chao-Sorenson index), 98.6% (estimated Chao-Sorenson index), 50.3% (Morisita-Horn index) and 44.0% (Bray-Curtis index) (Table 3); otherwise it rarely exceeded 50.0% between LLSE and HLSE or between MLSE and HLSE.

Table 3 Qualitative and abundance-based similarity scores between plant communities at desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria

Similarity estimator	Levels of sand encroachment (LSE)
	Low (LLSE) (S=11) vs. Moderate (MLSE) (S=14)
Shared species observed	
Estimated Chao-shared	
Classic Jaccard index (%)	66.7
Classic Sørensen index (%)	80.0
Raw Chao-Jaccard index (%)	93.2
Estimated Chao-Jaccard index (%)	97.2
Raw Chao-Sørensen index (%)	96.5
Estimated Chao-Sørensen index (%)	98.6
Morisita-Horn index (%)	50.3
Bray-Curtis index (%)	44.0

3.8 Interrelationship between vegetation diversity at different LSE

The relationships between abundance, cover, and diversity parameters of vegetation at different LSE in the study area revealed many significant ($P < 0.05$) and positive correlations (Fig. 6 [Figure 6: see original paper]). These correlations dominated under LLSE affecting the following pairs of parameters: VC VC:N′ ($P < 0.001$), VC VC:S ($P = 0.033$), VC H′ ($P = 0.027$), VC E ($P = 0.015$), N′ S ($P = 0.011$), N′ H′ ($P = 0.031$), N H′max ($P = 0.042$), N′ SRI ($P = 0.020$), S N′:S ($P = 0.041$), S H′ ($P = 0.028$), S H′max ($P = 0.003$), S SRI ($P = 0.047$), N′:S VC:S ($P = 0.014$), N′:S H′max ($P = 0.008$), VC:N′ VC:S ($P = 0.028$), VC:N′ H′ ($P = 0.014$), VC:N′ E ($P = 0.011$), VC:N′ SRI ($P = 0.034$), VC:S H′ ($P = 0.016$), CV:S H′max ($P = 0.017$), CV:S E ($P = 0.028$), H′ H′max ($P = 0.020$), H′ E ($P = 0.002$), H′ SRI ($P = 0.004$) and finally E SRI ($P = 0.014$).

Under MLSE, the significant correlations were observed between the pairs VC N ($P = 0.017$), S H′max ($P = 0.000$), H′ SRI ($P = 0.008$), E SRI:S ($P = 0.003$), whereas in HLSE, the significant correlations included S H′max ($P = 0.001$), S E ($P = 0.029$), S SRI:S ($P = 0.008$), VC:N′ VC:S ($P = 0.035$), H′max SRI:S ($P = 0.017$), and E SRI:S ($P = 0.004$). According to two-tail Mantel tests, different correlation matrices (Fig. 6) were positively associated, with a stronger correlation between MLSE HLSE ($P < 0.001$) compared with LLSE MLSE ($P = 0.035$) and LLSE HLSE ($P = 0.016$).

Fig. 6 Correlation matrices exposing correlations between plant characteristics (vegetation cover, plant abundance, and diversity parameters) at desert pavements under different levels of sand encroachment (LSE) in the Sahara Desert of Algeria. (a), low LSE (LLSE); (b), moderate LSE (MLSE); (c), high LSE (HLSE).

3.9.1 Lifeform

According to species- and abundance-based spectra (Table 4 ; Fig. 7 [Figure 7: see original paper]), chamaephytes predominated, while phenerophytes and therophytes were weakly represented. This finding is valid for both the whole study area and LSE when considered separately. Hemicryptophytes were moderately represented in all LSE.

3.9.2 Morphological type

Regardless of the type of spectra (abundance- or species richness-based), with the exception of HLSE, where annuals were absent, perennials predominated in LLSE and MLSE as well as in the study area when considered all LSE pooled (Fig. 7).

3.9.3 Dispersal type

For the whole study area and at each LSE, the predominance of anemochores was observed in plant dissemination types (Fig. 7). This type of plants with wind-borne seeds was also prominent in the density spectrum, but only in LLSE. Barochores co-dominated in second place in the study area, but it predominated in MLSE and HLSE. Zoochores were either absent or poorly represented, regardless of LSE.

