

TAXONOMIC, TRAIT-BASED, AND BETA-DIVERSITY PATTERNS OF PLANT COMMUNITIES ACROSS WADIS, DAYAS, AND OASIS MARGINS IN THE GHARDAÏA REGION, NORTHERN ALGERIAN SAHARA

Radhia BIAD*, Choayb BOUNAB*, Moussa HOUHAMDI**

*Laboratory of Valorization and Conservation of Arid Ecosystem, Faculty of Natural and Life Sciences and Earth Sciences, University of Ghardaïa, Ghardaïa, Algeria

**Biology, Water and Environment Laboratory (LBEE), Department of Ecology and Environmental Engineering, Faculty SNV-STU, University 8 May 1945 Guelma, Algeria

Corresponding author: Radhia Biad, University of Ghardaïa, Faculty of Natural and Life Sciences and Earth Sciences, Department of Biology, BP 455, Bounoura, Ghardaïa 47000, Algeria, phone: +213558642922, E-mail: biad.radhia@univ-ghardaia.edu.dz

Abstract. Wadis are azonal drainage systems that concentrate plant diversity in the northern Sahara, but how landform heterogeneity structures their floras remains poorly documented. We compared the taxonomic, trait-based, and beta-diversity dimensions of plant communities at six sites in the Ghardaïa region (northern Algerian Sahara): three sandy-rocky wadi channels, one open wadi, one clay endorheic daya, and one peri-urban oasis margin, using 18 quadrats of 400 m² sampled in spring 2025. We recorded 2,127 individuals of 53 taxa in 31 families; Asteraceae was the richest family (10 taxa), followed by Apiaceae, Brassicaceae, Fabaceae, and Poaceae (3 taxa each); Poaceae was the most abundant (21.4% of individuals). Saharo-Arabian elements dominated (47.2%), and therophytes and chamaephytes were equally frequent (34.0% each). Richness (highest at El Attéf, 39.7 taxa per quadrat), Hill numbers, and diversity indices differed among sites (Kruskal-Wallis, $p = 0.012$ – 0.033), but with three quadrats per site only richness at Oued Labyad versus El Attéf differed significantly after Bonferroni correction. Sørensen beta diversity was high (0.795) and dominated by turnover ($\beta_{SIM} = 0.711$) rather than nestedness ($\beta_{SNE} = 0.085$). PERMANOVA on Bray-Curtis dissimilarities (999 permutations) indicated strong compositional differences among sites (pseudo- $F = 2.14$, $R^2 = 0.47$, $p = 0.001$), with heterogeneous dispersions (PERMDISP, $p = 0.001$). Indicator species analysis identified *Phragmites communis* (IndVal = 1.00) and *Juncus rigidus* (IndVal = 0.91) as markers of hygric sites. Trait-based indices (FRic, FEve, FDis) were computed from three categorical attributes compiled from floras (life span, ethnobotanical use, endemism), used as proxies for avoidance versus persistence strategies, grazing value, and range restriction under drought stress; FRic ignores abundance, whereas FEve and FDis are abundance-weighted. Functional richness tracked taxon richness, whereas functional evenness was low to moderate (0.41–0.83). Strong turnover among sites of contrasting landforms suggests that conservation should target the whole habitat mosaic.

Keywords: arid ecosystems; beta diversity; floristic diversity; functional traits; indicator species; Saharan Algeria.

INTRODUCTION

Drylands cover about 41% of Earth's land surface and sustain a substantial share of global plant diversity and ecosystem functioning despite chronically low productivity [37, 38, 55]. Their vegetation is expected to respond non-linearly to increasing aridity [11]. Within these landscapes, wadis are azonal systems: linear drainage networks that concentrate episodic run-off and shallow alluvial water and support vegetation distinct from the surrounding zonal reg and erg surfaces [23, 41, 48, 65]. Dayas, by contrast, are closed depressions within the rocky hamadas that receive local run-off and flood temporarily [13, 48]; they differ from wadis in genesis and hydrology and are not micro-habitats of the wadi network. Both landforms, together with oasis margins, contribute to landscape-scale geomorphological heterogeneity in the northern Sahara. Contemporary biodiversity assessment increasingly combines Hill numbers, which unify richness, Shannon entropy, and Simpson concentration [14, 28, 56], with the partitioning of beta diversity into turnover and nestedness [7, 9] and with trait-based indices of community structure [33, 67]. In deserts and global drylands, beta diversity is often dominated by turnover and is related to climate, soil, and dispersal [23, 30, 31, 66], and it informs both ecosystem functioning and conservation planning [42, 58], but such multi-dimensional analyses are scarce in North African wadi systems. Saharan botany has a long tradition [15, 48, 51], and recent work in Algeria has documented the flora, life-form spectra, and chorology of sandy habitats

and wadis, including the Ghardaïa region [6, 41], as well as plant diversity along a semi-arid North African watershed [60] and in urban plantations of the Algerian Sahara [62]. Global syntheses further show that trait diversity in drylands responds to aridity and grazing [27]. These studies, however, mostly describe individual habitat types, and comparatively few have contrasted wadi channels, dayas, and oasis margins within a single framework that couples Hill-number alpha diversity, turnover-nestedness partitioning, multivariate tests, indicator species, and trait-based indices. The M'Zab region of Ghardaïa, where sandy wadi channels, clay dayas, and oasis margins occur within a few kilometres, offers a suitable setting for this comparison. We therefore pursued five objectives: (1) to characterise the taxonomic and chorological structure of the flora (i.e., the distribution of taxa among biogeographic range types); (2) to quantify Hill-number alpha diversity across six sites; (3) to partition beta diversity and test compositional differences with PERMANOVA and PERMDISP; (4) to identify indicator taxa with indicator species analysis (IndVal), which is used only to describe taxon-site associations and not as a measure of functional diversity; and (5) to describe the trait-based functional structure of the communities (FRic, FEve, FDis) from categorical attributes and its coupling with taxonomic diversity. We hypothesised that geomorphological heterogeneity, namely sandy wadi channels versus a clay daya and an oasis margin, is associated with strong floristic turnover.

MATERIALS AND METHODS

Study Area

The study was conducted in the Ghardaïa region (M'Zab Valley, northern Algerian Sahara; 32°N, 3°E; 468 m a.s.l.). Climatic data were taken from the Ghardaïa station of the National Meteorological Office (ONM; period 2009-2018), as compiled by Zergoun [70]. Mean annual temperature was 22.3°C; monthly mean temperatures ranged from 12.1°C (January) to 34.2°C (July), monthly mean minima from 4.1°C (January) to 25.8°C (July), and monthly mean maxima from 20.1°C to 42.4°C. Mean annual precipitation was 65.4 mm, very irregularly distributed (e.g., September 15.7 mm, January 10.5 mm, March 8.4 mm). The mean wind speed was 2.27 m/s (monthly means from 1.78 m/s in December to 2.58 m/s in March); north-westerly winds prevail in autumn, winter, and spring, and hot southerly winds are frequent in summer. The Emberger pluviothermic quotient, calculated for Algeria with Stewart's formula ($Q2 = 3.43 P/(M - m)$, where P is annual precipitation, M the mean maximum of the hottest month, and m the mean minimum of the coldest month [63]), was 5.85 for this period, placing Ghardaïa in the Saharan bioclimatic stage [70]; the study area therefore lies at the northern margin of the Saharan bioclimatic stage, close to its transition with the steppes of the Saharan Atlas. The bedrock is a plateau of Upper Cretaceous (Turonian) limestone, the rocky hamada known as the Chebka of the M'Zab [5, 25, 70], dissected by wadi channels and locally covered by alluvial and aeolian deposits. Fieldwork was carried out in spring (February-April 2025). Six sites representing three geomorphologically distinct landform types were investigated (the term Oued, i.e. wadi, is kept only as part of local site names). Three are sandy to rocky-bottomed wadi channels of varying watershed size (Oued Ourighnou, Oued Labyad, and Oued Madagh; Fig. 1), which are fluvial drainage systems. One is a clay-floored endorheic daya (Daya), a closed depression within the hamada receiving local slope run-off [15]; dayas differ from wadis in genesis and hydrological dynamics, so the daya is not treated as a micro-habitat of the wadi network. The remaining two are a peri-urban oasis margin under moderate anthropogenic pressure

(Bounoura) and a relatively well-preserved open wadi system (El Attef). The six sites thus span a gradient of substrate texture, hydrological connectivity, and disturbance that was defined qualitatively from field observation; no soil, hydrological, or disturbance variables were measured. Local lithological variation (calcareous bedrock, alluvial and aeolian cover, clayey infill) may influence water infiltration and retention, but this is a working hypothesis that was not tested here.

Sampling Design and Vegetation Survey

Floristic sampling was conducted at the vegetation peak (spring, February-April 2025). Each sampling unit was a 20 m × 20 m (400 m²) plot (hereafter "quadrat", equivalent to a phytosociological relevé); this size was selected with the minimal-area method [45]: preliminary species-area curves reached an asymptote at this size. Sampling was stratified by geomorphological unit (channel bed, terrace, and clay depression), and three independent quadrats were sampled per site (18 quadrats in total), a number that balances spatial independence and logistical feasibility in hyper-arid terrain. The six sites are distinct habitat units along a gradient of soil texture, hydrology, and disturbance rather than true replicates of one habitat type, and each landform type is represented by one site (one daya, one oasis margin) or three sites (sandy wadi channels); replication therefore occurs only at the quadrat level ($n = 3$ per site), and inferences concern the six sites sampled rather than landform types in general. All vascular plant taxa were recorded in each quadrat. Abundance was recorded as a direct count of individuals per quadrat (no cover-abundance scale such as Braun-Blanquet was used); absolute abundance was the total number of individuals across quadrats, and absolute frequency the number of quadrats (0-18) in which a taxon occurred; relative abundance and relative frequency are the corresponding percentages of the totals. These data are provided in Supplementary Table S1, which also lists, for each taxon, the genus, family, Raunkiaer life form [54], chorological type, and life cycle. Botanical identification followed Quézel and Santa [52], updated with Dobignard and Chatelain [20] and Ozenda [48]; chorological affinity followed Ozenda [48] and Pottier-Alapetite [50]. In the chorological codes, SA-Med denotes Saharo-Arabian taxa extending into the Mediterranean region, whereas Med-SA denotes Mediterranean taxa extending into the Saharo-Arabian region; the two are distinct categories. The trait-based analysis used three categorical attributes assigned to each taxon from floras and the ethnobotanical literature rather than measured in the field: life span (annual/ephemeral versus perennial), ethnobotanical use category (pastoral, medicinal, medicinal-toxic, medicinal/food, food, ecological, both, or none), and endemism status (non-endemic, cultivated, or endemic to the Saharo-Arabian, North African, Algero-Tunisian, or Algero-Moroccan area) [20, 49]. No continuous traits (e.g., specific leaf area, plant height, seed mass) were measured. These attributes were retained because life

