

# Patterns of plant diversity change across arid landscapes of the Aral Sea region (Central Asia)

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## Abstract

Arid and semi-arid ecosystems of Central Asia are undergoing rapid transformation due to climate change, large-scale anthropogenic pressure, and desertification processes, particularly following the desiccation of the Aral Sea. The vegetation cover of the Aral Sea region (Uzbekistan) represents a unique natural laboratory for studying long-term changes in biodiversity and community structure under increasing aridity and environmental stress. This study aims to assess temporal and spatial changes in plant biodiversity in the Aral Sea region by comparing historical and contemporary geobotanical data, with a focus on  $\alpha$ - and  $\beta$ -diversity patterns across major vegetation types and landscape units. We analysed historical vegetation records (1960s–1990s) and contemporary field data collected during expeditions in 2020–2023 across five natural–geographical regions (Ustyurt Plateau, Eastern Chink, dried Aral Sea bed, North-Western Kyzylkum, Amu Darya Delta) and five vegetation

complexes (halophytic, gypsophytic, psammophytic, tugai, and takyr communities). Alpha diversity was quantified using species richness, Shannon diversity index, and dominance index, while beta diversity was assessed using Whittaker's approach and SDR simplex decomposition (similarity, species replacement, and richness difference). Multivariate analyses (NMDS), kernel density estimation, and generalized linear models were applied using R software. Comparative analysis revealed pronounced shifts in vegetation structure and biodiversity over time. Most vegetation types exhibited a decline in species richness and Shannon diversity, accompanied by increased dominance of a limited number of stress-tolerant species. Halophytic and gypsophytic communities showed substantial losses of species richness in the dried Aral Sea bed and North-Western Kyzylkum, whereas psammophytic communities demonstrated partial recovery in some areas. Beta-diversity patterns indicated that species loss dominated in highly degraded regions, while species turnover prevailed in relatively stable landscapes such as the Amu Darya Delta and parts of the Ustyurt Plateau. The observed changes reflect ongoing desertification, climate-driven aridisation, and anthropogenic pressure across the Aral Sea region. Spatial heterogeneity in  $\alpha$ - and  $\beta$ -diversity responses highlights differing ecosystem resilience among vegetation types. These findings underscore the importance of long-term biodiversity monitoring and provide a scientific basis for conservation and restoration strategies in arid landscapes of Central Asia.

### Keywords

Arid ecosystems, desertification, alpha diversity, beta diversity, vegetation dynamics, Aral Sea region, Central Asia

## Introduction

Arid and semi-arid ecosystems occupy a significant proportion of the Earth's land surface and are among the most vulnerable natural systems under conditions of global climate change and increasing anthropogenic pressure. Rising aridity is accompanied by a decline in biological productivity, simplification of vegetation structure, and disruption of key ecosystem functions, including regulation of carbon and water balances (Hooper et al. 2005; Cardinale et al. 2012; Newbold et al. 2015). In drylands, threshold responses to aridification have been demonstrated, beyond which abrupt shifts occur in biodiversity and community stability (Maestre et al. 2015; Berdugo et al. 2020, 2022).

Climate-driven degradation of dry ecosystems is intensified by land-use transformation, grazing pressure, and soil disturbance, leading to vegetation homogenization and loss of local mosaic structure (Reynolds et al. 2007; Bestelmeyer et al. 2015). Under these conditions, biodiversity is considered not only an indicator of ecosystem state but also a key factor determining ecosystem stability and recovery capacity under climatic extremes (Yachi and Loreau 1999; Isbell et al. 2017).

The Aral Sea region represents one of the most striking examples of rapid and large-scale transformation of dry ecosystems in Eurasia. The desiccation of the Aral Sea resulted in the formation of vast new surfaces of the former seabed, intensified deflation and salt-dust transport, and restructuring of hydrological and salinity regimes in adjacent territories (Shomurodov et al. 2021; Anming et al. 2024). These

processes have led to the emergence of new extreme habitats and initiated primary succession under conditions of high salinity and moisture deficit.

Long-term studies of vegetation dynamics on the exposed Aral Sea bed indicate that colonization is not linear and is determined by the interaction of soil texture, salinity, groundwater depth, and landscape position. A 35-year analysis demonstrated that plant community formation follows different successional trajectories – from sparse halophytic formations to relatively stable psammophytic complexes accompanied by increasing species richness (Adilov et al. 2025). These findings are consistent with the high spatial heterogeneity of vegetation cover in the Aral Sea region and its sensitivity to microrelief and local moisture conditions (Korolyuk et al. 2024).

The Ustyurt Plateau is of particular importance for assessing the resilience of dry ecosystems in Central Asia, as it hosts gypsophytic, halophytic, and shrub communities formed under conditions of extreme aridity. Population-based studies show that vegetation status in this region is determined not only by climatic factors but also by local habitat conditions and anthropogenic impacts. Analyses of ontogenetic structure in rare species have revealed population fragmentation and a reduction in the proportion of generative individuals, indicating limited potential for natural regeneration (Rakhimova et al. 2020).

Assessment of the current state of individual species and formations on the Ustyurt Plateau (*Crambe edentula* and shrub halophytic communities) revealed signs of degradation and instability of coenopopulations associated with aridification and grazing pressure (Rakhimova et al. 2021; Rakhimova and Rakhimova 2022). Similar trends were identified in analyses of coenopopulations of *Xylosalsola chiwensis* and *Scorzonera bungei*, where changes in age structure reflect decreasing community stability even under apparently stable species composition (Rakhimova et al. 2023). For certain xerophytic species of the north-western Ustyurt Plateau, high sensitivity to ongoing aridification has also been demonstrated (Rakhimova et al. 2024).

Degradation processes in dry ecosystems also affect rangeland landscapes, including saxaul woodlands. Studies conducted in the north-western Kyzylkum indicate a reduction in projective cover, simplification of spatial structure, and changes in the role of dominant species under desertification, directly affecting biodiversity and forage value of pastures (Sharipova et al. 2025). These changes are consistent with global assessments of the impact of degradation and grazing pressure on dry-land vegetation (Milchunas and Lauenroth 1993).

For accurate diagnosis of such transformations, biodiversity metrics that account for both local community structure and differences among communities are required. Alpha diversity reflects vegetation condition at the plot level, whereas beta diversity analysis allows identification of whether species replacement processes dominate or whether overall floristic impoverishment occurs. Partitioning of  $\beta$ -diversity into turnover and richness difference components has proven effective in analysing degradation and succession processes in dry ecosystems (Baselga 2010; Legendre and De Cáceres 2013).

The application of multivariate analytical methods (NMDS) and regression models enables detection of hidden environmental gradients and quantitative assessment of the effects of aridification, salinization, and soil disturbance on community structure (Borcard et al. 2018; Oksanen et al. 2022). Such studies demonstrate that biodiversity changes in dry regions are often associated not only with productivity shifts but also with environmental constraints and disruption of soil–biotic interactions (Delgado-Baquerizo et al. 2016).

Despite numerous studies addressing ecosystem degradation and transformation in the Aral Sea region, a comprehensive spatial–temporal assessment of biodiversity dynamics across major vegetation types is still lacking. Most previous research has focused either on individual species or on specific plant communities and local territories, without integrating historical and contemporary geobotanical data at the regional scale. Moreover, assessment of vegetation change in arid ecosystems of Central Asia has most often been limited to local species richness ( $\alpha$ -diversity), whereas analysis of  $\beta$ -diversity and its structural components (species turnover and richness difference), which allow identification of mechanisms of community restructuring, has been applied considerably less frequently. As a result, a significant knowledge gap remains regarding whether vegetation transformation in the Aral Sea region is driven primarily by species loss, by species replacement along environmental gradients, or by a combination of these processes, and to what extent these mechanisms differ among halophytic, gypsophytic, psammophytic, tugai, and takyr ecosystems under ongoing aridification and anthropogenic pressure.

The present study represents the first integrated regional assessment of long-term vegetation dynamics in the Aral Sea region based on comparison of historical (1960s–1990s) and contemporary (2020–2023) geobotanical data. A comprehensive multi-level approach was applied, including  $\alpha$ -diversity analysis,  $\beta$ -diversity decomposition (including SDR analysis), NMDS ordination, spatial analysis using Kernel Density, and generalized linear models.