3.9.4 Noy-Meir's strategy

The spectra of species richness and density of Noy-Meir's strategy showed a very clear dominance of arido-active plants compared with arido-passive species for all LSE and the whole study area (Fig. 7).

3.9.5 Grime's strategy

Species-based spectrum of Grime's strategy showed a predominance of CS strategy (competitive and stress-tolerant) throughout the study area and in different LSE (Fig. 7). The same was true for the density-based spectrum, but except in MLSE, where stress tolerant plants predominated. Plants with CSR and SR strategies were very poorly represented both in terms of species richness and abundance and both at the scale of LSE, and even at the whole study area.

3.9.6 Chorological type

Based on species richness spectrum (Fig. 7), the Saharo-Arabian category was well represented in the whole study area and different LSE. In terms of abundance, the chorological type 'Saharo-Arabian' was exclusively dominating in LLSE and the study area. In MLSE, Mediterranean-Saharo-Arabian plants predominated, while Saharan plants colonized HLSE. Finally, the endemic plants to Algerian-Moroccan Sahara were very weakly represented in all sandy gravels both in terms of plant richness and density.

3.10 Plant ecological category and rarity status

Regardless of LSE, a predominance in relative frequency of species richness of psammophytes (S = 48.0%, N' = 26.2%–65.3%) was recorded. This was accompanied by a weak representation of gypsovags and ruderals (Table 5). For the rarity status in the flora of Algeria, based on species relative frequency, there was an absence of plants of CCC in LLSE. CC and C plant species were well represented (27.3% for each), accompanied by a significant percentage of RR species (S = 18.2%). Abundance-based frequencies showed a predominance of C species (N' = 75.9%). The species richness of the category CC and C predominated in MLSE with S = 28.6%. Based on abundance, CC species predominated with 59.4%. In HLSE, species richness of CC type was well represented (S = 40.0%), while species with AC status was absent. In terms of abundance, AR predominated with N' = 47.3%. In the whole study area, CC status predominated in terms of species richness (S = 31.6%), while it was the category of C that predominated in terms of abundance (N' = 42.5%).

3.11 Vegetation pattern associated to desert pavements under SLA

MFA result confirmed totaled 100.00% of explained variance, with 62.89% on the first dimension and 37.11% on the second dimension (Fig. 8 [Figure 8: see original paper]). This analysis highlighted the associations between the measured traits and attributed characteristics of vegetation according to LSE. We distinguished the latter from each other according to the variables of vegetation. According to first axis of MFA, we distinguished desert pavements with HLSE from the other two LSE by morphological type, phytogeographic type, rarity status, density parameter, lifeform, and Noy-Meir's strategy. While the second axis differentiated between MLSE and LLSE according to Grime's strategy, diversity score, dispersal type, and common species. The plant communities encountered in LLSE and MLSE converged mainly by similarities in morphological type and Noy-Meir's strategy, and then by rarity status, density parameter, and lifeform. Plant community of desert pavement under HLSE presented similar schemes with MLSE following the effects of plant diversity parameter and dispersal type, while the density of common species between these LSE contributed to their segregation apart. The converging variables between communities of LLSE and HLSE were scores of diversity parameters and common species densities. The MFA indicated that with the increase in LSE, i.e., along the gradient from LLSE to HLSE, plant communities strike sharp changes in plant variables including decrease in plant densities with changes in chorological categorie, rarity status, lifeform, morphological type, and Noy-Meir's strategy. Indeed, the variants and sub-traits of these variables were significantly related to each other. Considering the PFT patterns of plant communities shown in Figure 7, chamaephyte, perennial, plant density (N′), anemochorous, arido-active, and CC species were positively correlated (Fig. S1).

Fig. 8 Vegetation pattern associated to desert pavements under different levels of sand encroachment in the Sahara Desert of Algeria. L1, low LSE; L2, moderate LSE; L3, high LSE. The vegetation of each sand encroachment level was projected on MFA (multiple factor analysis) dimensions using ten vectors representing different plant characteristics.