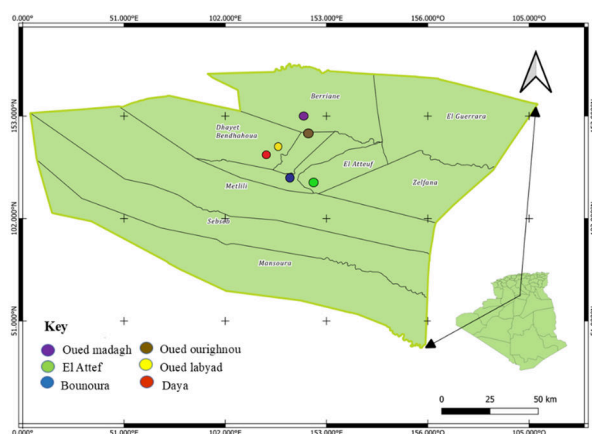


Figure 1. Location of the study area

span separates avoidance (ephemeral) from persistence (perennial) strategies, the main contrast in arid-zone plant ecology [19, 46]; ethnobotanical use summarises grazing and harvesting value, which is relevant in grazed drylands where trait diversity responds to grazing [27]; and endemism describes range restriction and habitat specialisation, which is relevant to conservation value. They are not physiological traits and are therefore interpreted as proxies.

Data Analysis

All analyses were performed in R v.4.6.0 [53]. Biological and chorological spectra were computed and plotted with ggplot2 [69]. Alpha diversity was quantified with the Shannon index ($H' = -\sum p_i \ln p_i$), the Simpson index ($1 - D = 1 - \sum p_i^2$), Pielou's evenness ($J' = H'/\ln S$), where p_i is the relative abundance of taxon i and S is taxon richness [39], and Hill numbers ($qD = (\sum p_i^q)^{1/(1-q)}$; $q = 0, 1, 2$, i.e., taxon richness, the exponential of Shannon entropy, and the inverse Simpson concentration; iNEXT [29]), which are non-increasing functions of q [14, 28]. Among-site differences were tested with Kruskal-Wallis tests ($\alpha = 0.05$) followed by Dunn's post hoc tests with Bonferroni correction [22]; with $n = 3$ quadrats per site these tests have low power, and non-significant pairwise results are interpreted as inconclusive rather than as evidence of equivalence. Because several indices were tested, the Kruskal-Wallis p-values of the seven non-redundant indices (richness, Shannon, Simpson, Pielou, FRic, FEve, FDis; Hill numbers of order 1 and 2 are monotonic transformations of Shannon and Simpson) were also adjusted with the Benjamini-Hochberg false discovery rate procedure [10]. Beta diversity was partitioned into the turnover (βSIM) and nestedness (βSNE) components of multiple-site Sørensen dissimilarity (βSOR) with betapart [7, 9]. The Sørensen-based decomposition was chosen as the standard formulation of this framework and because βSIM is independent of differences in richness among sites; the Jaccard-based components (βJTU , βJNE) are monotonic transformations of the Sørensen-based ones [8], so the relative importance of turnover and nestedness is not expected to change with the choice of family. Compositional differences were tested by

PERMANOVA (adonis2; Bray-Curtis dissimilarity on abundance data; 999 permutations; reported as pseudo- F , R^2 , and p ; [1]) and multivariate dispersion by PERMDISP (betadis; 999 permutations; [2, 4]) in vegan [47], and were visualised with NMDS ($k = 2$), PCoA, and hierarchical clustering. To relate compositional differences to geomorphology, a second PERMANOVA grouped the quadrats a priori by landform type (wadi systems: Oued Ourighnou, Oued Labyad, Oued Madagh, and El Attef; daya; oasis margin: Bounoura) on the same Bray-Curtis matrix with 9,999 permutations. Indicator species were identified with IndVal/multipatt (indicspecies; 999 permutations; site-group combinations allowed; [17, 18, 21]). Because permutation p-values vary among runs, the IndVal and PERMANOVA p-values reported here are from a single run; repeated runs changed them by up to about 0.02. Trait-based indices (FRic, FEve, FDis) were computed with dbFD in the FD package [33, 67] from the taxon $\times$ trait matrix described above, using Gower dissimilarity because all traits are categorical [26]. FRic was expressed as the number of distinct trait combinations (functional entities) represented in a quadrat and does not depend on abundance, whereas FEve and FDis were weighted by taxon abundance (number of individuals per quadrat) [40, 43]. Before correlation analysis, normality was checked with Shapiro-Wilk tests and Q-Q plots; because several variables departed from normality (Simpson, Pielou, FEve), Spearman's rank correlation (r_s) was used throughout, and the p-values of the 21 pairwise correlations were adjusted with the Benjamini-Hochberg procedure [10]. Exact p-values are reported throughout.

RESULTS

Taxonomic Composition and Floristic Structure

The 18 quadrats yielded 2,127 individuals belonging to 53 taxa, 51 genera, 31 families, 19 orders, and 2 classes (Fig. 2; Supplementary Table S1). Magnoliopsida dominated (48 taxa in 28 families), whereas Liliopsida contributed 5 taxa in 3 families (Poaceae, Juncaceae, and Arecaceae). Asteraceae was the most diverse family (10 taxa), followed by Apiaceae, Brassicaceae, Fabaceae, and Poaceae (3 taxa each) (Fig.

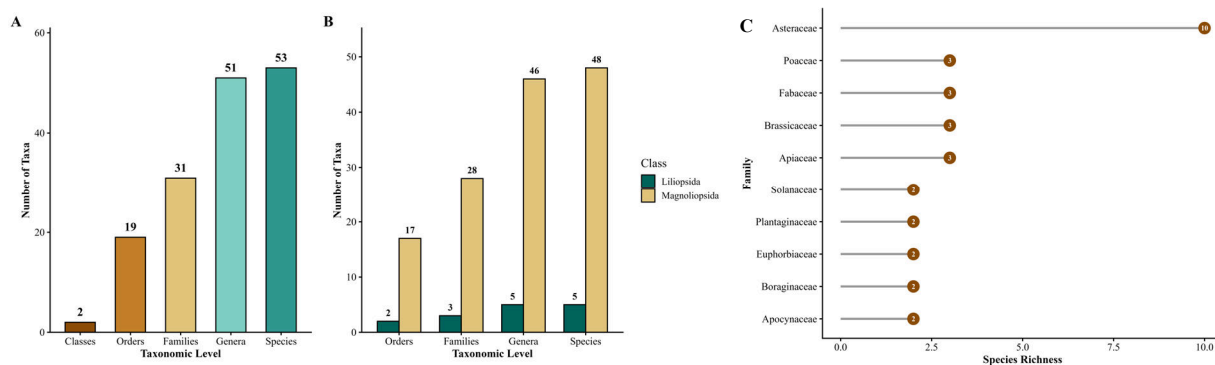


Figure 2. Taxonomic composition of the recorded flora: (A) number of taxa at each of five hierarchical ranks; (B) breakdown of taxa between Liliopsida and Magnoliopsida; (C) cumulative abundance of the dominant botanical families (Poaceae is the most abundant family, Asteraceae the most diverse).

2C). In terms of abundance, Poaceae was the leading family (455 individuals, 21.4%), mainly because of *Phragmites communis* (346 individuals, 16.3%), the most abundant taxon, which occurred in only six of the 18 quadrats; Asteraceae accounted for 327 individuals (15.4%).

Life cycle. Perennial taxa accounted for 63.7% (Oued Madagh) to 79.3% (Bounoura) of the individuals at each site (Daya 65.1%, Oued Labyad 67.4%, Oued Ourighnou 71.2%, El Attef 76.6%), the remainder being ephemeral taxa (Fig. 3A; Supplementary Table S2). **Ethnobotanical use.** Taxa used for pastoral/livestock purposes represented 55.1% (Daya) to 81.5% (Bounoura) of the individuals (El Attef 68.9%, Oued Labyad 63.1%, Oued Madagh and Oued Ourighnou 57.7%), followed by medicinal taxa (including medicinal-toxic taxa), which ranged from 14.1% at Bounoura to 41.6% at Daya; food, ecological, mixed-use, and unused categories were minor (Fig. 3B). **Endemism.** Non-endemic taxa (including cultivated taxa) represented 75.7% (Oued Ourighnou) to 93.2% (Bounoura) of the individuals; North African endemics ranged from 6.2% (Bounoura) to 22.0% (Oued Ourighnou), and Algero-Moroccan endemics, which were more abundant at Daya (4.7%) and Oued Labyad (5.9%), reached at most 5.9% (Fig. 3C).

Biological and Chorological Spectra

The biological spectrum (Fig. 4A) was co-dominated by therophytes and chamaephytes (18 taxa each; 33.96%), followed by hemicryptophytes and phanerophytes (7 taxa each; 13.21%) and geophytes (3 taxa; 5.66%), which sum to 100% apart from rounding. The chorological spectrum (Fig. 4B) comprised 11 categories totalling 53 taxa (100%): Saharo-Arabian (SA; 25 taxa; 47.17%), SA-Med (9 taxa; 16.98%), Cosm and Med-SA (5 taxa each; 9.43%), Med and SA-Sind (2 taxa each; 3.77%), and five further categories (Trop, SA-Trop, SA-Cosm, SA-Med-IrT, and cultivated taxa) with one taxon each (1.89%). The SA, SA-Med, and Med-SA elements together accounted for 73.6% of the flora (39 of 53 taxa); including all categories with a Saharo-Arabian component, the share rises to 83.0% (44 of 53 taxa). This composition indicates a predominantly Saharo-Arabian floristic affinity, in line with the Saharo-Arabian region of the Holarctic Kingdom [64].