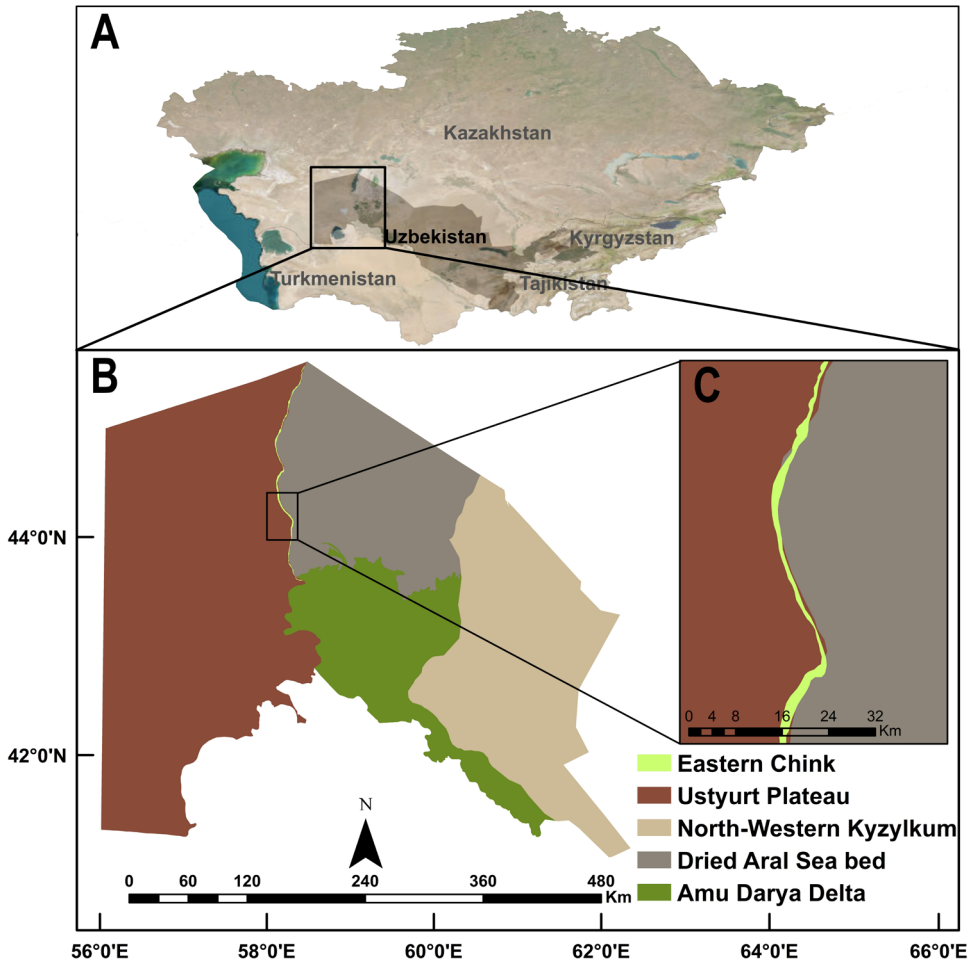
The results demonstrate that vegetation responses to aridification are heterogeneous and differ substantially among ecosystem types. In some communities, processes of species loss and homogenization prevail, whereas in others species replacement and structural reorganization dominate. Distinguishing the relative contributions of species loss and turnover provides deeper insight into mechanisms of resilience and restructuring in arid ecosystems and establishes a quantitative basis for biodiversity monitoring and vegetation restoration strategies under changing climatic conditions in Central Asia.

## Materials and methods

### Study area and regionalization

The territory of the Republic of Uzbekistan is located in the central part of Central Asia and is characterised by a sharply continental climate dominated by arid and

semi-arid natural conditions. The object of this study was the vegetation of the Aral Sea region within the territory of Uzbekistan. The study area encompasses five natural–geographical regions differing in geomorphology, hydrological conditions, and degree of anthropogenic transformation: the Ustyurt Plateau, the Eastern Chink, the dried Aral Sea bed, the North-Western Kyzylkum, and the Amu Darya Delta (Fig. 1). These regions represent key elements of the arid belt of Central Asia and are characterised by high spatial heterogeneity of habitat conditions.



**Figure 1.** Study area and distribution of the five analysed natural–geographical regions of the Aral Sea region, Uzbekistan, Central Asia. (A) Location of the study area within Central Asia. (B) Distribution of the five analysed regions: Ustyurt Plateau, Eastern Chink, dried Aral Sea bed, North-Western Kyzylkum, and Amu Darya Delta. (C) Enlarged view of the Eastern Chink region, provided to show its narrow linear structure and spatial position between the Ustyurt Plateau and the dried Aral Sea bed more clearly.

## Data sources

Two datasets were used in this study: historical geobotanical descriptions conducted during the 1960s–1990s and published in regional scientific works and reports, and contemporary field data collected by the authors during expeditions carried out between 2020 and 2023. To compare the historical and contemporary state of the vegetation cover, geobotanical relevés of model plant communities were grouped according to the main vegetation types.

In total, 60 relevés were analysed for the historical period, and an equivalent number of relevés was used for the contemporary period. The relevés were distributed among vegetation types as follows: gypsophytic vegetation – 12 relevés per period; takyr vegetation – 8 relevés per period; halophytic vegetation – 28 relevés per period; psammophytic vegetation – 4 relevés per period; and tugai vegetation – 8 relevés per period.

Contemporary geobotanical relevés were conducted on standard plots of 100–400 m<sup>2</sup>, depending on vegetation type. For each relevé, species composition, projective cover of individual species, total projective cover, life forms, and dominant ecological groups were recorded.

## Vegetation types

Five major vegetation types were included in the analysis: halophytic (salt-tolerant and solonchak communities); gypsophytic; psammophytic (sandy communities); tugai; and takyr communities (Fig. 2). This typological classification enabled comparison of biodiversity dynamics under varying degrees of aridity, salinity, and anthropogenic impact.

## $\alpha$ -diversity metrics

Assessment of  $\alpha$ -diversity in plant communities was carried out using a set of complementary indices reflecting both floristic richness and abundance distribution structure. Species richness ( $S$ ), defined as the total number of vascular plant species recorded within a single geobotanical plot, was used as the basic metric. Species richness is one of the most widely applied indicators of local biodiversity and is sensitive to degradation processes associated with aridification, salinisation, and anthropogenic pressure (Whittaker 1960; Magurran 2004).

To account for the evenness of species abundance distribution, the Shannon–Wiener diversity index (Shannon 1948) was calculated using the standard formula:

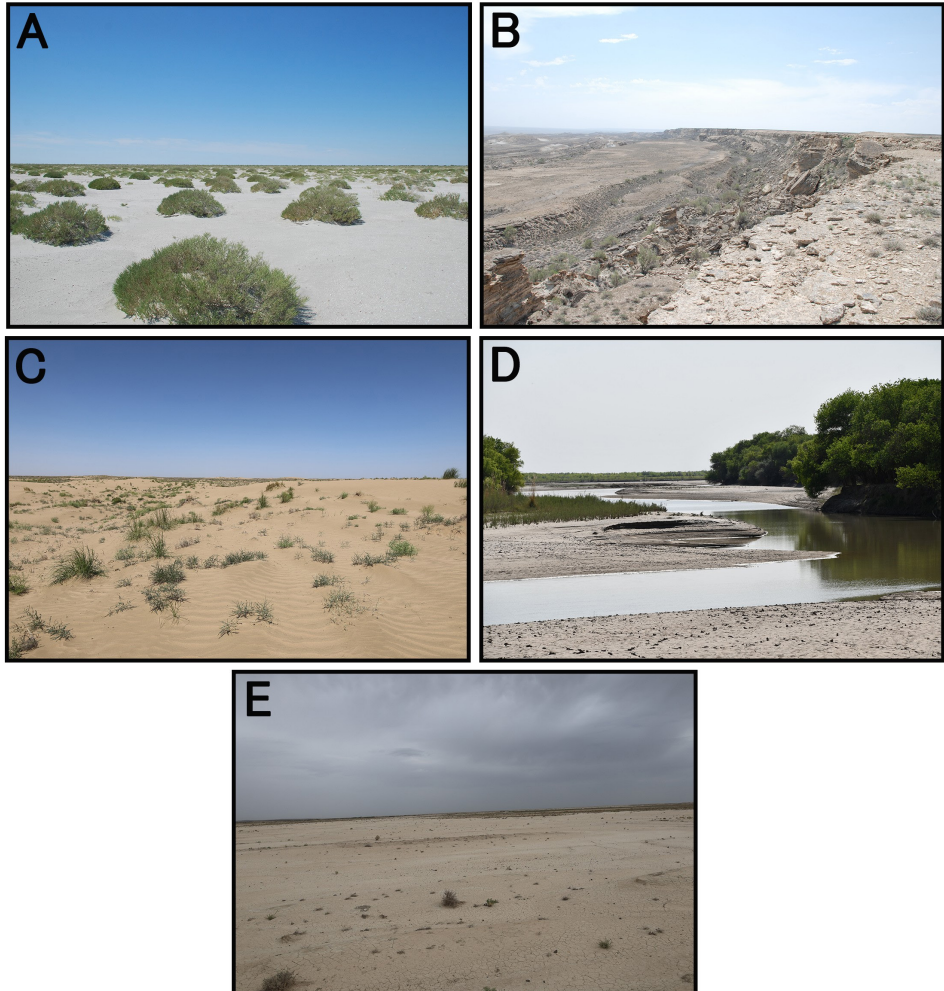
$$H = - \sum_{i=1}^S P_i \ln P_i$$

where:

$H$  – diversity index;

$S$  – total number of species;

$P_i$  – relative abundance of the  $i$ -th species, expressed as the proportion of its projective cover relative to the total projective cover of the community. The Shannon index simultaneously accounts for dominant and subdominant species and is widely used in analysing structural changes in plant communities of arid and semi-arid ecosystems (Magurran 2004; Maestre et al. 2015).



**Figure 2.** Main vegetation types analysed in the Aral Sea region (Uzbekistan). (A) Halo-phytic communities (*Halochnemum strobilaceum*) on the dried Aral Sea bed; (B) gypsophytic communities of the Eastern Chink; (C) psammophytic (sandy) communities of the North-Western Kyzylkum; (D) tugai communities along the Amu Darya River; (E) takyr communities of the Ustyurt Plateau.

Additionally, the dominance index was calculated to reflect the degree of unevenness in species abundance distribution within the community. Increased values of this index were interpreted as strengthening of the role of one or several dominant species and reduction in the structural complexity of the phytocoenosis, which is typical of degraded communities in dry regions (Eldridge et al. 2011; Berdugo et al. 2020).

Dominance was calculated as:  $\text{Dominance} = 1 - \text{Simpson index}$ . The index ranges from 0 (all taxa are equally represented) to 1 (one taxon completely dominates the community).

Based on quantitative species representation, the Shannon biodiversity index (H) reflects community structural complexity and may vary from 0 to 5 (Orlova 2013). The dominance index (D) is considered the inverse of Simpson's index ( $1/D$ ) (Lebedeva et al. 1999).

The combined analysis of species richness, Shannon index, and dominance allowed identification of both quantitative and structural aspects of  $\alpha$ -diversity changes across vegetation types and natural–geographical regions of the Aral Sea area.

## $\beta$ -diversity metrics

### SDR index calculation

Calculations were performed using the SDR Simplex computer program (Podani and Schmera 2011). Three indices were calculated as follows. Similarity (S) was calculated using the Jaccard similarity coefficient:

$$1) S_{Jac} = a/n ,$$

where:

a – number of species shared between plots;

n – total number of species.

Richness difference (D) was calculated as the ratio of the absolute difference between species numbers at each site (b, c) to the total number of species n:

$$2) D = 1 - (a + 2\min\{b, c\})/n ,$$

Finally, species replacement (R) was defined as:

$$3) R = 2\min\{b, c\}/n ,$$

where in formulas (2) and (3),

b – number of species present only at the first site;

c – number of species present only at the second site;

$\min\{b, c\}$  – the smaller value between  $b$  and  $c$ , representing the number of species at the less species-rich site that are replaced by new species at the more species-rich site.

$\beta$ -diversity indices were also calculated using *R* functions within the packages *ggtern*, *purrr*, and *tidyr*.

## Statistical analysis

To analyse spatial–temporal vegetation structure and identify biodiversity change patterns, a combination of multivariate and regression-based statistical methods was applied. Differences in species composition among communities were visualised using non-metric multidimensional scaling (NMDS), widely applied in ecological data analysis (Minchin 1987; Borcard et al. 2018). Ordination was performed based on Jaccard dissimilarity matrices, corresponding to the binary nature of the initial data.

The quality of ordination solutions was assessed using stress values; stress < 0.2 was considered acceptable for ecological interpretation (Clarke 1993). NMDS diagrams were used to analyse differences among vegetation types, natural-geographical regions, and time periods, as well as to identify directions of successional changes.

To quantitatively assess factors influencing  $\alpha$ -diversity metrics and structural community characteristics, generalized linear models (GLM) were applied. GLMs are widely used in ecological research for analysing non-normally distributed data (Müller 2004). Response variables included species richness, Shannon index, and total projective cover, whereas explanatory variables included time period, region, and vegetation type.

All analyses were performed in the *R* environment using the *vegan* package for biodiversity analysis and ordination (Oksanen et al. 2022), as well as standard regression modelling tools. Interpretation of results considered ecological features of arid ecosystems and spatial heterogeneity of the dataset.

## Results and discussion

### Changes in $\alpha$ -diversity indices of vegetation in the Aral Sea region

Analysis of  $\alpha$ -diversity indices revealed clear spatial and temporal differences in the structure of plant communities in the Aral Sea region. Species richness, Shannon diversity, and dominance varied depending on vegetation type and natural–geographical region, reflecting the combined influence of aridification, substrate conditions, hydrological regime, and anthropogenic disturbance (Fig. 3A–E; Table 1).

Halophytic communities showed contrasting changes among regions. In the Amu Darya Delta and on the dried Aral Sea bed, Shannon diversity slightly in-

creased in the contemporary period, while dominance decreased. For example, on the dried Aral Sea bed, the Shannon index increased from 1.57 to 1.73, and dominance decreased from 0.23 to 0.20. This indicates a moderate increase in evenness, probably related to the redistribution of species abundance within contemporary halophytic communities. However, the relatively low diversity values and narrow floristic composition of these communities indicate that halophytic vegetation remains strongly constrained by salinity and moisture deficit.

Gypsophytic communities were characterised by comparatively high Shannon diversity and low dominance in both periods. In the Eastern Chink, Shannon values remained almost unchanged between the historical and contemporary datasets, whereas dominance stayed at a low level. This suggests that gypsophytic vegetation retains a relatively stable community structure under extreme edaphic conditions. At the same time, some gypsophytic sites showed a moderate decline in diversity, indicating local effects of environmental filtering and disturbance.