4 Discussion

After characterizing the vegetation cover to water stress in hot and arid environments [**?**, **?**], this study shed light on plant communities of the desert pavements, which are one of the most characteristic landscapes of the Sahara Desert. In the Sahara Desert, the vegetation cover with geomorphological determinism is closely linked to the habitat. Apart from the wadis and dry valleys that are colonized by plant groups, erg, Hamada- and Reg-type habitats have a low floristic diversity.

4.1 Evaluation of taxonomic diversity

The study area shelters 19 plant species belonging to 18 genera and 13 families, dominated in particular by *A. articulata* with rare species *D. scoparia*, *R. raetam*, and *S. pungens*. The floristic composition and abundance vary according to LSE, with a more marked representation of *A. articulata* in LLSE, *T. microphylla* in MLSE, and *C. saharae* in HLSE. On the other hand, the distribution of botanical families at different LSE is favoring the families of Asteraceae (richer in genera), Poaceae, Fabaceae, Scrophulariaceae, Amaranthaceae, and Thymeleaceae compared with Apiaceae. The same families are reported in previous studies in arid and semi-arid North Africa [**?**, **?**, **?**, **?**, **?**]. According to Heywood [**?**, **?**], these families are not only restricted to arid environments, but they are the largest families of flowering plants in the world. According to Giulietti et al. [**?**, **?**], the predominance of these families reflects their establishment ability in habitats with high solar radiation, shallow soils, steep slopes, and major factors of low availability of water and nutrients in these ecosystems. It also indicates their effective strategies of wind dispersal of their diaspores [**?**, **?**].

With regard to the distribution of 19 species identified, the range fluctuates between 10 in LLSE and HLSE, and 14 species in MLSE, with dominance of ubiquitous and common species, such as *A. articulata*, *C. forsskaolii*, *M. halimi-*

folius, and *T. microphylla.* However, some species showed some exclusivity such as *S. acutiflora* in LLSE, *E. guyoniana* and *R. raetam* in MLSE, and *D. scoparia*, *E. alata*, *C. saharae* and *S. pungens* in HLSE. In active sand dune fields and sandy habitats, species composition is associated with spatial heterogeneity and dynamics that can be determined by aeolian erosion, sand accumulation, and siltation [**?**, **?**, **?**, **?**].

The low vegetation cover characterizing hot and arid environments, especially in the Sahara Desert, prompts to apply purposive sampling technique in the study area, but the greater the sampling effort is, the more the number of species is expected to increase [**?**, **?**]. At the beginning, the collection includes the most common species, and then increasingly rare species. In this study, the total number of observed species was 19, varying from 10 to 14 species depending on LSE. The use of non-parametric estimators revealed that there is a difference between observed richness and that estimated both for the area as a whole and for each LSE. For 4 estimators applied (Chao1, Chao2, Jack1, and Jack2), additional sampling effort is required to complete the inventory of missing rare species. In the study area as a whole, this additional sampling is estimated at 7% (Chao1), 23% (Chao2), 16% (Jack1), and 27% (Jack2). However, these predictions vary according to LSE. In LLSE, with its 11 observed species, the increase was 6% for Chao1, 7% for Chao2, 18% for Jack1, and 23% for Jack2. In MLSE ($S_{\text{obs}} = 14$), the increase was 30% for Chao1, 10% for Chao2, 19% for Jack1, and 25% for Jack2. Finally, in HLSE ($S_{\text{obs}} = 10$), the increase was 9% for Chao1, 2% for Chao2, 14% for Jack1, and 13% for Jack2. In any case, regardless of estimator used, the sampling effort turned out to be relatively insufficient. Although the Jackknife's estimator is known for its robustness [**?**, **?**], the values obtained are not far from the other estimators.

At 150 samples (10 times more than the reference sample) and independently of LSE, the observed richness (19 species) would reach 24 species, i.e., an increase of 29% for a number of individuals of 5910. In LLSE ($S_{\text{obs}} = 11$, n=224 individuals), at 150 samples (30 times more than the reference sample), the number of estimated species (S_{est}) would be 12.80 for n=6720. For MLSE ($S_{\text{obs}} = 14$, n=217), the predicted richness would reach 17.00 species for n=6510 individuals. For HLSE ($S_{\text{obs}} = 10$, n=150), the estimated richness would be 10.53 species for 4500 individuals. Although there is a difference between observed and estimated species richness with different estimators applied, the missing sampling effort is not great, since the extrapolation curves reveal a plateau very quickly even before reaching the 20th sample or a little more, regardless of LSE.

