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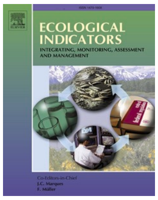

Original Articles

Vegetation colonization and biodiversity dynamics on the exposed Aral Sea bed: A 35 years investigation

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ABSTRACT

The Aral Sea, formerly a large saltwater lake in Central Asia, has almost disappeared due to unsustainable water management practices. This desiccation has resulted in a profound ecological catastrophe, characterized by the emergence of vast, barren landscapes. This study investigates the dynamics of vegetation colonization and biodiversity on the desiccated Aral Sea bed, focusing on the interplay of soil gradations, plant species composition, and the development of distinct ecosystem types. Over a 35-years investigation period, 30 dominant species were identified across five ecosystem types: ephemeral ecosystems, wasteland ecosystems, post-ecosystems, remnant ecosystems, and neo-ecosystems. Community analysis revealed generally low similarity between these ecosystem types, with significant floristic overlap observed only between ephemeral and neo-ecosystems (41.4 %) and between neo-ecosystems and post-ecosystems (54.1 %). An ecological scale was developed, categorizing 65 distinct ecotypes based on soil mechanical composition, salinity levels, and groundwater depths; this framework revealed clear patterns in species dominance and biodiversity distribution. Considerable variability in soil factors was evident across the study area. Gradients in mechanical composition and salinity significantly impacted vegetation cover and the activity of dominant species. Higher vegetation activity was generally associated with sandy soils (clay content less than 10 %) and lower salinity (<4.0 g/L). Groundwater levels exhibited varied effects on vegetation, with the highest vegetative cover typically observed where groundwater was at a depth of 1.0–1.5 m. Regression models and canonical correspondence analysis highlighted the strong influence of soil gradations on the differentiation of ecosystem types, indicating a dynamic interplay between prevailing soil conditions and the processes of species colonization. The study concludes that ecosystem development on the desiccated Aral Sea bed is shaped by complex interactions among various soil factors and underscores the critical importance of considering landscape-scale interference and heterogeneity in understanding vegetation succession patterns.

1. Introduction

Vegetation restoration in degraded landscapes is a key indicator of the final stage of ecological succession, culminating in the formation of zonal vegetation. Primary succession processes under extreme conditions-such as those in saline areas (Dimeyeva, 2007), on spoil heaps (Simanchuk et al., 2023), in degraded fallow lands (Bugubaeva et al., 2023), and on volcanic islands (Magnússon et al., 2014)-are of particular interest, especially where plant colonisation adheres to autogenic development principles (Poorter et al., 2024).

In this context, solonchak massifs constitute complex dynamic systems where successful halophyte colonisation and subsequent successional processes are governed by multiple factors. These include soil cracking (Jiang et al., 2023), microrelief (Davy et al., 2011), groundwater level (Sutton & Price, 2020), soil moisture (Yan & Guo, 2019), precipitation (Gessner et al., 2013; Duan et al., 2022a), and salinity

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(Jiang et al., 2023). These factors suggest that the direction and rate of succession are determined by both the isolated impacts of individual elements and their synergistic interactions within the self-organising vegetation systems of saline landscapes.

The Aral Sea, having undergone catastrophic desiccation since the 1960s, presents a unique natural laboratory for observing the formation of new ecosystems under large-scale anthropogenic transformation and intense salinisation. The desiccated seabed, now exceeding 55,000 km^2, consists predominantly of neo-terrains where extensive solonchak and takyr massifs surpass similar landscapes elsewhere in Central Asia in spatial extent (Micklin, 2016). Takyrs and solonchaks, which develop under arid conditions with periodic inundation, are classified as low-productivity soil types. Takyrs are characterised by a heavy mechanical composition, a surface crust, and a platy soil structure, while solonchaks are distinguished by high concentrations of readily soluble salts. Collectively, these properties limit their biological productivity (World Reference BaseforSoilResources, 2014). In highly saline environments, such as the desiccated Aral Sea bed, soil salinity primarily governs vegetation structure and species distribution (Koull and Chehma, 2016; Gonzáles et al., 2021). Consequently, the transformation extent of takyr and solonchak massifs, driven by self-organising soil formation processes, decisively influences plant colonisation success and the stability of successional trajectories within this extremely arid and saline landscape.