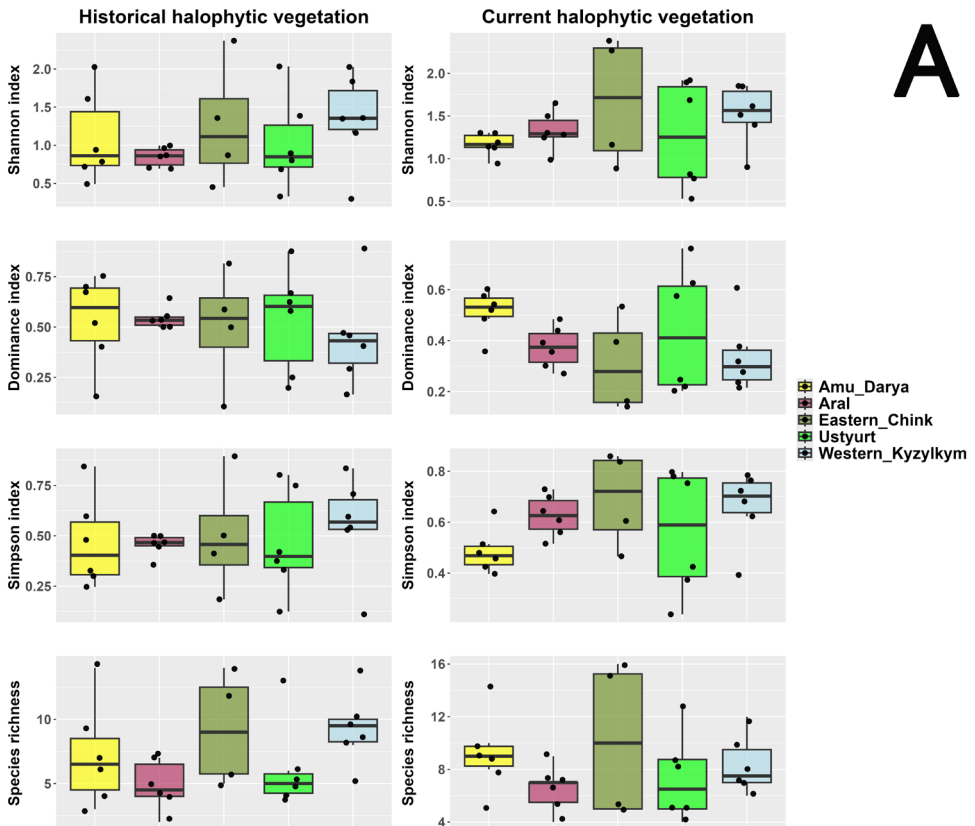


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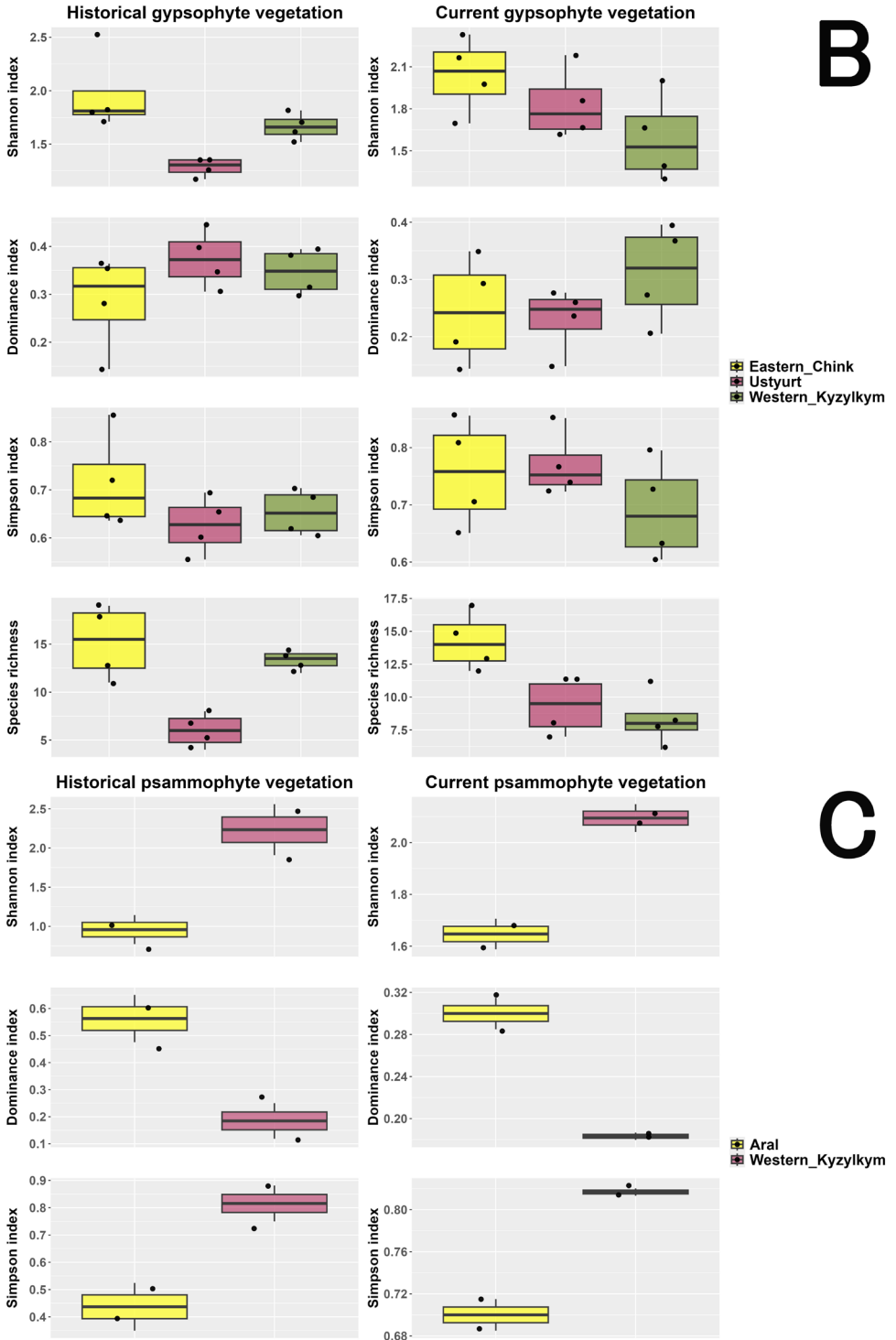


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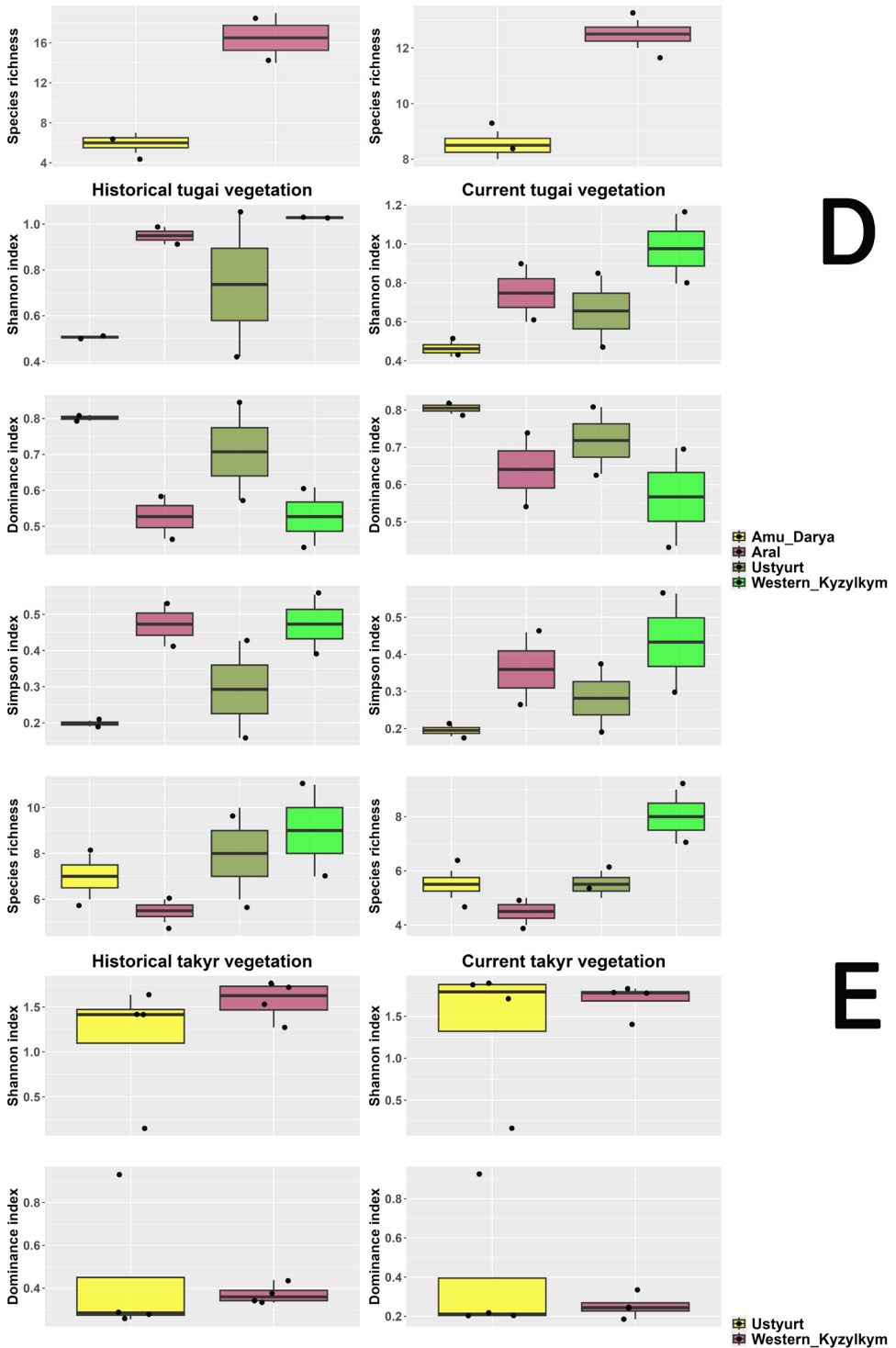
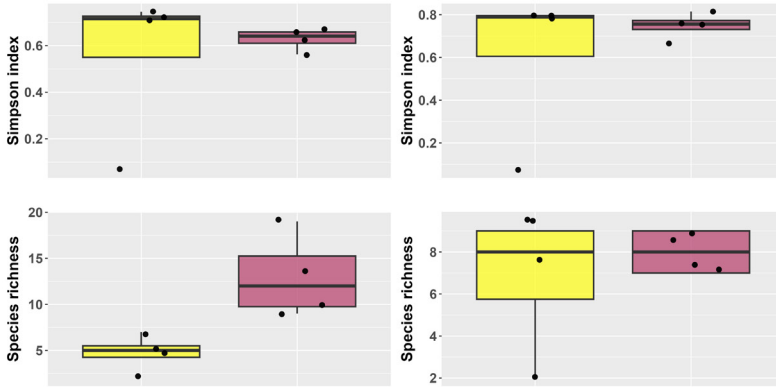