Alpha Diversity

Alpha diversity varied among sites (Table 1). El Attef had the highest mean richness (39.7 taxa per quadrat; 1SD: 2.1), whereas Oued Labyad had the lowest mean richness (16.7 taxa; 1SD: 6.0). Shannon entropy ranged from 2.08 to 3.51 among quadrats, with

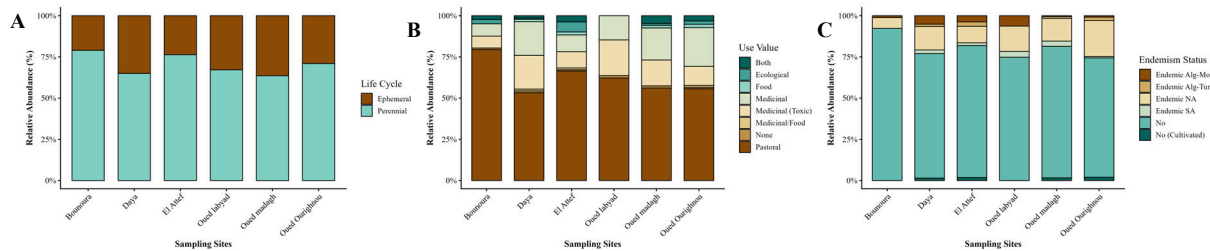


Figure 3. (A) Life-cycle spectrum (perennial vs. ephemeral taxa) expressed as relative abundance (% of individuals) per site. (B) Ethnobotanical use categories, expressed as relative abundance (% of individuals). (C) Endemism spectrum, showing the relative abundance of non-endemic (including cultivated), North African (NA), Saharo-Arabian (SA), Algero-Tunisian (Alg-Tun), and Algero-Moroccan (Alg-Mor) endemic taxa.

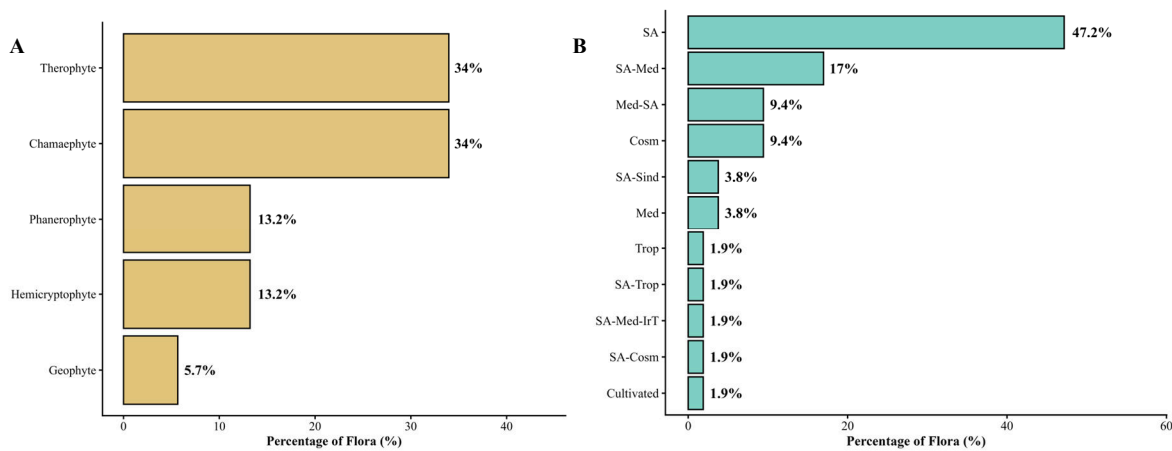


Figure 4. (A) Biological spectrum and (B) chorological spectrum of the study flora (n = 53 taxa). Chorological abbreviations: SA, Saharo-Arabian; Med, Mediterranean; Cosm, Cosmopolitan; Sind, Sindian; Trop, Tropical; IrT, Irano-Turanian. Compound codes denote composite ranges: SA-Med, Saharo-Arabian taxa extending into the Mediterranean region; Med-SA, Mediterranean taxa extending into the Saharo-Arabian region. The abbreviation of each taxon is given in Supplementary Table S1.

the highest site means at Oued Ourighnou (3.34) and Oued Madagh (3.33). Bounoura had markedly lower Simpson values ($1 - D = 0.72-0.83$, versus $0.88-0.97$ at the other sites) and Pielou evenness ($J' = 0.67-0.78$, versus $0.82-0.97$), El Attef being intermediate for evenness ($J' = 0.82-0.87$) (Table 1; Figs 5-6). In every quadrat $q = 0 \geq q = 1 \geq q = 2$, as expected for Hill numbers. El Attef showed the highest richness ($q = 0$: 38-42 taxa) but low diversity of dominant taxa ($q = 2$: 8.5-13.0 effective taxa), indicating high richness with strong dominance asymmetry. Oued Ourighnou, Oued Madagh, and Daya had high $q = 2$ values (16.8-29.4). Bounoura showed the steepest decline across orders, from $q = 0$ (22-33 taxa) through $q = 1$ (8.0-15.1 effective

taxa) to $q = 2$ (3.6-6.0 effective taxa), indicating numerical dominance by a few taxa. Kruskal-Wallis tests detected significant among-site differences in Hill numbers of order $q = 0$ ($p = 0.033$), $q = 1$ ($p = 0.023$), and $q = 2$ ($p = 0.012$) (Fig. 5), and in Shannon entropy ($p = 0.023$), Simpson diversity ($p = 0.012$), and Pielou evenness ($p = 0.031$) (Fig. 6). After Benjamini-Hochberg adjustment across the seven non-redundant indices (richness, Shannon, Simpson, Pielou, FRic, FEve, FDis), the tests for richness, Shannon, Simpson, and Pielou, as well as for FRic (see below), remained significant (adjusted $p = 0.047$); the tests for Hill numbers of order 1 and 2 are rank-equivalent to those

Table 1. Site means (1SD in parentheses; $n = 3$ quadrats per site) of the alpha-diversity and trait-based indices, and Kruskal-Wallis p-values among the six sites (unadjusted). Hill numbers $q = 1$ and $q = 2$ are expressed as effective numbers of taxa. FRic is the number of distinct trait combinations.

Index	Oued Ourighnou	Oued Labyad	Oued Madagh	Daya	Bounoura	El Attef	p (K-W)
Richness ($q = 0$)	34.0 (4.6)	16.7 (6.0)	33.7 (2.5)	29.3 (4.0)	29.0 (6.1)	39.7 (2.1)	0.033
Hill $q = 1$	28.5 (5.6)	13.9 (4.0)	28.1 (3.3)	24.9 (5.2)	11.9 (3.6)	22.4 (3.2)	0.023
Hill $q = 2$	24.8 (5.9)	11.8 (2.8)	24.4 (4.1)	21.8 (5.5)	4.8 (1.2)	10.6 (2.3)	0.012
Shannon H'	3.34 (0.21)	2.60 (0.30)	3.33 (0.11)	3.20 (0.20)	2.44 (0.32)	3.10 (0.14)	0.023
Simpson $1 - D$	0.96 (0.01)	0.91 (0.02)	0.96 (0.01)	0.95 (0.01)	0.78 (0.06)	0.90 (0.02)	0.012
Pielou J'	0.95 (0.03)	0.94 (0.02)	0.95 (0.02)	0.95 (0.03)	0.73 (0.05)	0.84 (0.03)	0.031
FRic	20.3 (3.1)	12.0 (2.6)	18.0 (2.0)	17.0 (1.0)	17.0 (2.6)	22.7 (0.6)	0.033
FEve	0.56 (0.05)	0.67 (0.13)	0.49 (0.07)	0.54 (0.09)	0.48 (0.02)	0.49 (0.02)	0.120
FDis	0.42 (0.01)	0.38 (0.02)	0.41 (0.05)	0.41 (0.03)	0.36 (0.01)	0.42 (0.01)	0.157

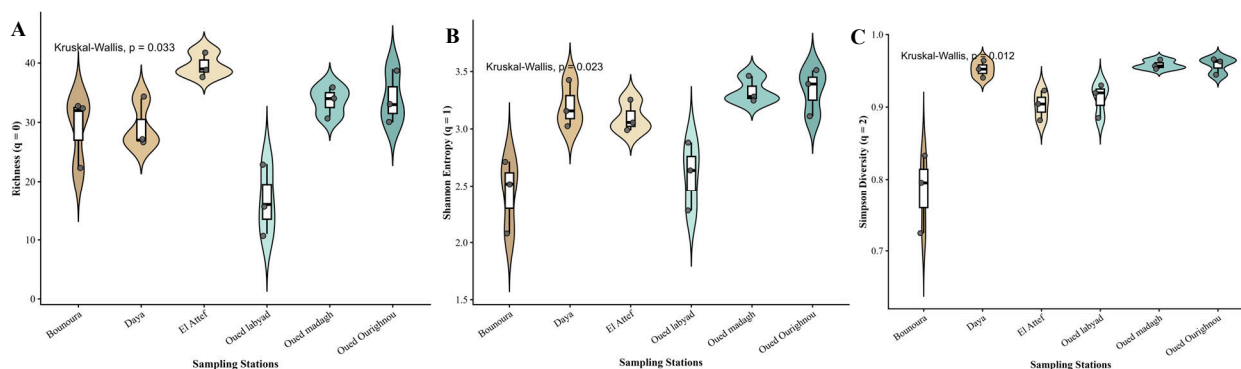


Figure 5. Variation in alpha diversity across the quadrats of the six sites, expressed as Hill numbers of order (A) $q = 0$ (taxon richness; Kruskal-Wallis $p = 0.033$), (B) $q = 1$ (exponential of Shannon entropy; $p = 0.023$), and (C) $q = 2$ (inverse Simpson concentration; $p = 0.012$).