Vegetation colonisation on the desiccated Aral Sea bed progresses through halosere, psammosere, and potamosere succession stages (Dimeyeva, 2007). According to the IUCN ecosystem typology (Keith et al., 2020), the Aral Sea is classified as a collapsed freshwater wetland system. However, natural landscape-forming processes have led to the emergence of a new botanical-geographical region on its former bed –the Aralkum (Tojibaev et al., 2016)-characterised by mosaic combinations of various ecosystem types. Floristic enrichment originated from the Amudarya Delta, the Ustyurt Plateau, and the northwestern Kyzylkum Desert. Nevertheless, the nature of ecosystem formation is shaped not only by species influx but also by landscape structure, which influences the direction and stability of successional processes.

Existing research on vegetation dynamics on the desiccated Aral seabed has primarily analysed vegetation indices using remote sensing, identifying relationships with factors such as salinity, groundwater depth, and precipitation (Löw et al., 2021; Shi et al., 2014; Kim et al., 2020; Cui et al., 2023). However, these studies largely overlook spatial self-organisation processes within the landscape, thereby limiting a comprehensive understanding of colonisation mechanisms and ecosystem stability. The specific factor combinations promoting sustainable vegetation establishment in arid conditions—particularly under high salinity, variable soil texture, and fluctuating groundwater levels—remain poorly understood. Furthermore, how these combinations correspond to ecosystem types and successional trajectories within saline landscapes is unclear.

In this context, the development of modern soil profiles and the stabilisation of colonised vegetation patches are crucial for sustainable landscape self-organisation and ecosystem functioning (Setyawan, 2004; Vítovcová et al., 2021; Qi et al., 2023; Poorter et al., 2024). Concurrently, solonchak formation processes and hydrological conditions on the desiccated Aral seabed remain in flux, driven by intensifying aridification. This leads to the stepwise development of sandy-desert soils amidst persistent interactions between variable salinity, diverse soil textures, and groundwater fluctuations (Toderich, Adilov, 2024). Due to the high dynamism of these processes, landscape transformation occurs so rapidly that reliably assessing colonisation success of and emerging ecosystem stability becomes challenging.

This study aims to characterise ecosystem formation processes on the desiccated Aral seabed, considering plant colonisation degree and soil conditions. It addresses the following research questions: (1) How do interactions among soil mechanical composition, salinity, and groundwater depth influence ecosystem formation and species composition? (2) Which soil conditions promote stable ecosystem development? (3) What are the direction and resilience of successional processes under various ecological factor combinations? Accordingly, we undertake a comprehensive evaluation of vegetation self-organisation processes in the Aralkum's post-collapse landscape by analysing spatial relationships among gradations in soil texture, salinity, and groundwater depth using 35 years of field monitoring data.

2. Materials and methods

2.1. Study site

The study site encompasses the desiccated part of the Aral Sea (Fig. 1). Historically, the Aral Sea was the fourth-largest freshwater lake on Earth, covering approximately 67,000 km2 in 1960 (Micklin, 2016). Over the past six decades, significant anthropogenic interventions have led to the loss of about 90 % of its original water volume (Löw et al., 2021). The sea's total area within Uzbekistan is 30,861.76 km2, of which the desiccated area now occupies 28,791.93 km^2 (Dukhovniy et al., 2020). Biogeographically, the desiccated part of the Aral Sea belongs to the Aral district of the Central Kazakhstan province, Phytogeographically, it is part of the South Aral district of the Turanian province (Tojibaev et al., 2016).

The climate in the Aral Sea basin is continental, and its continentality has increased significantly since the sea's desiccation (Adilov et al., 2021). According to long-term meteorological data (meteorological station Ak-Tumsuk, 2000–2018), key climatic parameters are: Tmax = 43.4 °C, Tmin = -35.5 °C, Tmean = 9.9 °C, with an average annual precipitation of 62.7 mm (Dukhovniy et al., 2020).