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**Figure 3.** Temporal shifts in  $\alpha$ -diversity indices across major vegetation types of the Aral Sea region, comparing historical and contemporary states: (A) Halophytic communities; (B) gypsophytic communities; (C) psammophytic communities; (D) tugai communities; (E) takyr communities. For each vegetation type,  $\alpha$ -diversity is shown by species richness, Shannon index, Simpson index, and dominance index. Boxplots show the distribution of values among geobotanical relevés within each region and period. The horizontal line inside each box indicates the median, the box represents the interquartile range, and the whiskers extend to the most extreme values within 1.5 times the interquartile range. Black points indicate individual relevés. Colours indicate natural–geographical regions.

Psammophytic communities displayed more variable dynamics. In the North-Western Kyzylkum, Shannon diversity decreased from 2.66 to 2.42, indicating a reduction in structural complexity of sandy vegetation. In contrast, psammophytic communities on the dried Aral Sea bed showed an increase in diversity and a decline in dominance, suggesting ongoing successional development on newly formed sandy substrates. These opposite trends indicate that sandy communities respond differently depending on substrate stability, colonisation stage, and local disturbance.

Tugai communities showed clearer signs of degradation. In the Ustyurt Plateau, Shannon diversity decreased from 1.94 to 1.62, while dominance increased from 0.17 to 0.22. Similar tendencies in other tugai sites indicate simplification of community structure and strengthening of dominant species. These changes are consistent with hydrological disturbance, reduction of suitable floodplain habitats, and increasing anthropogenic pressure.

Takyr communities showed the most heterogeneous  $\alpha$ -diversity pattern. Mean diversity values varied widely, and some communities were characterised by very low Shannon diversity and high dominance. In the most stressed takyr sites, Shannon values declined to approximately 0.50–0.60, while dominance reached up to 0.68. This indicates strong structural simplification and the prevalence of a small number of stress-tolerant species under conditions of soil desiccation, salinity, and surface disturbance.

**Table 1.** Temporal changes in  $\alpha$ -diversity metrics (Shannon index  $H'$  and dominance  $D$ ) across vegetation types and natural-geographical regions of the Aral Sea region

Vegetation type	Region	$H'$ (H, M $\pm$ SD)	$H'$ (C, M $\pm$ SD)	$D$ (H, M $\pm$ SD)	$D$ (C, M $\pm$ SD)	$H'$ (min–max)	$D$ (min–max)
Halophytic	Amu Darya Delta	1.87 $\pm$ 0.52	2.02 $\pm$ 0.28	0.18 $\pm$ 0.08	0.15 $\pm$ 0.03	1.27–2.67	0.08–0.31
Halophytic	Dried Aral Sea bed	1.57 $\pm$ 0.34	1.73 $\pm$ 0.26	0.23 $\pm$ 0.08	0.20 $\pm$ 0.05	1.04–2.08	0.14–0.38
Gypsophytic	Eastern Chink	2.58 $\pm$ 0.02	2.53 $\pm$ 0.13	0.09 $\pm$ 0.02	0.09 $\pm$ 0.01	1.28–2.83	0.06–0.31
Psammophytic	North-Western Kyzylkum	2.66 $\pm$ 0.18	2.42 $\pm$ 0.05	0.08 $\pm$ 0.02	0.09 $\pm$ 0.01	1.52–2.84	0.07–0.24
Tugai	Ustyurt Plateau	1.94 $\pm$ 0.27	1.62 $\pm$ 0.11	0.17 $\pm$ 0.05	0.22 $\pm$ 0.02	1.31–2.22	0.12–0.33
Takyr	Ustyurt Plateau	1.41 $\pm$ 0.47	1.65 $\pm$ 0.67	0.29 $\pm$ 0.17	0.27 $\pm$ 0.23	0.50–2.78	0.08–0.68

Note:  $H'$  – Shannon diversity index;  $D$  – dominance index; M – mean value; SD – standard deviation; H – historical state; C – contemporary state.

Overall,  $\alpha$ -diversity patterns indicate that vegetation responses in the Aral Sea region are strongly type-specific. Halophytic and takyr communities show the clearest signs of structural simplification, whereas gypsophytic communities remain comparatively stable. Psammophytic communities demonstrate both degradation and successional recovery, depending on region and substrate conditions. Tugai vegetation occupies an intermediate position but shows a clear tendency toward reduced diversity and increased dominance under altered hydrological conditions.

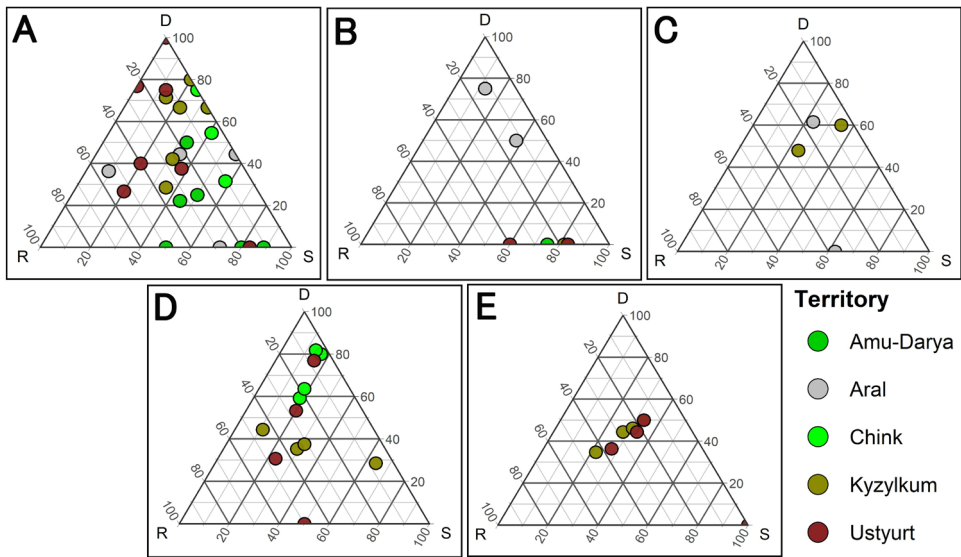
### Changes in $\beta$ -diversity indices of vegetation in the Aral Sea region

Analysis of  $\beta$ -diversity indices revealed spatial differentiation of vegetation cover and identified leading mechanisms of species composition change under aridification. Comparison of historical and contemporary data demonstrated that  $\beta$ -diversity is shaped by both species replacement and species richness loss processes, with their relative contributions varying substantially among vegetation types and natural-geographical regions (Fig. 4 A–E).