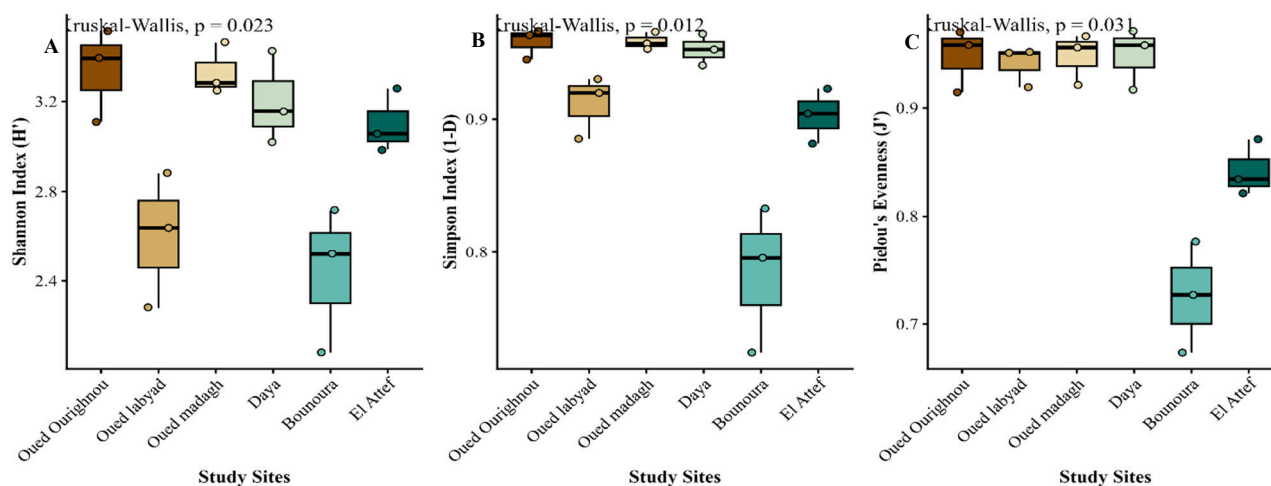


Figure 6. Within-site alpha diversity assessed with three complementary indices across the quadrats of the six sites: (A) Shannon H' (Kruskal-Wallis $p = 0.023$), (B) Simpson $1 - D$ ($p = 0.012$), and (C) Pielou J' ($p = 0.031$).

for Shannon and Simpson and were not adjusted separately. Dunn's post hoc tests with Bonferroni correction showed that richness was significantly lower at Oued Labyad than at El Attef (adjusted $p = 0.017$); for Hill numbers of order 1 and 2 and for the Shannon, Simpson, and Pielou indices no pairwise contrast was significant (smallest adjusted $p = 0.055$, Bounoura versus Oued Madagh and Oued Ourighnou for Simpson diversity). With $n = 3$ quadrats per site, pairwise comparisons have low power, so the remaining site-specific contrasts should be read as overall among-site heterogeneity whose pairwise structure remains to be resolved with larger samples.

Beta Diversity and Compositional Turnover

Total Sørensen beta diversity ($\beta_{SOR} = 0.795$) was dominated by spatial turnover ($\beta_{SIM} = 0.711$; 89.3%), with low nestedness ($\beta_{SNE} = 0.085$; 10.7%), indicating that inter-site differences reflect species replacement rather than progressive impoverishment of a shared core flora. Pairwise Bray-Curtis dissimilarities among the 18 quadrats ranged from 0.31 to 0.94, the highest value being between Oued Labyad R3 and Bounoura R3 (BC = 0.945); the mean dissimilarity between quadrats of different sites was 0.65. Within-site dissimilarities were

lowest at El Attef (0.31-0.35) and Bounoura (0.37-0.46) and highest at Oued Labyad (0.73-0.81) and Daya (0.53-0.73) (Figs. 7 and 8).

PERMANOVA and PERMDISP

Compositional differences among the six sites were highly significant (PERMANOVA on Bray-Curtis dissimilarities, 999 permutations: pseudo- $F(5, 12) = 2.136$, $R^2 = 0.471$, $p = 0.001$), so site identity explained 47.1% of the total variance. PERMDISP was also significant ($F(5, 12) = 6.663$, $p = 0.001$), indicating heterogeneous within-site dispersions: quadrats were compact at El Attef and Bounoura and dispersed at Oued Labyad and Daya (see within-site dissimilarities above). Because PERMANOVA is sensitive to unequal dispersions, a significant PERMDISP can by itself produce a significant PERMANOVA [4]. Grouping the quadrats a priori by landform type (wadi systems, $n = 12$; daya, $n = 3$; oasis margin, $n = 3$; Bray-Curtis, 9,999 permutations) also explained a significant but smaller share of the variance (pseudo- $F(2, 15) = 1.80$, $R^2 = 0.193$, $p = 0.027$), i.e., about 41% of the among-site variance was associated with landform type and the rest with differences among sites within landform types. The large effect size ($R^2 = 0.471$) and the clear separation of

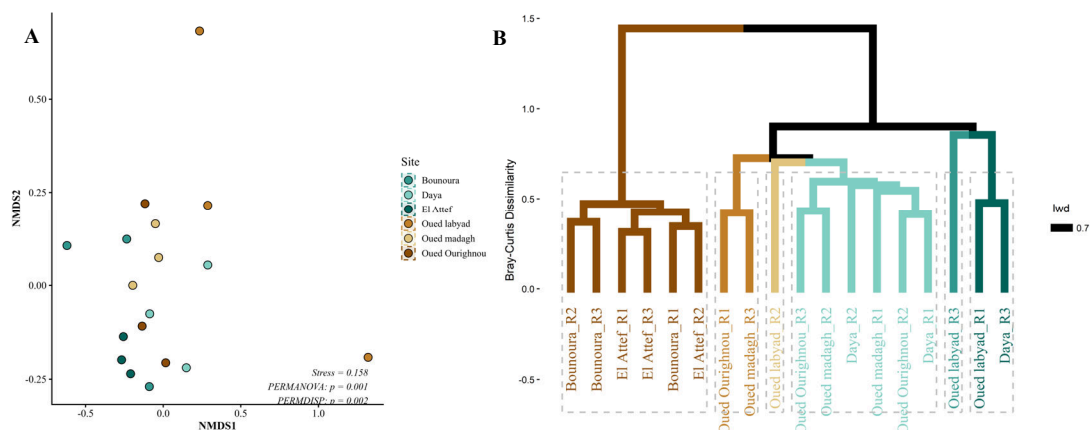


Figure 7. (A) Non-metric multidimensional scaling (NMDS) ordination of the quadrats based on Bray-Curtis dissimilarity, showing floristic differentiation among the six sites (stress = 0.158). (B) Hierarchical cluster analysis dendrogram of the quadrats based on Bray-Curtis dissimilarity.

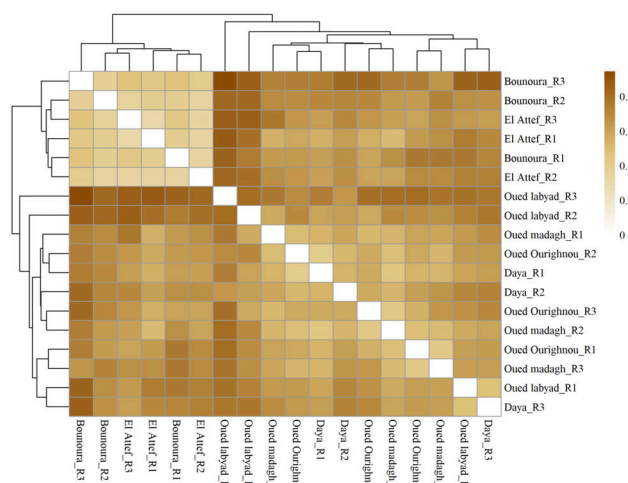


Figure 8. Heatmap of pairwise Bray-Curtis dissimilarity between all quadrats of the six sites, with hierarchical clustering applied to both rows and columns.

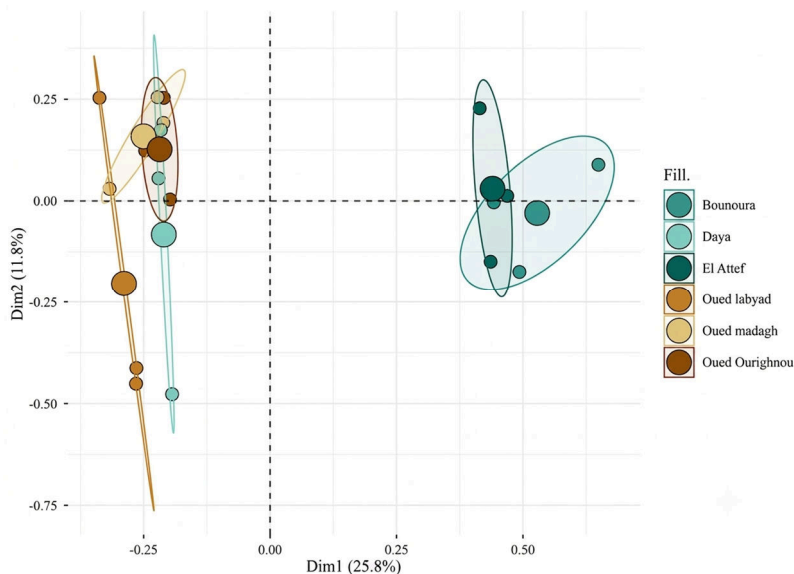


Figure 9. Principal Coordinates Analysis (PCoA) ordination of the quadrats of the six sites, with 95% confidence ellipses illustrating among-site floristic differentiation (Dim1 = 25.8%, Dim2 = 11.8%).

sites in the NMDS and PCoA ordinations (Figs 7A and 9) nevertheless indicate that the site differences involve shifts in community centroids in addition to differences in dispersion; the sites therefore differ in both mean composition and internal variability (Fig. 9).

Indicator species analysis

IndVal/multipatt identified six taxa with IndVal ≥ 0.87 (Fig. 10); five were significant at $p < 0.05$ and one was marginal. *Phragmites communis* (IndVal = 1.000, $p = 0.001$) and *Juncus rigidus* (IndVal = 0.913, $p = 0.014$) were associated with Bounoura and El Attef. *Ziziphus lotus* (IndVal = 0.931, $p = 0.040$) and *Tamarix gallica* (IndVal = 0.930, $p = 0.050$, marginal) were associated with the combination of Bounoura, El Attef, Oued Madagh, and Oued Ourighnou. *Cynodon dactylon* (IndVal = 0.886, $p = 0.027$) was associated with Oued Labyad, Oued Madagh, and Oued Ourighnou, and *Phoenix dactylifera* (IndVal = 0.870, $p = 0.038$) with El

Attef, Oued Madagh, and Oued Ourighnou. No indicator taxon was associated with Daya. IndVal describes taxon-site associations; it does not quantify functional traits or functional diversity.