The desiccated part of the Aral Sea is characterized by low soil formation intensity, low humus content, and a propensity for salinization, with primitive soil types predominating. Several natural-territorial complexes are distinguished in this area. Grey-brown soils dominate island territories (Rebirth Island); sandy soils with a honeycomb-hummocky character or takyr solonchaks with a sandy cover prevail in the initial water retreat zones; and large areas are covered by saline swamps, corky, and corky-puffy solonchaks (Dukhovniy et al., 2020;

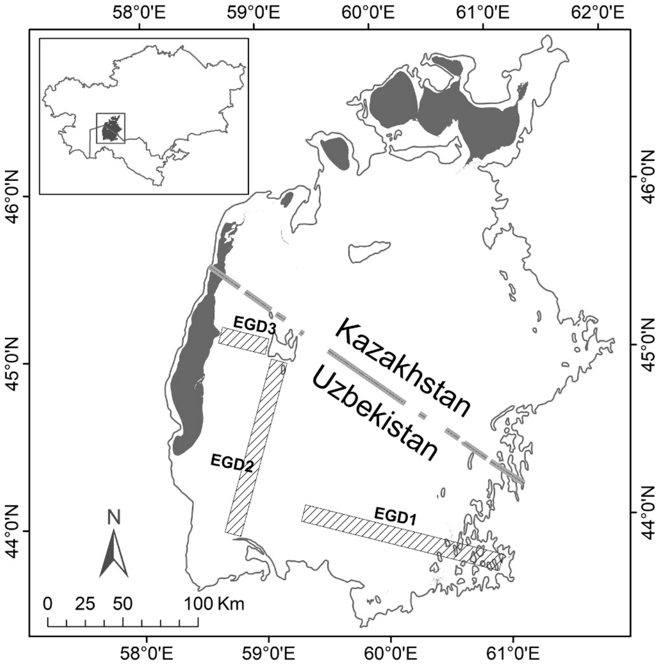

Fig. 1. The desiccated portion of the Aral Sea within Kazakhstan and Uzbekistan. The numbering of eco-gradient directions (EGD1, EGD2, EGD3) corresponds to the observed degree of shoreline recession.

Shomurodov et al., 2021). In areas with subsoil saturation, marsh-meadow, alluvial-meadow, and alluvial-marsh-meadow soils have developed (Dukhovniy et al., 2020).

2.2. *Data collection and investigation of vegetation*

From 1986 to 2021, we studied the degree of vegetation colonization along three eco-gradient directions (EGD) corresponding to the three directions of Aral Sea shoreline recession. EGD1 extends from east to west (135 km), EGD2 from south to north (115 km), and EGD3 from west to east (34 km) (Fig. 1). The width of all EGDs was 1.5 km. Permanent monitoring points (MPs) were established every 3 km intervals.

For vegetation analysis, we utilised our field data accumulated from 2005 to 2021, supplemented by archival data on the vegetation of the desiccated Aral Sea bed (Kabulov, 1990; Sherimbetov et al., 2015). Due to the sparse vegetation, descriptions were made on 100 m^2 transects at each MP using descriptive geobotanical approaches (Granitov, 1980). Plant nomenclature follows Plants of the World Online (POWO) (POWO, 2024). Landscape characteristics were assessed based on regional topography, edaphic factors, and vegetation cover (Tirnakci and Özer, 2018; Swanwick, 2002).

A total of 870 geobotanical descriptions of the desiccated Aral Sea bed vegetation were collected. This allowed us to identify the most active (dominant) species at the MPs across different observation years. Species activity was determined by their prevailing abundance percentage (%) in plant communities (Granitov, 1980).

2.3. *Measurement of environmental factors*

Key ecological factors affecting vegetation colonization included marine soil mechanical composition (MC, %), weighted average soil salinity (%), and groundwater level (m). Analyses were conducted according to the “Guide for Chemical Analysis of Soils” (Arinushkina, 1970).