Halophytic communities of the dried Aral Sea bed are characterised by low similarity values among plots and predominance of the richness difference component. This indicates pronounced biotic impoverishment and spatial homogenisation of vegetation cover. Contemporary halophytic communities formed with participation of *Halocnemum strobilaceum*, *Suaeda physophora*, *Salsola nitraria*, and *Atriplex tatarica* demonstrate reduction of accompanying species and high fragmentation.

The dominance of species loss within  $\beta$ -diversity structure reflects degradation dynamics driven by extreme substrate salinity and hydrological instability.

Gypsophytic vegetation of the Ustyurt Plateau is characterised by relatively low  $\beta$ -diversity values, indicating high floristic homogeneity within the region. The species composition of gypsophytic communities dominated by *Anabasis salsa*, *Zygo-phyllyum xanthoxylon*, and *Salsola orientalis* remains relatively stable over time. The low proportion of both species replacement and richness loss reflects resilience of gypsophytic communities to contemporary climatic changes and limited anthropogenic influence.



**Figure 4.** SDR simplex diagram showing the proportional contribution of similarity (S), species replacement (R), and richness difference (D) to  $\beta$ -diversity across major vegetation types of the Aral Sea region in historical and contemporary periods. (A) Halophytic; (B) tugai; (C) psammophytic; (D) gypsophytic; (E) takyr communities.

In psammophytic communities,  $\beta$ -diversity is primarily formed by species replacement, reflecting high spatial heterogeneity of habitat conditions and diversity of successional stages. On stabilised sands of the dried Aral Sea bed and the North-Western Kyzylkum, a shift of dominants is observed from grasses such as *Aristida pennata* and *Stipagrostis pennata* to shrub forms including *Calligonum setosum*, *Calligonum elatum*, and *Eremosparton aphyllum*. The predominance of species replacement indicates preservation of adaptive potential and capacity for structural reorganisation without drastic floristic impoverishment.

Tugai communities of the Amu Darya Delta exhibit a mixed  $\beta$ -diversity pattern, where the contribution of species replacement is comparable to richness difference.

Changes in the proportion of woody and herbaceous components, represented by *Populus pruinosa*, *Elaeagnus angustifolia*, and *Tamarix ramosissima*, reflect local hydrological alterations and anthropogenic pressure. Takyr communities are characterised by low  $\beta$ -diversity values and high floristic homogeneity, associated with extreme habitat conditions and dominance of a limited number of xeromorphic species such as *Climacoptera lanata* and *Haloxylon aphyllum*.

Overall,  $\beta$ -diversity analysis shows that multiple mechanisms of vegetation restructuring coexist in the Aral Sea region. Halophytic communities are dominated by biotic impoverishment processes, whereas psammophytic systems are characterised mainly by species replacement. Gypsophytic communities demonstrate the highest stability, while tugai and takyr complexes occupy an intermediate position. These differences emphasise the key role of substrate type, hydrological regime, and degree of aridity in shaping vegetation spatial structure.

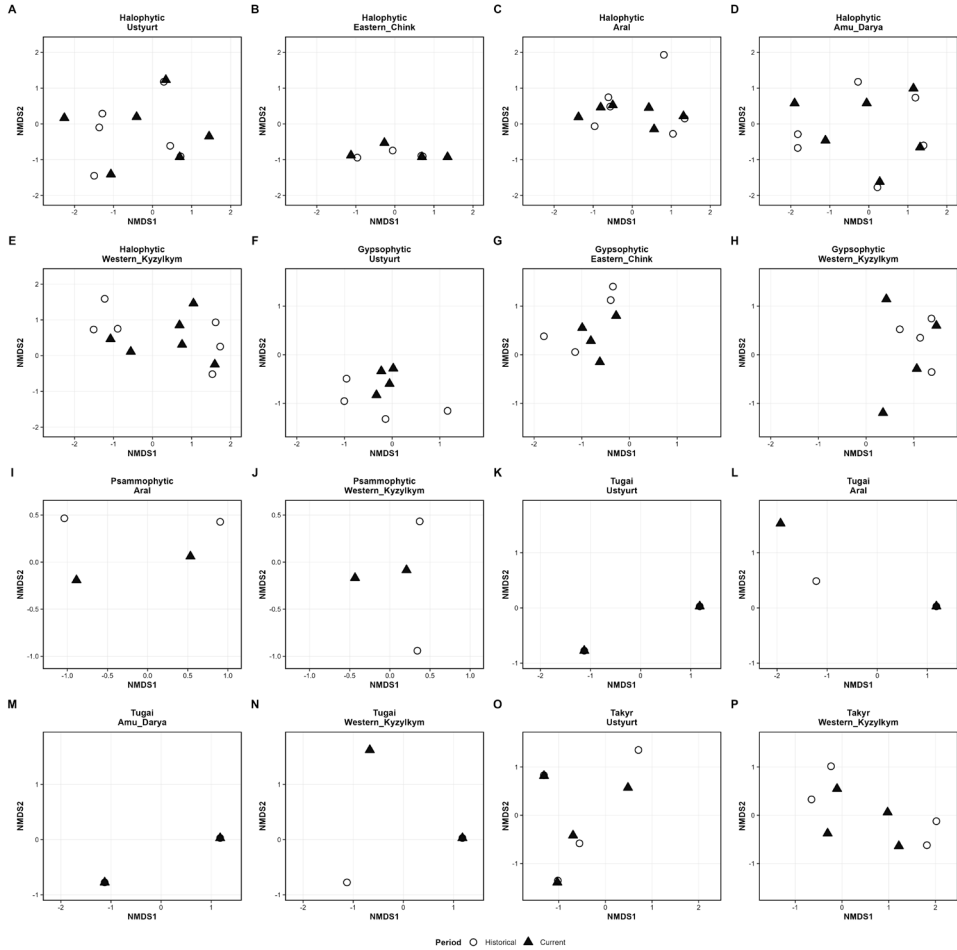
### Spatial differentiation of plant communities based on NMDS ordination

Non-metric multidimensional scaling (NMDS) revealed key spatial and ecological gradients determining contemporary vegetation structure and highlighted differences among vegetation types and time periods. Ordination space clearly reflects heterogeneous community responses to aridification, salinity changes, and hydrological transformation (Fig. 5).

The generalised analysis of floristic similarity based on the Sørensen index (Table 2) showed predominantly low to moderate similarity levels among regions across all vegetation types. In the historical period, minimum  $C_s$  values ( $<0.20$ ) were characteristic mainly of gypsophytic and halophytic communities, reflecting strong spatial differentiation under contrasting edaphic and hydrological regimes.

In the contemporary period, most vegetation types show increased mean Sørensen index values, particularly in gypsophytic and halophytic communities (up to  $C_s = 0.35\text{--}0.45$ ). This trend indicates partial convergence of floristic composition, likely associated with increased anthropogenic impact and habitat homogenisation. At the same time, tugai and psammophytic communities retain high variability in similarity values, reflecting differences in ecosystem resilience and specificity.

In general, NMDS ordination confirms that vegetation structure in the Aral Sea region is shaped by the combined influence of climatic aridification, substrate salinity, and hydrological factors. The most pronounced structural shifts are characteristic of halophytic and psammophytic communities, while gypsophytic complexes demonstrate the greatest stability. Tugai communities occupy a transitional position, combining signs of degradation and spatial reorganisation. These ordination patterns are consistent with  $\alpha$ - and  $\beta$ -diversity analyses and underline heterogeneous vegetation responses to contemporary environmental changes.



**Figure 5.** NMSD ordination of plant community composition across vegetation types and natural–geographical regions of the Aral Sea region. Panels show separate ordinations for each combination of vegetation type and territory: halophytic communities in the Ustyurt Plateau (A), Eastern Chink (B), dried Aral Sea bed (C), Amu Darya Delta (D), and North-Western Kyzylkum (E); gypsophytic communities in the Ustyurt Plateau (F), Eastern Chink (G), and North-Western Kyzylkum (H); psammophytic communities on the dried Aral Sea bed (I) and in the North-Western Kyzylkum (J); tugai communities in the Ustyurt Plateau (K), dried Aral Sea bed (L), Amu Darya Delta (M), and North-Western Kyzylkum (N); and takyr communities in the Ustyurt Plateau (O) and North-Western Kyzylkum (P). Open circles indicate historical relevés, and filled triangles indicate contemporary relevés. NMSD ordination was based on Bray–Curtis dissimilarity calculated from species composition data.