Functional Diversity

FRic ranged from 10 (Oued Labyad R3) to 23 (El Attef, Oued Ourighnou) and closely tracked taxonomic richness ($r_s = 0.873$, $p < 0.001$) (Fig. 12). FRic differed among sites (Kruskal-Wallis $p = 0.033$), whereas FEve ($p = 0.120$) and FDis ($p = 0.157$) did not (Fig. 11); Dunn's tests with Bonferroni correction showed that FRic was lower at Oued Labyad than at El Attef (adjusted $p = 0.019$). FEve was low to moderate across quadrats (0.407-0.825) with no clear site-level pattern, and FDis ranged from 0.350 to 0.449. With $n = 3$ quadrats per site, the non-significant FEve and FDis tests are inconclusive rather than evidence of equivalence.

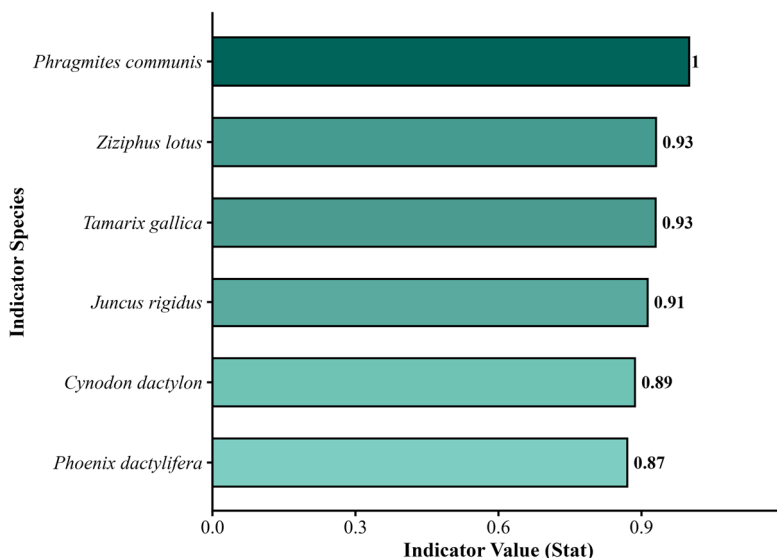


Figure 10. Indicator species analysis (IndVal): the six taxa with the highest indicator values (IndVal ≥ 0.87). Five are significant at $p < 0.05$; *Tamarix gallica* is marginal ($p = 0.050$).

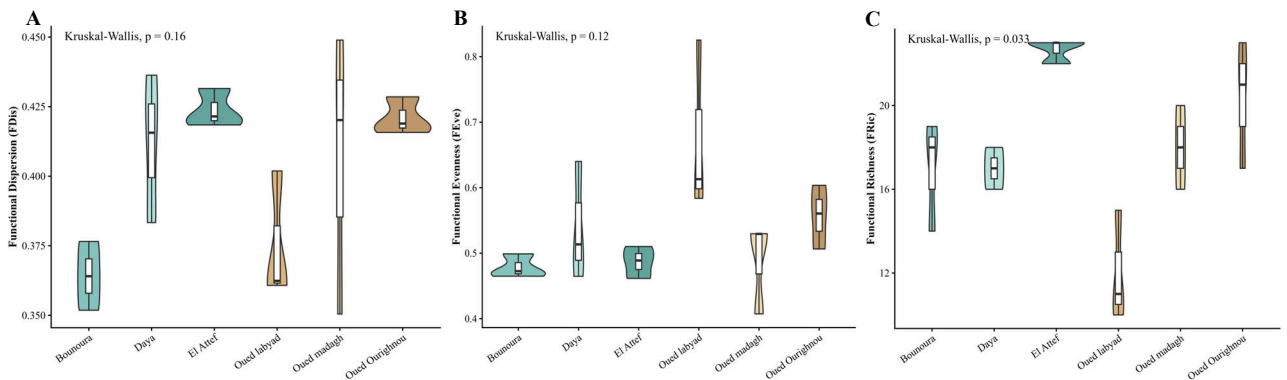


Figure 11. Among-site variation in trait-based indices: (A) functional dispersion (FDis; Kruskal-Wallis $p = 0.157$), (B) functional evenness (FEve; $p = 0.120$), and (C) functional richness (FRic; $p = 0.033$) across the six sites.

Spearman correlations (Fig. 12) showed a strong association between Shannon and Simpson indices ($r_s = 0.92$), whereas richness was moderately correlated with Shannon ($r_s = 0.64$; adjusted $p = 0.015$) and not significantly with Simpson ($r_s = 0.31$; adjusted $p = 0.31$). FRic showed the strongest trait-taxonomic coupling ($r_s = 0.87$ with richness, adjusted $p < 0.001$; $r_s = 0.56$ with Shannon, adjusted $p = 0.042$), indicating that taxon-rich quadrats occupy a larger trait space. FDis was positively correlated with richness ($r_s = 0.69$; adjusted $p = 0.006$) and Shannon ($r_s = 0.61$; adjusted $p = 0.022$) but not with Pielou evenness ($r_s = 0.28$; adjusted $p = 0.38$), so trait-taxonomic coupling operated mainly through richness rather than evenness. FEve was negatively correlated with richness ($r_s = -0.52$; unadjusted $p = 0.027$), but this association was not significant after adjustment (adjusted $p = 0.062$). With $n = 18$ quadrats, coefficients with $|r_s|$ below about 0.47 are not significant at $\alpha = 0.05$ before adjustment.

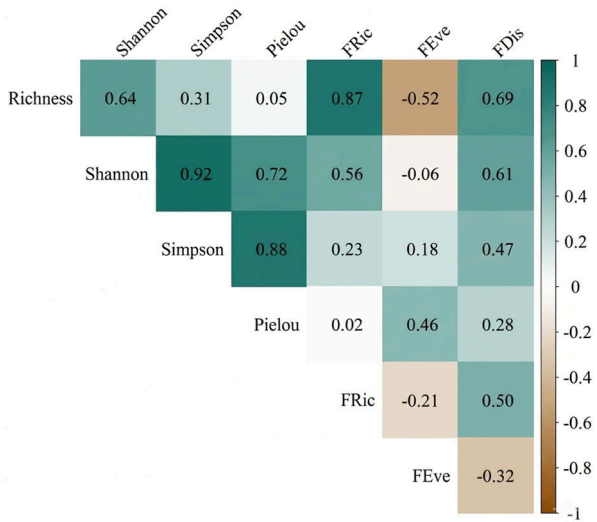


Figure 12. Pairwise Spearman rank correlation matrix between taxonomic diversity indices (Richness, Shannon, Simpson, Pielou) and trait-based indices (FRic, FEve, FDis) across the 18 quadrats.

DISCUSSION

The inventory of 53 taxa in 31 families lies within the range reported for other northern Saharan and North

African dryland systems, although direct comparisons are limited by differences in habitat type, plot size, and sampling effort. Merchela *et al.* [41] recorded only 15 taxa in 20 surveys of sandy wadis of the same Ghardaïa region, and Azizi *et al.* [6] recorded 29 taxa in 18 families, mainly Poaceae and Brassicaceae, on sandy soils and dunes of the northern Sahara; our larger total reflects the inclusion of contrasting landforms and of a hygic site. In the wadis of the Saint Katherine Protectorate (Egypt), where mean annual rainfall is also about 60 mm, El-Barougy *et al.* [23] recorded 67 native taxa in 84 plots of 20 m $\times$ 20 m, a comparable order of magnitude. In urban plantations of the Algerian Sahara, Souddi *et al.* [62] recorded 29 taxa in 12 families, with Poaceae the best-represented family and therophytes and wind-dispersed taxa dominant, which is consistent with the importance of Poaceae and short-lived taxa found here, although that survey used 1 m² plots under tree canopies and is not directly comparable. Around water towers in hyper-arid Adrar, Souddi and Bouallala [61] likewise recorded a Saharo-Arabian-dominated flora (43 taxa in 22 families) in which annual therophytes prevailed, whereas chamaephytes were as frequent as therophytes in our wadi, daya, and oasis-margin sites, a contrast that may reflect the buffering of water availability along drainage lines. The prominence of Asteraceae, Poaceae, Brassicaceae, and Fabaceae is a recurrent feature of North African arid floras [15, 48, 51] and is commonly attributed to traits such as efficient dispersal, short life cycles, and, in Fabaceae, nitrogen fixation, although this explanation was not tested here. In theoretical terms, the modest richness of individual sites alongside a larger pool across the six habitat types is consistent with the view that diversity in arid regions depends strongly on habitat heterogeneity and on the temporal pulses of water availability [46, 57].

The co-dominance of therophytes and chamaephytes (34.0% each) is consistent with two complementary strategies under chronic resource limitation: stress avoidance through rapid life-cycle completion (therophytes) and stress tolerance through persistent woody or suffrutescent forms (chamaephytes) [46]. Merchela *et al.* [41] found that hemicryptophytes (51.7% of individuals), followed by chamaephytes (33.1%), dominated sandy wadis of the same region; the

difference probably reflects the different metrics (taxa versus individuals) and the narrower habitat range of that study. The proportion of therophytes is lower than the values above 50% commonly reported for hyper-arid Saharan cores [48], which is compatible with the position of Ghardaïa at the northern margin of the Saharan bioclimatic stage ($Q_2 = 5.85$, annual precipitation 65.4 mm) and, as a hypothesis, with edaphic buffering in wadi habitats; this requires testing with direct soil moisture and salinity measurements. The Saharo-Arabian dominance (47.2%) reflects a Saharo-Arabian floristic affinity (Saharo-Arabian region of the Holarctic Kingdom [64]), and the substantial SA-Med and Med-SA components (26.4% together) underline the position of Ghardaïa as a contact zone between Saharan and Mediterranean floras [51]. Wadis are, however, azonal habitats that differ from the zonal hyper-arid reg and erg surfaces around them [48], so the flora recorded here should not be taken as representative of general zonal Saharan vegetation.