Soil samples were collected at three locations within each MP where vegetation descriptions were made. At each location, cores were taken from the upper 0–20 cm and 20–40 cm soil layers in three replicates. For determining MC, the physical clay content (particles < 0.01 mm) was analyzed. Soil salinization was determined after categorising samples by MC. Soil salinity was measured using the dry residue method from soil extracts. The groundwater level was measured in the field during vegetation description using a 10 cm diameter soil auger. Drilling was performed to a depth of 4 m, checking for infiltrated water with liquid clay every 50 cm.

2.4. *Data design*

To assess changes in vegetation colonization scale and types, data were ranked and tabulated to represent cross-sections (termed ecotopes) of the following indicators: species activity (%), soil salinity (%) in the 0–20 cm and 20–40 cm horizons, MC (%) in the 0–20 cm and 20–40 cm horizons, and groundwater level (m) from 0-400 cm.

Four MC gradations were identified based on clay content classifications by Akzhigitova (1982) (pelitophytes, hemipelitophytes, hemipsammophytes): MC1: clay content > 45 %; MC2: clay content 20–45 %; MC3: clay content 10–20 %; MC4: clay content < 10 %.

Under evaporative and periodically leaching regimes on hydromorphic solonchaks, maximum salinity typically occurs in the surface horizons (0–10 and 0–20 cm) (Dukhovniy et al., 2020). Therefore, the 0–20 cm horizon was selected as the indicator horizon for soil salinity. Including recalculations for the 20–40 cm horizons was considered to significantly diminish observable differences in salinity ranges for various species. Initially, salinity classes were empirically identified with detailed breakdowns (<0.2, 0.2–1, 1–4, 4–7, 7–10, >10 %). Subsequently, during plant distribution analysis, these were consolidated into three classes for clays (MC1), loams (MC2), and sandy loams (MC3) (soil salinity 1: 0.2–4.0 %; soil salinity 2: 4.0–7.0 %; soil salinity 3: >7.0 %), and sands (MC4) (soil salinity 4: ≤ 1%; soil salinity 5: 1.0–4.0 %; soil salinity 6: 4.0–7.0 %; soil salinity 7: >7.0 %).

Groundwater levels in hydromorphic conditions can exhibit significant seasonal fluctuations; for instance, *Salicornia europaea*, typically dominant at a groundwater level up to 1 m, can also be found at groundwater level up to 2 m. Therefore, groundwater depth data were presented considering the conditions necessary for normal halophyte regeneration in desert environments. Depending on the groundwater depth, five gradations were identified: groundwater level 1: <1.0 m, groundwater level 2: 1.0–1.5 m, groundwater level 3: 1.5–2.0 m, groundwater level 4: 2.0–3.0 m, groundwater level 5: >3.0 m. The unequal interval sizes for these gradations reflect the varying significance of groundwater levels for plants of different ecobiomorphs.

The obtained results for the 65 ecotopes were spatially analysed using Canonical Correspondence Analysis and the Gradient Boosting Model.

Five ecosystem classifications were proposed. These classifications are based on three soil factors and determined by both the activity of dominant species and the naturalness of their communities. The degree of naturalness was assessed as the proximity of the successional stage to the theoretically optimal vegetation type, according to the nomenclature for vegetation explication in Uzbekistan (Granitov, 1980). The ecosystem classifications, based on the degree of naturalness, include: 1. ephemeral ecosystems; 2. neo-ecosystems; 3. remnant ecosystems; 4. post-ecosystems; 5. wasteland ecosystems.