**Table 2.** Sørensen similarity index (Cs) among vegetation types in historical and contemporary periods

Vegetation type	Cs (H, min–max)	Cs (H, mean)	Cs (C, min–max)	Cs (C, mean)
Gypsophytic	0.119–0.218	0.172	0.196–0.452	0.307
Takyr	0.203	0.203	0.333	0.333
Halophytic	0.200–0.379	0.289	0.260–0.465	0.350
Tugai	0.242–0.413	0.323	0.190–0.461	0.311
Psammophytic	0.243	0.243	0.176	0.176

Note: Cs – Sørensen floristic similarity index; H – historical state; C – contemporary state.

### Spatial concentration of vegetation types (Kernel Density)

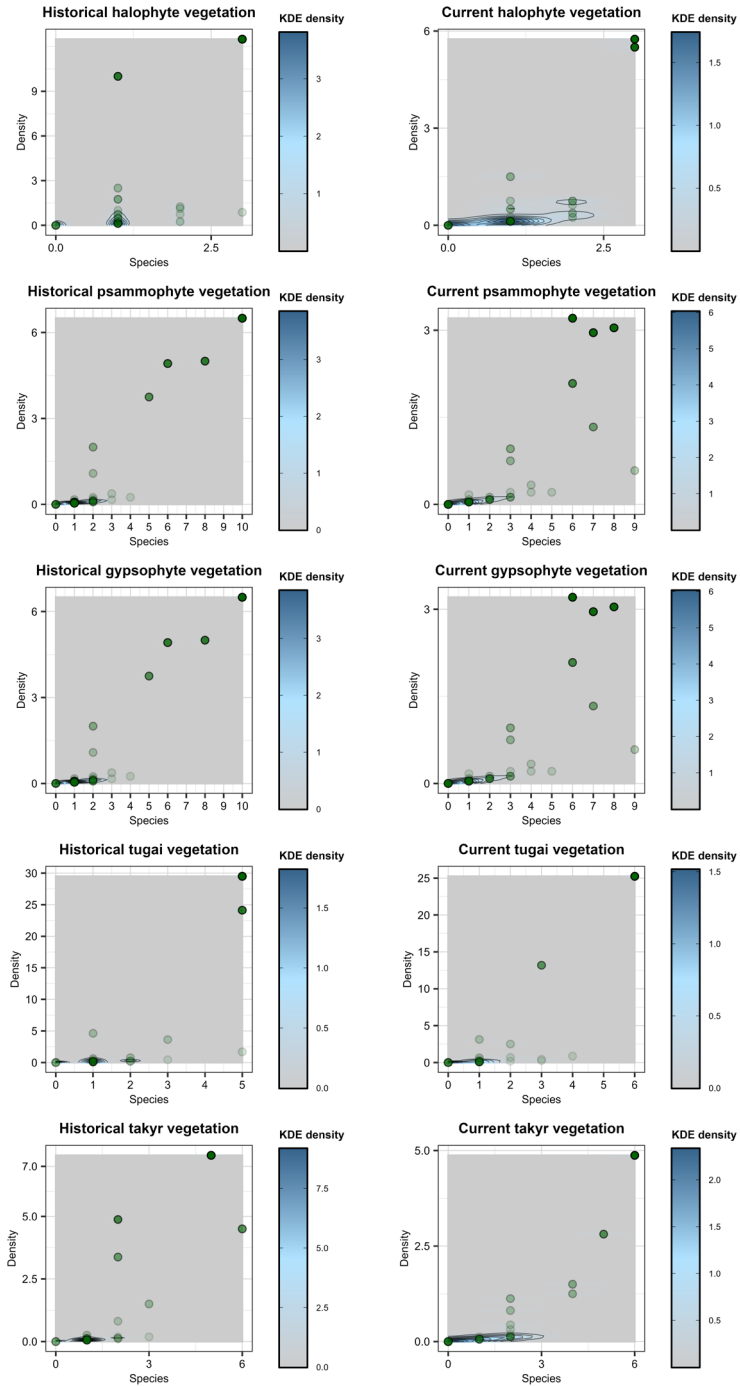
Spatial concentration analysis using the Kernel Density method revealed areas of aggregation and dispersion of major vegetation types and linked them with  $\alpha$ -diversity,  $\beta$ -diversity, and NMDS results. Unlike ordination methods, which reflect similarity gradients, Kernel Density emphasises spatial organisation and identifies concentration centres within the landscape (Fig. 6).

Kernel Density Analysis revealed pronounced differences in vegetation spatial organisation between historical and contemporary periods (Table 3). Gypsophytic vegetation shows a decline in total projective cover accompanied by increased species occurrence, indicating formation of a more mosaic community structure. Takyr ecosystems demonstrate the most negative dynamics, manifested in reduced density and species number. Halophytic vegetation is characterised by a sharp decrease in dominant density, reflecting a successional shift toward xerophytic forms. Tugai communities exhibit structural reorganisation associated with hydrological regime disruption, while psammophytic vegetation demonstrates a decline in density of specialised species under aridification and anthropogenic pressure. Collectively, these changes indicate directed transformation of ecosystems in the Aral Sea region.

Overall, Kernel Density analysis complements ordination and diversity analyses by linking abstract similarity gradients to concrete landscape patterns. Areas of high concentration of halophytic and takyr communities reflect limited suitable habitats and degradation tendencies, whereas dispersed psammophytic concentration indicates successional dynamics and potential resilience.

### Linear regression models linking vegetation diversity and environmental gradients

To quantitatively assess factors determining spatial–temporal vegetation structure changes, linear regression models were applied linking  $\alpha$ - and  $\beta$ -diversity metrics with key ecological and spatial variables.



**Figure 6.** Kernel density plots illustrating the relationship between species richness and vegetation density across major vegetation types of the Aral Sea region in historical and contemporary periods.

**Table 3.** Changes in vegetation density and occurrence in historical and contemporary periods (Kernel density analysis)

Vegetation type	Historical period	Contemporary period	Main trend	Ecological interpretation
Gypsophytic	Higher total projective cover; moderate occurrence	Decrease in projective cover; increase in occurrence	Diffuse distribution	Adaptation of gypsophytes to aridification and increased habitat mosaicism
Takyr	Relatively high density at certain levels	Overall decrease in density and species number	Degradation	Desiccation, soil degradation, anthropogenic impact
Halophytic	High density of dominant species	Nearly twofold decrease in density	Reduction of dominants	Succession and replacement of mesophytic species by xerophytic species
Tugai	Fluctuating density and high occurrence	Increase in density with decreased occurrence	Structural reorganisation	Hydrological regime disturbance, degradation of tugai ecosystems
Psammophytic	Increase in density with increasing occurrence	Decrease in density of several characteristic species	Reduction of specialised species	Aridification and anthropogenic pressure

Note: Density and species occurrence were assessed using Kernel density analysis.

Linear regression analysis revealed statistically significant relationships between vegetation density and species number for all vegetation types (Table 4). Coefficient of determination ( $R^2$ ) values indicate high explanatory power of the models, especially for gypsophytic and halophytic communities in the historical period.

For gypsophytic vegetation in the historical state, the strongest relationship between density and species richness was observed ( $R^2 = 0.88$ ), whereas in the contemporary period this relationship weakened, indicating increasing influence of additional ecological and anthropogenic factors. A similar trend was detected in halophytic and tugai vegetation, where decreasing density and habitat fragmentation altered regression relationships.