Hill numbers allow richness, Shannon entropy, and Simpson concentration to be compared within one framework [14, 28, 56]. The divergence between the $q = 0$ and $q = 2$ profiles at El Attef and Bounoura points to community structures dominated by few taxa. These are the only two sites where *Phragmites communis* occurred, a taxon that alone accounted for 16.3% of all individuals; numerical dominance by this hygrophyte is a plausible explanation for the low $q = 2$ and evenness values at both sites, although per-site abundances were not analysed for this purpose. At El Attef, high richness combined with low dominant-taxon diversity is also consistent with an open, well-connected wadi system that receives propagules from its surroundings, in line with mass-effect and species-sorting concepts [35, 57]. At Bounoura, the steepest decline from $q = 0$ to $q = 2$ (22-33, 8.0-15.1, and 3.6-6.0 effective taxa, respectively) may additionally be associated with the anthropogenic disturbance of this peri-urban margin; this interpretation is hypothetical because disturbance was not measured. The significant Kruskal-Wallis results ($p = 0.012-0.033$; adjusted $p = 0.047$) indicate overall heterogeneity among sites in richness, Hill numbers, and evenness, whereas the Dunn-Bonferroni tests resolved only the contrast between the poorest site (Oued Labyad) and the richest (El Attef); with three quadrats per site, the remaining site-level contrasts are descriptive and require confirmation with larger samples.

Turnover dominated over nestedness in beta diversity ($\beta_{SIM} = 0.711$; 89.3% of $\beta_{SOR} = 0.795$), a turnover-to-nestedness ratio of about 8.4. This is higher than the average ratio of 5.7 reported in a meta-analysis across organisms and ecosystems [59], and agrees with the turnover-dominated species beta diversity (82.5% of total) reported for desert plant communities in north-western China [30] and with turnover-driven patterns in global drylands, which are related to climate and soil attributes [66]. Because β_{SIM} is independent of richness differences among sites [7, 8], this result indicates

species replacement among sites rather than nested subsets of a shared flora, even though richness differed among sites. The PERMANOVA result ($R^2 = 0.471$, $p = 0.001$), together with the significant PERMDISP, shows that sites differ both in mean composition and in within-site variability [2, 4]; the clear separation of centroids in the ordinations supports a true location effect, but the unequal dispersions caution against interpreting R^2 as a pure centroid effect. This caution agrees with work showing that distance-based tests such as PERMANOVA confound location and dispersion effects when dispersions are heterogeneous [4, 68]; reporting both tests and inspecting the ordinations, as done here, is therefore the appropriate way to read the site differences, and a formal separation of location from dispersion would require more quadrats per site. High turnover among habitats is compatible with strong, habitat-specific environmental filtering, but dispersal limitation can also generate turnover in desert plant communities [30, 31]; because neither environmental nor spatial variables were measured, the present design cannot separate these processes [3, 34]. The highest Bray-Curtis dissimilarity (0.945, between Oued Labyad and Bounoura) is plausibly linked to substrate-mediated hydrological differences, which remains to be tested.

Wadis and dayas should be interpreted as geomorphologically and hydrologically distinct landforms rather than as nested habitats. Wadis are linear, channelised fluvial systems whose vegetation is shaped by episodic flood pulses, sediment transport, and shallow alluvial groundwater [65], whereas dayas are closed depressions of the hamada fed by local run-off, in which fine sediments accumulate and water is lost mainly through evaporation and infiltration [13, 15]; the hydrology of the studied daya was not monitored. These contrasting regimes may generate differences in substrate texture, water retention, and soil chemistry that could underlie the compositional distinctness of wadi and daya sites. In our data, landform type (wadi systems, daya, oasis margin) explained 19.3% of the Bray-Curtis variance ($p = 0.027$), about 41% of the among-site variance, whereas the remainder reflected differences among sites within a landform type, mainly among wadi systems; lithology itself was not measured, so its contribution cannot be separated from that of landform. None of the indicator taxa was associated with the studied daya, whereas historical accounts describe *Ziziphus lotus* and *Pistacia atlantica* in the dayas of the Laghouat-Ghardaïa region [13]; our single daya may therefore not be representative of all dayas. Local lithological variation (Cretaceous limestone bedrock versus alluvial, aeolian, and clayey infill) may further modulate infiltration and moisture availability, but this is a working hypothesis. Accordingly, the turnover reported here is best viewed as differentiation among sites of different landform type and origin within a shared regional species pool, i.e., as geomorphological landscape heterogeneity, rather than as micro-habitat partitioning within a single wadi network.

Functional richness, evenness, and dispersion were calculated from three categorical attributes (life span, ethnobotanical use, endemism) following the distance-based framework of Laliberté and Legendre [33] and the indices of Villéger *et al.* [67]. These attributes are only partial proxies for plant function: life span is functionally relevant, whereas ethnobotanical use and endemism describe human use and range size rather than resource-use strategies, so the indices describe the diversity of ecological and biogeographic attributes rather than of physiological functions [19, 49]. FRic tracked taxonomic richness ($r_s = 0.87$) and differed among sites ($p = 0.033$), indicating that taxon-rich quadrats contain more distinct trait combinations, whereas FEve (0.41-0.83) was low to moderate and FDis did not differ significantly among sites ($p = 0.157$). Compressed trait distributions along environmental gradients are a classic signature of environmental filtering [16], and the low-to-moderate FEve is consistent with such filtering, but this interpretation is provisional: trait convergence alone does not demonstrate filtering [32], the attributes are categorical and not measured on individuals, continuous traits such as specific leaf area, plant height, or seed mass [49] were not included, and the number of quadrats is small. Recent work in global drylands shows that trait diversity responds to aridity and grazing in ways that are not necessarily monotonic [11, 27], and in arid Egyptian wadis species contributions to beta diversity depend on traits such as plant height and specific leaf area [23]; continuous traits would therefore be a priority for future work; trait-based approaches are particularly informative about community responses to disturbance [44]. The negative association between FEve and richness ($r_s = -0.52$) did not remain significant after adjustment ($p = 0.062$) and should not be over-interpreted. If a decoupling between richness and evenness of trait space were confirmed with continuous traits, it would imply that management aimed only at maximising richness may not maintain functional redundancy, a component of resilience [24].

IndVal identified taxa that can serve as candidate indicators for conservation and monitoring. *Phragmites communis* (= *Phragmites australis*; IndVal = 1.000, $p = 0.001$) and *Juncus rigidus* (IndVal = 0.913, $p = 0.014$) are hygrophilous taxa generally associated with shallow groundwater, and their association with Bounoura and El Attef suggests that these sites function as hygric refugia within the landscape; this should be confirmed with groundwater measurements. *Ziziphus lotus* is a shrub that, like other dryland shrubs, probably creates islands of improved soil fertility and moisture [36] and may facilitate associated plants [12]; it warrants priority in restoration planning, although its facilitative role was not tested here. Community composition in these wadis is likely shaped by abiotic (edaphic and hydrological) and biotic filters acting together, but their relative importance cannot be assessed with the present data.

Taken together, the results suggest that landscape-level diversity in the Ghardaïa region is associated with

geomorphological heterogeneity among sandy wadi channels, a clay daya, and an oasis margin. Earlier studies in the region mainly described the floristic composition, life forms, and chorology of individual habitat types [6, 41]; the present study complements them by combining Hill-number alpha diversity, turnover-nestedness partitioning, multivariate tests, indicator taxa, and trait-based indices across a gradient of landform types, and its regional relevance lies in showing that turnover among contrasting landforms, rather than nestedness, accounts for most of the compositional variation, as reported for other desert systems [30, 66]. This perspective is relevant for the conservation of northern Saharan and Maghrebian drylands, particularly under declining water tables and land-use intensification. We recommend (1) a protected-area network that covers sandy wadis, clay dayas, and hygric refugia as a complementary mosaic, because high turnover means that no single site represents the whole flora [58]; (2) groundwater regulation near *Phragmites* and *Juncus* stands; (3) the consideration of *Ziziphus lotus* in restoration programmes; and (4) long-term monitoring as a baseline for climate-change projections. Limitations include the small number of quadrats per site ($n = 3$), a single spring season, six sites that are not replicates of a landform type (one daya and one oasis margin), the absence of environmental measurements, and categorical traits. Future work should add continuous traits, phylogenetic diversity, soil physicochemical predictors, and multi-year seasonal monitoring.

This study provides a multi-dimensional assessment of plant community structure across wadi, daya, and oasis-margin sites in the Ghardaïa region, combining taxonomic, trait-based, and beta-diversity approaches. Geomorphological heterogeneity among sandy wadis, a clay endorheic daya, and an oasis margin is associated with turnover-dominated beta diversity ($\beta\text{SIM} = 0.711$; 89.3% of $\beta\text{SOR} = 0.795$) and with significant among-site differences in richness and evenness, although, with three quadrats per site, only the contrast in richness between Oued Labyad and El Attef was significant in pairwise tests. The 53-taxon flora, dominated by Saharo-Arabian elements and equally by therophytes and chamaephytes, reflects both stress avoidance and stress tolerance. Low-to-moderate functional evenness is consistent with environmental filtering, a hypothesis to be tested with continuous traits. Conservation in this region should therefore consider the full mosaic of landforms, and indicator taxa such as *Phragmites communis* and *Ziziphus lotus* can serve as candidate proxies for monitoring ecosystem integrity at regional scale.

Acknowledgements. The authors would like to thank the Laboratory of Valorization and Conservation of Arid Ecosystem (Laboratoire de Valorisation et Conservation des Écosystèmes Arides (LVCAE)) for their support and for providing the necessary facilities to conduct this research.

Conflict of interest. There is no actual or potential conflict of interest in relation to this article.

Supplementary Table S1. Complete list of the 53 taxa recorded in the 18 quadrats (n = 2,127 individuals), ranked by absolute abundance. Taxa are listed under the names used in the field database; where the currently accepted name differs, it is given in the second column. Family, genus, Raunkiaer life form, chorological type, and life cycle are given for each taxon. Frequency is the number of quadrats (0-18) in which the taxon occurred.