2.5. *Long-term changes of ecosystems and their forecasts*

We studied the changes in the area of these five ecosystem types and the Aral Sea, along with their forecasted values. The land cover classes of these ecosystems (TELCC) for five different periods (1980–1985, 1990–1995, 2000–2005, 2010–2015, 2016–2022) were established using remote sensing data. Landsat 5 Thematic Mapper (TM) images from 1986 and 1996, Landsat 7 Enhanced Thematic Mapper (ETM) images from 2006, and Landsat 8 Operational Land Imager (OLI) images from 2016 and 2022, available through the U.S. Geological Survey (USGS, 2024), formed the basis of this analysis. Image processing was performed using ENVI 5.3 software. Standard pre-processing of Landsat images included geometric and radiometric calibration, conversion to top-of-atmosphere reflectance, and subsequent retrieval of surface reflectance (Ali et al., 2018). Additionally, the FLAASH module in ENVI 5.3 was used for radiometric and atmospheric correction of all images, converting pixel values to reflectance values ranging from 0 to 1 (Maas et al., 2010; Zhai et al., 2022). ENVI 5.3 software also enabled the application of the ISODATA unsupervised classification method to all images, resulting in the identification of six TELCC classes: 1. ephemeral ecosystems; 2. neo-ecosystems; 3. remnant ecosystems; 4. post-ecosystems; 5. wasteland ecosystems; 6. Waterbody (Aral Sea).

For spatial-dynamic forecasting of TELCC changes, data from 2006, 2016, and 2022 were used, and the multilayer perceptron (MLP) neural network method was implemented within a GIS environment. QGIS 2.18.0 software with the Modules for Land Use Change Simulations (MOLUSCE) plugin was used for the analysis. The MOLUSCE plugin employs a four-step workflow for predicting TELCC changes. In the initial stage, the change between successive TELCC maps is quantified, with 2006 and 2016 serving as the first and second recording years, respectively. This change is then mapped and used as input for the subsequent stage. During the transition potential modeling stage, the MOLUSCE plugin offers four methods for predicting TELCC changes: artificial neural network (MLP), weights of evidence, multi-criteria evaluation, and logistic regression. The MLP method was chosen for training the prediction model in this study. The training process concludes with the calculation of a validation kappa value. If this kappa value meets established standards, the prediction of the third year’s LULC map (in this case, 2022) is performed using the cellular automata simulation method. Initially, one iteration is performed for validation. The simulated map (predicted TELCC for 2022) is then compared with the reference map (actual TELCC for 2022) using an overall kappa calculation. If the overall kappa meets the criteria, the cellular automata simulation step is repeated to predict future TELCC. The forecast horizon is determined by the time interval between the first and second input years. In this study, four iterations were performed, leading to forecasts for 2030.

The MLP method was used to predict TELCC in 2022. The predicted TELCC map for 2022 was compared with the actual TELCC map for 2022, yielding an overall kappa value of 76 %. This satisfactory kappa value indicated that the model was suitable for further TELCC predictions.

2.6. Statistical analysis

To compare soil factor gradations and identify significant differences among categorical groups, Tukey's Honest Significant Difference (HSD) test was utilized at $p \leq 0.05$. The mean vegetation activity (*MA*) within each of the 14 soil gradations (*Fg*) was calculated using formula (1):

$$MA(Fg) = \frac{\sum Spi}{Ec} \tag{1}$$

where:

MA(Fg) – mean activity (%) of vegetation within a specific soil gradation,

$\sum Sp_i$ – sum of the activity values for all species present in the ecotopes of that soil gradation,

Ec – number of ecotopes within that specific soil gradation.

To assess the distinct influence of the 14 soil gradations on species frequency and activity, the relative abundance (*RA*) of species within each soil gradation (*Fg*) was calculated using formula (2):

$$RA(Fg) = \frac{\sum_{i=1}^{n}\left(\frac{f_i}{\sum_{j=1}^{n} f_i}\right) \times \sum Sp_i}{\sum_{j=1}^{n}\left(\frac{f_i}{\sum_{k=1}^{n} f_k}\right)} \tag{2}$$

where:

RA(*Fg*) – relative activity (%) of species within a specific soil gradation,

n – number of species,

f_i – frequency of occurrence of species,

$\sum Sp_i$ –sum of the activity values for all species present in the ecotopes of that soil gradation,

$\sum_{j=1}^{n} f_j$ – total sum of frequencies for all species,

$\sum_{k=1}^{n} f_k$ – normalization of the total sum of species frequency for all species.