By comparing the plant communities recorded at desert pavement with different LSE, a dissimilarity is reported among LLSE, MLSE, and HLSE. This species compositional dissimilarity may be due to the effect of native plants to form nabkhas following the trapping of mobile aeolian sediments and sand accumulations [**?**, **?**, **?**].

As for vegetation parameters, the low rate of cover (14%–16%) accompanied by a decreasing abundance with the increase in LSE, represents a main indicator of climatic aridity in hot environments [?, ?]. As vegetation is the major component determining the nature of ecosystems [?, ?], its distribution is modulated by water availability and habitat quality [?, ?, ?]. On the other hand, the diversity indices (H′, E, and SRI) showed high values with a tendency to balance in MLSE and HLSE vs. low values in LLSE. According to Mota et al. [?, ?], the high values of diversity in these habitats could be explained by the installation of herbaceous and shrubby communities, which vary according to the landform, microclimate, soil depth, generating a mosaic character to this vegetation. According to Batanouny [?, ?], local topography not only controls water, but also affects its physical and chemical attributes. A slight depression of a few centimeters can lead to the accumulation of a thin layer of soil/sand transported by the water and/or wind, which contributes to the creation of a relatively favorable habitat to the growth of plants, despite the hostile desert conditions [?, ?].

4.2 Evaluation of plant functional diversity

According to Wang et al. [?, ?], plant functional traits provide information about adaptations to climate and environmental conditions, and can be used to explore the existence of alternative plant strategies within ecosystems. The analysis of plant ecological groups highlighted the predominance of psammophytes and a low quantity of gypsovag plants (gypsicoles or gypsophytes), and ruderals in LLSE and HLSE, while MLSE is colonized by saxicolous species. This diversity of ecological groups is linked to the nature of the soil, in particular particle size composition in sand. Moreover, the analysis of the rarity/abundance status of the flora showed good representations of C and CC types. Whereas CCC, AC, and R plants are poorly represented and less abundant.

Active dunes, whether continental or marine, are unfavorable for the survival of most plants due to the instability of the support except for psammophytes [?, ?, ?]. The latter are defined as the pioneering dune plant species [?, ?]. Therefore, only psammophytes adapting to wind–sand activity are established [?, ?, ?]. Topographic depressions serve as vegetation islands, composed of psammophytes and non-psammophytes [?, ?], among which endemic or rare species occur [?, ?]. In all cases, vegetation distribution is scale-dependent. However, sand dune encroachment and wind–sand activity (sand burial and erosion) also contribute to shaping vegetation pattern [?, ?, ?]. Vegetation pattern is very likely to be associated with the scale level [?, ?, ?]. Microheterogeneity regulates erosion and soil nutrient distribution, and causes small-scale vegetation heterogeneity [?, ?, ?]. Observed vegetation patterns frequently reflect differences of natural conditions [?, ?].

Lifeform composition of plant community is a faithful indicator of adaptations of its constituent species to climatic conditions [?, ?]. Since phanerophytes prefer humid climates, such as equatorial regions [?, ?], and while chamaephytes indicate a temperate phytoclimate [?, ?], the dominance of therophytes in any region indicates an arid climate and disturbed habitat [?, ?]. Unlike some studies on the vegetation of arid and semi-arid environments, where therophytes dominated the lifeform spectrum [?, ?, ?, ?, ?], this study showed that chamaephytes dominated in desert pavements invaded by aeolian sand deposits. Regardless of LSE, chamaephyte propositions exceeded the percentages of hemicryptophytes, therophytes, and phanerophytes. Therophytes are weakly present in the studied desert pavements, although the vegetation sampling was carried out during the optimal period of plant growth (February–April). This is in disagreement to plant biological spectra established in other arid and semi-arid zones of Algeria [?, ?, ?]. This biological type is dependent on rainfall [?, ?]. According to Harrison et al. [?, ?], therophytes are generally dominant in some of the planet's driest and coldest environments. This lifeform can be rare due to a combination of short growing seasons and low nutrient inputs to rock surfaces that prevent rapid establishment and growth [?, ?]. It is most likely that their low presence in desert pavement with gravels and different LSE is associated with the instability of physical support resulting from the dominance of sandy soil texture [?, ?]. In arid environments of the Middle East, Al-Shaye et al. [?, ?] reported that the dominance of therophytes and chamaephytes over other plant lifeforms is a response to the hyper-arid climate with insufficient rainfall; whereas some microhabitats can support a high percentage of perennials.