No.	Taxon (as recorded)	Accepted name (if different)	Genus	Family	Life form	Chorotype	Life cycle	Abund.	Freq.
1	<i>Phragmites communis</i>	<i>Phragmites australis</i>	<i>Phragmites</i>	Poaceae	Ge	Cosm	Perennial	346	6
2	<i>Zilla macroptera</i>		<i>Zilla</i>	Brassicaceae	Ch	SA	Perennial	77	14
3	<i>Cymbopogon schoenanthus</i>		<i>Cymbopogon</i>	Poaceae	He	SA-Trop	Perennial	66	12
4	<i>Plantago notata</i>		<i>Plantago</i>	Plantaginaceae	Th	SA	Ephemeral	65	8
5	<i>Oudneya africana</i>		<i>Oudneya</i>	Brassicaceae	Ch	SA	Perennial	57	11
6	<i>Launea glomerata</i>	<i>Launea glomerata</i>	<i>Launea</i>	Asteraceae	Th	SA	Ephemeral	54	14
7	<i>Rhanterium adpressum</i>		<i>Rhanterium</i>	Asteraceae	Ch	SA	Perennial	54	13
8	<i>Pituranthos chloranthus</i>	<i>Deverra chlorantha</i>	<i>Deverra</i>	Apiaceae	Ch	SA	Perennial	50	15
9	<i>Pteranthus dichotomus</i>		<i>Pteranthus</i>	Caryophyllaceae	Th	SA	Ephemeral	50	14
10	<i>Moricandia arvensis</i>		<i>Moricandia</i>	Brassicaceae	Ch	Med-SA	Perennial	49	12
11	<i>Ruta tuberculata</i>	<i>Haplophyllum tuberculatum</i>	<i>Haplophyllum</i>	Rutaceae	Ch	SA	Perennial	48	14
12	<i>Plantago ciliata</i>		<i>Plantago</i>	Plantaginaceae	Th	SA	Ephemeral	47	14
13	<i>Cleome arabica</i>		<i>Cleome</i>	Cleomaceae	Ch	SA	Perennial	45	13
14	<i>Cynodon dactylon</i>		<i>Cynodon</i>	Poaceae	Ge	Cosm	Perennial	43	9
15	<i>Colocynthis vulgaris</i>	<i>Citrullus colocynthis</i>	<i>Citrullus</i>	Cucurbitaceae	He	SA-Sind	Perennial	40	12
16	<i>Convolvulus supinus</i>		<i>Convolvulus</i>	Convolvulaceae	Th	SA	Ephemeral	40	13
17	<i>Malva aegyptiaca</i>		<i>Malva</i>	Malvaceae	Th	SA-Med	Ephemeral	40	12
18	<i>Emex spinosa</i>		<i>Emex</i>	Polygonaceae	Th	Med	Ephemeral	39	12
19	<i>Launea mucronata</i>	<i>Launea mucronata</i>	<i>Launea</i>	Asteraceae	He	SA-Med	Perennial	38	11
20	<i>Peganum harmala</i>		<i>Peganum</i>	Nitrariaceae	Ch	SA-Med-IrT	Perennial	38	11
21	<i>Euphorbia guyoniana</i>		<i>Euphorbia</i>	Euphorbiaceae	Ch	SA	Perennial	37	11
22	<i>Fagonia glutinosa</i>		<i>Fagonia</i>	Zygophyllaceae	Ch	SA	Perennial	37	11
23	<i>Pergularia tomentosa</i>		<i>Pergularia</i>	Apocynaceae	Ch	SA-Sind	Perennial	37	13
24	<i>Ziziphus lotus</i>		<i>Ziziphus</i>	Rhamnaceae	Ph	Med-SA	Perennial	36	12
25	<i>Ammodaucus leucotrichus</i>		<i>Ammodaucus</i>	Apiaceae	Th	SA	Ephemeral	35	12
26	<i>Tamarix gallica</i>		<i>Tamarix</i>	Tamaricaceae	Ph	Med-SA	Perennial	35	12
27	<i>Echinops spinosus</i>		<i>Echinops</i>	Asteraceae	He	SA-Med	Perennial	31	12
28	<i>Genista saharae</i>		<i>Genista</i>	Fabaceae	Ch	SA	Perennial	31	10
29	<i>Ferula vesicertensis</i>		<i>Ferula</i>	Apiaceae	He	SA	Perennial	30	7
30	<i>Anvillea radiata</i>		<i>Anvillea</i>	Asteraceae	Ch	SA	Perennial	28	8
31	<i>Retama retam</i>		<i>Retama</i>	Fabaceae	Ph	SA-Med	Perennial	28	11
32	<i>Chamomilla pubescens</i>	<i>Matricaria pubescens</i>	<i>Matricaria</i>	Asteraceae	Th	SA	Ephemeral	27	8
33	<i>Phoenix dactylifera</i>		<i>Phoenix</i>	Arecaceae	Ph	Cult	Perennial	27	9
34	<i>Reseda villosa</i>		<i>Reseda</i>	Resedaceae	Ch	SA	Perennial	27	14
35	<i>Trigonella anguina</i>		<i>Trigonella</i>	Fabaceae	Th	SA-Med	Ephemeral	26	11
36	<i>Atractylis delicatula</i>		<i>Atractylis</i>	Asteraceae	Th	SA	Ephemeral	25	10
37	<i>Centaurea dimorpha</i>		<i>Centaurea</i>	Asteraceae	Th	SA-Med	Ephemeral	25	11
38	<i>Spitzelia coronopifolia</i>		<i>Spitzelia</i>	Asteraceae	Th	SA	Ephemeral	23	10
39	<i>Aizoon canariense</i>		<i>Aizoon</i>	Aizoaceae	Th	SA-Med	Ephemeral	23	10
40	<i>Nerium oleander</i>		<i>Nerium</i>	Apocynaceae	Ph	Med	Perennial	23	9
41	<i>Erodium glaucophyllum</i>		<i>Erodium</i>	Geraniaceae	He	SA	Perennial	23	8
42	<i>Juncus rigidus</i>		<i>Juncus</i>	Juncaceae	Ge	Med-SA	Perennial	23	5
43	<i>Echium humile</i>		<i>Echium</i>	Boraginaceae	Ch	SA	Perennial	22	10
44	<i>Calendula aegyptiaca</i>		<i>Calendula</i>	Asteraceae	Th	SA-Med	Ephemeral	22	8
45	<i>Samolus valerandi</i>		<i>Samolus</i>	Primulaceae	He	Cosm	Perennial	22	8
46	<i>Megastoma pusillum</i>		<i>Megastoma</i>	Boraginaceae	Th	SA	Ephemeral	21	10
47	<i>Thymelaea microphylla</i>		<i>Thymelaea</i>	Thymelaeaceae	Ch	SA	Perennial	21	5
48	<i>Datura stramonium</i>		<i>Datura</i>	Solanaceae	Th	Cosm	Ephemeral	19	8
49	<i>Helianthemum lippii</i>		<i>Helianthemum</i>	Cistaceae	Ch	SA-Med	Perennial	18	9
50	<i>Solanum nigrum</i>		<i>Solanum</i>	Solanaceae	Th	Cosm	Ephemeral	17	6
51	<i>Ricinus communis</i>		<i>Ricinus</i>	Euphorbiaceae	Ph	Trop	Perennial	16	7
52	<i>Suaeda fruticosa</i>		<i>Suaeda</i>	Amaranthaceae	Ch	SA-Cosm	Perennial	13	6
53	<i>Capparis spinosa</i>		<i>Capparis</i>	Capparaceae	Ph	Med-SA	Perennial	13	6

Abbreviations. Life form (Raunkiaer): Th, therophyte; Ch, chamaephyte; He, hemicyrptophyte; Ph, phanerophyte; Ge, geophyte. Chorological types: SA, Saharo-Arabian; Med, Mediterranean; Cosm, Cosmopolitan; Sind, Sindian; Trop, Tropical; IrT, Irano-Turanian; Cult, cultivated. Compound codes denote composite ranges: SA-Med, Saharo-Arabian taxa extending into the Mediterranean region; Med-SA, Mediterranean taxa extending into the Saharo-Arabian region. Life cycle: therophytes are ephemeral (annual), all other life forms perennial. Taxonomy follows Dobignard and Chatelain; chorology follows Ozenda and Pottier-Alapetite.

Supplementary Table S2. Relative abundance (% of individuals) of life-cycle, ethnobotanical-use, and endemism categories at each site, as plotted in Fig. 3 (values derived from the figure, precision about ± 1 percentage point; rows sum to 100% within each block). NA, North African; SA, Saharo-Arabian; Alg-Tun, Algero-Tunisian; Alg-Mor, Algero-Moroccan.

Category	Bounoura	Daya	El Attef	Oued Labyad	Oued Madagh	Oued Ourighnou
0	1	2	3	4	5	6
Life cycle						
Perennial	79.3	65.1	76.6	67.4	63.7	71.2
Ephemeral	20.7	34.9	23.4	32.6	36.3	28.8

Supplementary Table S2 (continued)

0	1	2	3	4	5	6
Ethnobotanical use						
Pastoral	81.5	55.1	68.9	63.1	57.7	57.7
Medicinal	7.2	20.8	10.1	14.4	19.6	24.0
Medicinal (Toxic)	6.9	20.8	9.7	21.6	15.7	11.5
Medicinal/Food	0.0	0.5	0.6	0.0	0.1	0.6
Food	0.0	1.0	1.3	0.0	1.1	1.5
Ecological	2.1	0.2	5.8	0.0	0.5	1.6
Both	1.9	1.0	3.4	0.0	4.4	2.8
None	0.4	0.6	0.2	0.9	0.8	0.4
Endemism status						
No	93.2	77.5	82.2	75.9	81.9	74.1
No (Cultivated)	0.0	1.0	1.4	0.0	1.2	1.6
Endemic NA	6.2	14.2	9.7	15.1	13.7	22.0
Endemic SA	0.0	1.7	1.2	3.1	2.7	0.4
Endemic Alg-Tun	0.0	0.9	2.2	0.0	0.5	1.6
Endemic Alg-Mor	0.6	4.7	3.4	5.9	0.0	0.3