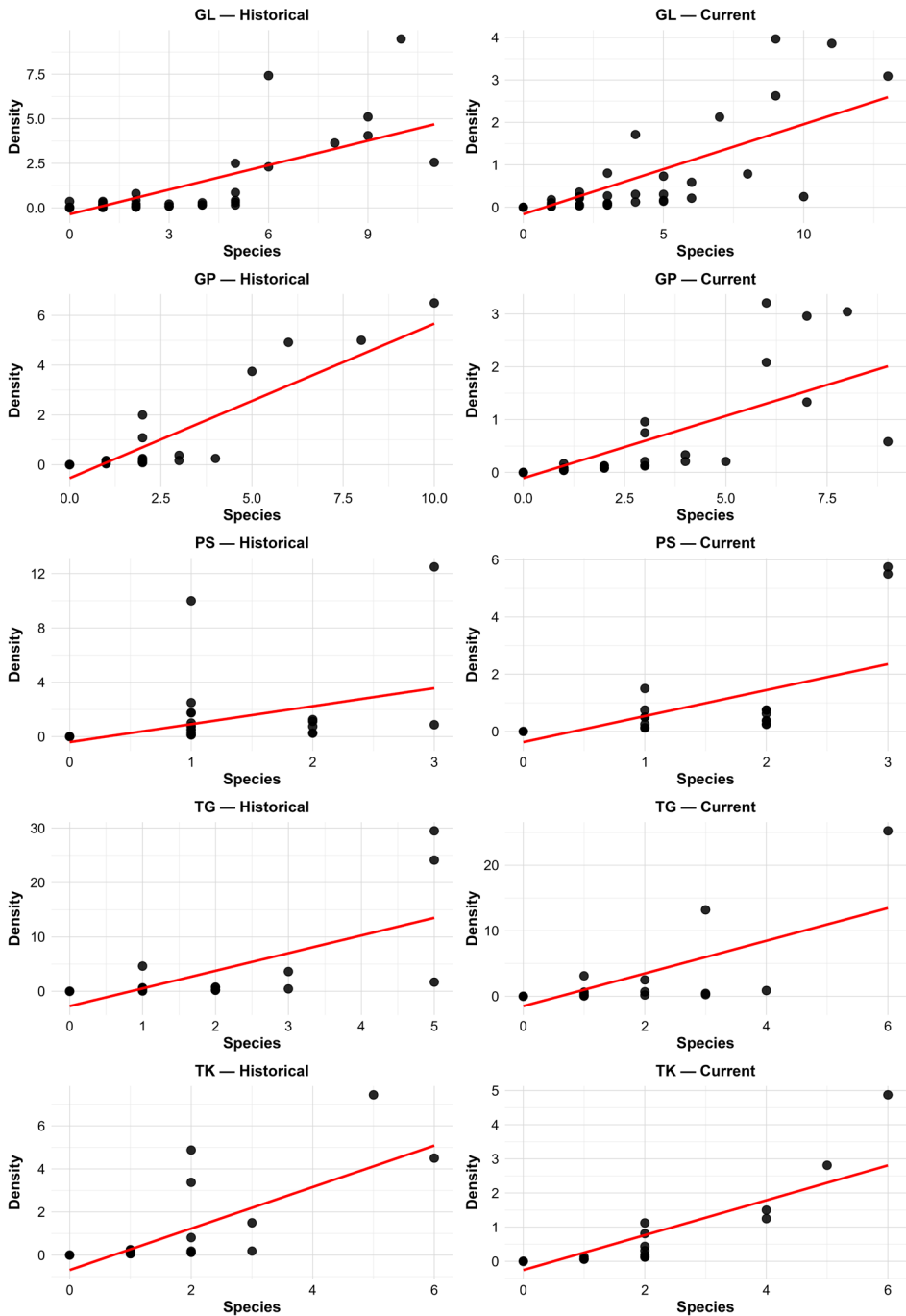
In takyr and psammophytic communities, regression models demonstrate restructuring of the density–species number relationship, reflecting substrate degradation and intensification of aridification. Overall, results confirm that in the historical past vegetation density played a more decisive role in shaping species diversity, whereas in the contemporary period community structure is increasingly determined by a complex of climatic and anthropogenic factors.

**Table 4.** Summary statistics of linear regression models for different vegetation types in historical and contemporary periods

Vegetation type	Period	R <sup>2</sup>	Adjusted R <sup>2</sup>	F-test	p-value	Interpretation of relationship
Gypsophytic	Historical	0.88	0.78	367.5	2.2e-16	Strong positive relationship between vegetation density and species richness
Gypsophytic	Contemporary	0.76	0.57	139.3	2.2e-16	Weakening of relationship; increasing influence of additional factors
Takyr	Historical	0.74	0.54	55.14	2.731e-09	Moderately strong relationship
Takyr	Contemporary	0.83	0.69	104.0	3.615e-13	Strengthening of statistical relationship under degrading conditions
Halophytic	Historical	0.75	0.56	184.4	2.2e-16	High sensitivity of species composition to vegetation density
Halophytic	Contemporary	0.78	0.61	220.8	2.2e-16	Significant relationship maintained despite density decline
Tugai	Historical	0.69	0.47	39.16	1.86e-07	Moderate relationship under stable hydrological conditions
Tugai	Contemporary	0.71	0.49	41.91	9.174e-08	Reduced stability of the relationship
Psammophytic	Historical	0.42	0.16	10.04	0.002719	Weak to moderate relationship
Psammophytic	Contemporary	0.65	0.41	34.42	4.586e-07	Increased role of density under overall decline in species richness

Note: R<sup>2</sup> – coefficient of determination; Adjusted R<sup>2</sup> – adjusted coefficient of determination; F-test – model significance statistic; p-value – level of statistical significance.

Synthesis of modelling results indicates that structural changes in vegetation of the Aral Sea region are shaped by combined climatic, edaphic, and spatial influences, with their relative importance varying among vegetation types. Halophytic and takyr communities are at highest risk of degradation, whereas psammophytic and partially tugai systems retain structural reorganisation potential through species replacement. Gypsophytic communities demonstrate the greatest resilience and weakest response to contemporary environmental changes (Fig. 7).



**Figure 7.** Linear regression models showing the relationship between species richness and vegetation density across major vegetation types of the Aral Sea region in historical and contemporary periods.

Thus, linear regression models confirm conclusions obtained from  $\alpha$ - and  $\beta$ -diversity analyses, NMDS ordination, and Kernel Density assessment, completing the comprehensive evaluation of spatial–temporal vegetation dynamics in the Aral Sea region.

## Conclusions

The comprehensive analysis of vegetation cover in the Aral Sea region revealed pronounced spatial–temporal heterogeneity of biodiversity changes driven by the combined effects of climatic aridification, edaphic conditions, and hydrological regime transformation. The application of an integrated approach, including  $\alpha$ - and  $\beta$ -diversity analysis, NMDS ordination, Kernel Density assessment, and linear regression modelling, made it possible to identify different trajectories of vegetation change depending on community type and natural–geographical context.

Analysis of  $\alpha$ -diversity indices showed that the most pronounced decline in local biodiversity is characteristic of halophytic and takyr communities of the dried Aral Sea bed, where increasing dominance of specialised species is accompanied by simplification of phytocoenotic structure. In contrast, gypsophytic communities of the Ustyurt Plateau demonstrate relative stability of  $\alpha$ -diversity metrics, reflecting high adaptation of their flora to extreme edaphic conditions. Psammophytic and tugai communities occupy an intermediate position, combining degradation processes with elements of successional recovery.

Results of  $\beta$ -diversity analysis and SDR decomposition demonstrated that mechanisms of vegetation restructuring differ substantially among vegetation types. In halophytic and takyr communities, processes of species richness loss and spatial homogenisation dominate, whereas in psammophytic and partly in tugai systems, species replacement along environmental gradients plays the leading role, indicating preservation of adaptive potential in these communities.

NMDS ordination confirmed clear spatial differentiation of plant communities and identified key ecological gradients determining their structure. The most pronounced ordination shifts were recorded for halophytic and psammophytic communities, whereas gypsophytic complexes are characterised by high floristic homogeneity and minimal temporal dynamics. Kernel Density analysis complemented these findings by identifying areas of vegetation concentration and dispersion and linking them to landscape features and degree of ecosystem degradation.

Linear regression models showed that vegetation diversity in the Aral Sea region is determined by the combined influence of climatic, edaphic, and spatial factors, with their relative importance varying substantially among vegetation types. Halophytic and takyr communities are at greatest risk of degradation, whereas psammophytic and partially tugai systems retain potential for structural reorganisation and recovery through species replacement. Gypsophytic communities demonstrate the highest resilience to contemporary environmental changes.

Overall, the results emphasise that vegetation responses to aridification in the Aral Sea region are not uniform and depend on the combination of local habitat conditions and biological characteristics of dominant species. The integrated approach applied in this study can serve as a methodological basis for vegetation monitoring and for the development of scientifically grounded management and restoration strategies for arid ecosystems of Central Asia.

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