The large representation of chamaephytes can be explained by plant adaptations to adverse weather conditions (dry winters), with protected buds on the soil surface and/or by scales and leaves [?, ?]. The predominance of this biological type in the Saharan environments has already been reported by other studies [?, ?, ?, ?, ?, ?]. As for hemicryptophytes, unlike the results of Bouallala [?, ?] and Bouallala et al. [?, ?], their low representation in the vegetation studied in desert pavement with gravels would probably be attributed to overgrazing in this rangeland. In any case, their low abundance reduces competition for soil moisture to the benefit of chamaephytes [?, ?, ?]. According to Rana et al. [?, ?], the low presence of hemicryptophytes indicates the effects of biotic factors on vegetation. While therophytes are typical of ruderal habitats, hemicryptophytes and phanerophytes require less disturbed habitats [?, ?]. Represented by two species (*E. alata* and *Retama retam* (Forssk.) Webb) in studied desert pavements, phanerophytic plants are a rare lifeform type in the Sahara Desert [?, ?, ?] except in habitats benefiting from a supply of water such as the case of valleys and wadi beds [?, ?]. These two xerophytes are pioneers of mobile and semi-stable sand dunes in deserts and steppes [?, ?, ?].

With regard to plant longevity and response to the xericity of climate, perennials dominate in the study area. These plants implement a set of morphological, physiological, and anatomical adaptation mechanisms to ensure slow survival in life during long periods of drought [?, ?, ?, ?]. As a result, these are less subject to seasonal variations, constituting the only rangelands still available in the hot-dry season [?, ?, ?]. However, the variation in life forms reflects species-specific responses to environmental variations, and represents functional traits of the species that may be an important driver of ecosystem functioning [?, ?].

The studied plants generally adopt a dispersal mode of anemochoric, barochoric, then zoochoric type in desert pavement with aeolian sand deposits. The importance of wind in desert environments no longer needs to be demonstrated [?, ?, ?]. Wind dispersal reaches a peak synchronized with the dry season in Mediterranean [?, ?], desert [?, ?], and dry tropical [?, ?] climates. In contrast, zoochory is the most dominant dispersal mechanism in dry and humid forests, and it decreases in ecosystems with dry climates [?, ?], reflecting the low presence of mammals in the hostile desert conditions [?, ?]. Finally, barochory is significant in temperate areas [?, ?]. Gentry [?, ?] and Jara-Guerrero et al. [?, ?] suggest that dispersal mechanisms may be associated with climatic factors and most likely with temporal patterns of water availability. These factors have the greatest impact on plant propagation in hyper-arid hot deserts [?, ?]. Plant dispersal strategy plays an essential role in the colonization of new habitats, population dynamics, species interactions, community structures, and plant diversity [?, ?]. It can be considered as a key factor in the conservation biology and restoration planning [?, ?].

Our findings revealed that arido-active plants exceed arido-passives. According to Jauffret [?, ?], arido-active species have water reserves to function. These plants benefit from sandy soils, which are capable of creating edapho-climatic conditions, favoring the development of a specific plant cover. The evolution of proportions of arido-active and arido-passive plants in the plant populations of dry zones could provide information on the vulnerability and/or the resilience capacity of ecosystems in the face of aridity and consequently climate change. The regression of arido-actives could reflect a trend towards aridification. While all annuals (therophytes) are arido-passive, perennial species are not always arido-active [?, ?, ?]. The same is true for Grime's strategy, which competitive, stress-tolerant plants, and stress-tolerators predominate other classes. Generally, even after the destruction of aerial phytomass, long-lived plants (competitive and stress-tolerant plants) will be able to sprout after grazing or cutting wood [?, ?]. With regard to the chorology of identified species, plants with the Saharo-Arabic chorological type predominated throughout the study area with Mediterranean Saharo-Arabic type and endemic to the Algerian-Moroccan Sahara. These are the phytogeographic types best suited to the Saharan environments [?, ?, ?, ?, ?]. Plants with the Mediterranean Saharo-Arabian chorological types find in MLSE, a favorable environment to develop and thrive. The endemic plants to the Algerian-Moroccan Sahara, despite their low presence and abundance, have managed to develop and spread in desert pavements of the Algerian Sahara Desert.