REFERENCES

- [1] Anderson, M.J., (2001): A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1): 32-46.
- [2] Anderson, M.J., (2006): Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62(1): 245-253.
- [3] Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., (2011): Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14(1): 19-28.
- [4] Anderson, M.J., Walsh, D.C.I., (2013): PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecological Monographs*, 83(4): 557-574.
- [5] Anonymous, (2026): The M'Zab Valley conserved area: introduction. Office de Protection et de Promotion de la Vallée du M'Zab (OPVM), Ghardaïa, Algeria. <https://opvm.dz> (accessed October 7, 2026).
- [6] Azizi, M., Chenchouni, H., Belarouci, M.E.H., Bradai, L., Bouallala, M., (2021): Diversity of psammophyte communities on sand dunes and sandy soils of the northern Sahara desert. *Journal of King Saud University - Science*, 33(8): 101656. <https://doi.org/10.1016/j.jksus.2021.101656>
- [7] Baselga, A., (2010): Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1): 134-143.
- [8] Baselga, A., (2012): The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21(12): 1223-1232.
- [9] Baselga, A., Orme, C.D.L., (2012): betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5): 808-812.
- [10] Benjamini, Y., Hochberg, Y., (1995): Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B*, 57(1): 289-300.
- [11] Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J.J., Gross, N., Saiz, H., Maire, V., Lehmann, A., Rillig, M.C., Solé, R.V., Maestre, F.T., (2020): Global ecosystem thresholds driven by aridity. *Science*, 367(6479): 787-790.
- [12] Bruno, J.F., Stachowicz, J.J., Bertness, M.D., (2003): Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 18(3): 119-125.
- [13] Cannon, W.A., (1913): Botanical features of the Algerian Sahara. Carnegie Institution of Washington, Publication No. 178, Washington, USA.
- [14] Chao, A., Chiu, C.H., Jost, L., (2014): Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, 45: 297-324.
- [15] Chehma, A., (2006): Catalogue des plantes spontanées du Sahara septentrional algérien. Dar El-Houda, Ain M'lila, Algeria, 146 p.
- [16] Cornwell, W.K., Ackerly, D.D., (2009): Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79(1): 109-126.
- [17] De Cáceres, M., Legendre, P., (2009): Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90(12): 3566-3574.
- [18] De Cáceres, M., Legendre, P., Moretti, M., (2010): Improving indicator species analysis by combining groups of sites. *Oikos*, 119(10): 1674-1684.
- [19] Díaz, S., Cabido, M., (2001): Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16(11): 646-655.
- [20] Dobignard, A., Chatelain, C., (2010-2013): Index synonymique de la flore d'Afrique du Nord (Vol. 1-5). Conservatoire et Jardin Botaniques de la Ville de Genève, Genève, Switzerland.
- [21] Dufrêne, M., Legendre, P., (1997): Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67(3): 345-366.
- [22] Dunn, O.J., (1964): Multiple comparisons using rank sums. *Technometrics*, 6(3): 241-252.
- [23] El-Barougy, R.F., Bersier, L.-F., Gray, S.M., El-Keblawy, A., Galal, T., Ullah, F., Elgamal, I.A., Dakhil, M.A., (2025): Shaping beta diversity in arid landscape through native plant species contributions: synergy of climate, soil, and species traits. *Frontiers in Plant Science*, 16: 1521596. <https://doi.org/10.3389/fpls.2025.1521596>
- [24] Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J., (2003): Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9): 488-494.
- [25] Fabre, J., (1976): Introduction à la géologie du Sahara algérien et des régions voisines. Société Nationale d'Édition et de Diffusion (SNED), Alger, Algeria, 422 p.

- [26] Gower, J.C., (1971): A general coefficient of similarity and some of its properties. *Biometrics*, 27(4): 857-871.
- [27] Gross, N., Maestre, F.T., Liancourt, P., Berdugo, M., Martin, R., et al., (2024): Unforeseen plant phenotypic diversity in a dry and grazed world. *Nature*, 632: 808-814. <https://doi.org/10.1038/s41586-024-07731-3>
- [28] Hill, M.O., (1973): Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54(2): 427-432.
- [29] Hsieh, T.C., Ma, K.H., Chao, A., (2016): iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7(12): 1451-1456.
- [30] Jiang, L., Hu, D., Wang, H., Lv, G., (2022): Discriminating ecological processes affecting different dimensions of α - and β -diversity in desert plant communities. *Ecology and Evolution*, 12(3): e8710. <https://doi.org/10.1002/ece3.8710>
- [31] Jiang, L., Lv, G., Gong, Y., Li, Y., Wang, H., Wu, D., (2021): Characteristics and driving mechanisms of species beta diversity in desert plant communities. *PLoS ONE*, 16(1): e0245249. <https://doi.org/10.1371/journal.pone.0245249>
- [32] Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., (2015): Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29(5): 592-599.
- [33] Laliberté, E., Legendre, P., (2010): A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1): 299-305.
- [34] Legendre, P., De Cáceres, M., (2013): Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, 16(8): 951-963.
- [35] Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., et al., (2004): The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7(7): 601-613.
- [36] Maestre, F.T., Bowker, M.A., Puche, M.D., Hinojosa, M.B., Martínez, I., García-Palacios, P., Castillo, A.P., Soliveres, S., Luzuriaga, A.L., Sánchez, A.M., Carreira, J.A., Gallardo, A., Escudero, A., (2009): Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters*, 12(9): 930-941.
- [37] Maestre, F.T., Eldridge, D.J., Soliveres, S., Kéfi, S., Delgado-Baquerizo, M., Bowker, M.A., García-Palacios, P., Gaitán, J., Gallardo, A., Lázaro, R., Berdugo, M., (2016): Structure and functioning of dryland ecosystems in a changing world. *Annual Review of Ecology, Evolution, and Systematics*, 47: 215-237.
- [38] Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., et al., (2012): Plant species richness and ecosystem multifunctionality in global drylands. *Science*, 335(6065): 214-218.
- [39] Magurran, A.E., (2004): Measuring biological diversity. Blackwell Publishing, Oxford, UK, 265 p.
- [40] Mason, N.W.H., Moullot, D., Lee, W.G., Wilson, J.B., (2005): Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111(1): 112-118.
- [41] Merchela, W., Bouallala, M., Bradai, L., Souddi, M., (2023): Floristic diversity of plant communities in sandy wadis of the northern Algerian Sahara (Ghardaïa region). *Biodiversity: Research and Conservation*, 72: 1-10. <https://doi.org/10.14746/biorc.2023.72.1>
- [42] Mori, A.S., Isbell, F., Seidl, R., (2018): β -diversity, community assembly, and ecosystem functioning. *Trends in Ecology & Evolution*, 33(7): 549-564.
- [43] Mouchet, M.A., Villéger, S., Mason, N.W.H., Moullot, D., (2010): Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4): 867-876.
- [44] Moullot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., (2013): A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28(3): 167-177.
- [45] Mueller-Dombois, D., Ellenberg, H., (1974): Aims and methods of vegetation ecology. John Wiley & Sons, New York, USA, 583 p.
- [46] Noy-Meir, I., (1973): Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, 4: 25-51.
- [47] Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., et al., (2022): vegan: Community Ecology Package. R package version 2.6-4.
- [48] Ozenda, P., (2004): Flore et végétation du Sahara. 3rd Edition. CNRS Éditions, Paris, France, 660 p.
- [49] Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Cornelissen, J.H.C., (2013): New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3): 167-234.
- [50] Pottier-Alapetite, G., (1979): Flore de la Tunisie. Angiospermes-Dicotylédones. Ministère de l'Enseignement Supérieur, Tunis, Tunisia, 651 p.
- [51] Quézel, P., (1978): Analysis of the flora of Mediterranean and Saharan Africa. *Annals of the Missouri Botanical Garden*, 65(2): 479-534.
- [52] Quézel, P., Santa, S., (1962-1963): Nouvelle flore de l'Algérie et des régions désertiques méridionales (2 Vols.). CNRS Éditions, Paris, France, 1170 p.
- [53] R Core Team, (2026): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- [54] Raunkiaer, C., (1934): The life forms of plants and statistical plant geography. Clarendon Press, Oxford, UK, 632 p.
- [55] Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., et al., (2007): Global desertification: building a science for dryland development. *Science*, 316(5826): 847-851.
- [56] Roswell, M., Dushoff, J., Winfree, R., (2021): A conceptual guide to measuring species diversity. *Oikos*, 130(3): 321-338.
- [57] Shmida, A., Wilson, M.V., (1985): Biological determinants of species diversity. *Journal of Biogeography*, 12(1): 1-20.
- [58] Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., (2016): How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, 31(1): 67-80. <https://doi.org/10.1016/j.tree.2015.11.005>
- [59] Soininen, J., Heino, J., Wang, J., (2018): A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27(1): 96-109.
- [60] Souahi, H., Gacem, R., Chenchouni, H., (2022): Variation in plant diversity along a watershed in the semi-arid lands of North Africa. *Diversity*, 14(6): 450. <https://doi.org/10.3390/d14060450>
- [61] Souddi, M., Bouallala, M., (2024): Comparative study of plant diversity around water towers in hyper-arid areas (Adrar, Algeria). *Biodiversity: Research and Conservation*, 74: 31-42. <https://doi.org/10.14746/biorc.2024.74.5>

- [62] Souddi, M., Chenchouni, H., Bouallala, M., (2024): Thriving green havens in baking deserts: Plant diversity and species composition of urban plantations in the Sahara Desert. *Journal of Arid Land*, 16(9): 1270-1287. <https://doi.org/10.1007/s40333-024-0083-2>
- [63] Stewart, P., (1969): Quotient pluviométrique et dégradation biosphérique: quelques réflexions. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord*, 59: 23-36.
- [64] Takhtajan, A., (1986): *Floristic regions of the world*. University of California Press, Berkeley, USA, 522 p.
- [65] Tooth, S., (2000): Process, form and change in dryland rivers: a review of recent research. *Earth-Science Reviews*, 51(1-4): 67-107.
- [66] Ulrich, W., Soliveres, S., Maestre, F.T., Gotelli, N.J., Quero, J.L., Delgado-Baquerizo, M., *et al.*, (2014): Climate and soil attributes determine plant species turnover in global drylands. *Journal of Biogeography*, 41(12): 2307-2319.
- [67] Villéger, S., Mason, N.W.H., Mouillot, D., (2008): New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8): 2290-2301.
- [68] Warton, D.I., Wright, S.T., Wang, Y., (2012): Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, 3(1): 89-101.
- [69] Wickham, H., (2016): *ggplot2: Elegant graphics for data analysis*. Springer, New York, USA.
- [70] Zergoun, Y., (2020): *Inventaire et bioécologie de quelques Orthoptères dans la vallée du M'Zab (Ghardaïa)*. Thèse de doctorat ès sciences, Université Kasdi Merbah, Ouargla, Algérie.

Received: June 18, 2026

Accepted: October 19, 2026

Published Online: October 21, 2026

Analele Universității din Oradea, Fascicula Biologie

Print-ISSN: 1224-5119

e-ISSN: 1844-7589

CD-ISSN: 1842-6433

Oradea University Press

<https://www.bioresearch.ro/revistaen.html>

<https://doi.org/10.61215/auofb.2026.2.07>