5 Conclusions

Based on the climatic and geomorphological characteristics, desert pavements of the northern Sahara represent hyper-arid environments with low vegetation cover and plant diversity. The analysis of this floristic diversity in the desert pavements gave insightful indicators on the state of evolution of the Saharan ecosystem through the presence and abundance of so-called exclusive species, which are good indicators of soils and sub-surface substrates. The present study showed that LLSE is characterized by an exclusive species, MLSE by two exclusive species, and HLSE by four exclusive species. The lifeform type best adapted to the environmental conditions of sandy desert pavements is chamaephytes. Generally, the dispersion of the majority of plants that constitute the phytocenoses analyzed is ensured by anemochory. Competitive and stress-tolerant plants are dominant and are able to sprout after grazing or cutting of aerial parts. Despite the diversity of chorological types, the Saharo-Arabian type remains by far the best represented and the best adapted to the conditions of sandy desert pavement of the Sahara Desert. Psammophytes dominate in the community of desert pavement despite the diversity of soil substrates. Furthermore, it is necessary to extend this study to other types of ecosystems to better understand the evolution and dynamics of biodiversity in hot and arid regions, especially the Sahara Desert.

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Appendix

Fig. S1 Pearson's correlation matrix between sub-levels of all plant variables clustered in the bi-plot of multiple factorial analysis (MFA). CSR, competition-stress-ruderality; CS, competition-stress; SR, stress-ruderality; Str, stress-tolerant; NA, North African chorological type; M-SA, Mediterranean-Saharo-Arabian; Sah, Saharan chorological type; SA, Saharo-Arabian; CCC, widespread; CC, very common; C, common; AC, fairly common; AR, quite rare; R, rare; RR, very rare; VC, vegetation cover; N′, density; S, species richness; H′, Shannon's diversity index; H′max maximum Shannon's diversity index; E, Evenness index; SRI, Simpson's reciprocal index.

Table S1 Climatic information of the El-Guerrara region at the Ghardaia Province in the Sahara Desert of Algeria

Climatic information	Value/class
Latitude	32°46′N
Longitude	04°33′E
Altitude (m)	
Koeppen's climate classification	BWh (B=Arid climate; W=Desert; h=hot)
Budyko's climate	Desert Hyper-arid
Radiational index of dryness	
Budyko's evaporation (mm/a)	
Budyko's runoff (mm/a)	
Budyko's evaporation (%)	
Budyko's runoff (%)	
Aridity	
Aridity index	
Moisture index (%)	
de Martonne's index	1
Precipitation deficit (mm/a)	1639.0
Climatic NPP (g DM/(m^2	
NPP (Temperature)	
NPP (Precipitation)	
NPP is precipitation limited	
Gorczynski's continentality index	

Note: NPP, net primary production. DM, dry matter.

Table S2 Long-term monthly climatic data near the El-Guerrara region at the Ghardaia Province in the Sahara Desert of Algeria

Parameter	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Average
Mean temperature (°C)	11.1$±1.38	13.6±1.20	16.8±1.50	21.0±0.95	25.7±1.63	31.2±1.46	33.7±1.54	34.0±1.34	28.6±1.29	22.2			
Day length (h)													
Sunshine hours (h)													
Ground frost frequency (%)													
Effective rainfall (mm)													
Effective rainfall percentage (%)													
Number of rainy days (d)													
Solid precipitation ratio													

Note: mean±SD; LST, local standard time.

Note: Figure translations are in progress. See original paper for figures.