Using HSD analysis, RA(Fg) results were compared among soil gradations to identify conditions most consistently supporting vegetation formation. Species diversity was assessed using the Shannon-Wiener index (Shannon, 1948). The Shannon-Wiener index was calculated using formula (3):

$$H' = \sum_{i=1}^{R} p_i \ln p_i \tag{3}$$

where:

H' – Shannon-Wiener diversity index,

R –total number of species in the ecotope (species richness),

p_i – proportion of individuals belonging to the *i-th* species relative to the total number of individuals.

Correlation analysis was performed to explore relationships between vegetation activity metrics (MA(Fg) and RA(Fg) within the 14 soil gradations and the corresponding Shannon-Wiener index values. Due to the presence of numerous outliers in MA(Fg) and RA(Fg) data, Spearman's rank correlation was used. To quantify floristic similarity among the five identified ecosystems, Sørensen's similarity index (Sørensen, 1948) was calculated using formula (4):

$$CC = 2c/\,(a + b + 2c) \tag{4}$$

where:

c – number of species common to both ecosystems being compared,

a – number of species unique to the first ecosystem,

b – number of species unique to the second ecosystem.

To assess the relationship between dominant species activity, environmental factors, and ecosystem types, Canonical Correspondence Analysis was performed (Sekulová et al., 2013). Stepwise variable selection, based on Akaike's Information Criterion (AIC) using adjusted R^2 regression was employed to identify environmental variables significantly contributing to the variation in species composition. The significance of the relationship between these selected environmental variables and species activity was further tested using 999 permutations in the Canonical Correspondence Analysis, retaining predictors that significantly ($p < 0.05$) explained changes in species activity. This analysis was conducted using the "vegan 2.6–6.1″ package in R (version 4.3.2; R Core Team, 2023).

A regression model using Extreme Gradient Boosting (XGBoost) was developed to model the vegetation succession process as influenced by key environmental factors over the 35-year study period. The model aimed to predict a target variable representing successional stage or vegetation status based on the year of colonization, MC, soil salinity, groundwater level, and the Shannon-Wiener diversity index (H'). To enhance model interpretability, SHAP (SHapley Additive exPlanations) values were computed. These values provided insights into both the direction (positive or negative) and the magnitude of each predictor's contribution to the modeled dynamics of vegetation colonization.

To evaluate the accuracy and stability of the regression model, five-fold cross-validation was conducted. The feature matrix included variables representing MC, soil salinity, groundwater level, and the year of colonization. Early stopping was applied during model training to prevent overfitting, with the optimal number of boosting iterations determined by the lowest root mean square error (RMSE) on the test folds.

Model performance was assessed using two key metrics: the RMSE and an approximate coefficient of determination (R^2), calculated as follows:

$$R^2 = 1 - \frac{RMSE^2}{Var(y)} \tag{5}$$

where:

R^2 – approximate coefficient of determination, representing the proportion of variance in the response variable explained by the model,

RMSE – root mean square error on the test fold,

Var(y) – variance of the observed response variable. This analysis was conducted using the "xgboost 1.7.7.1″ package (Chen and Guestrin, 2016) in R (version 4.3.2; R Core Team, 2023).

3. Results

3.1. Species composition of dominants and similarities between ecosystem types

Analysis of geobotanical descriptions identified 30 dominant species across various ecotopes over several years of observation (Appendix A). These comprised 9 annual herb species, 6 perennial herb species, 3 subshrub species, 10 shrub species, and 2 tree species. Five ecosystem types were identified, each having undergone various successional series over a 35-year period. Representatives of haloseres were found in ephemeral ecosystems and wasteland ecosystems; psammosere representatives were associated with post-ecosystems; and potomosere representatives were characteristic of remnant ecosystems.

The floristic compositions of the five ecosystem types exhibited low

Sorensen index values (Table 1). The highest vegetation similarity values were observed between ephemeral ecosystems and neo-ecosystems (41.4 %) and between neo-ecosystems and post-ecosystems (54.1 %). Vegetation similarities between ephemeral ecosystems, remnant ecosystems, and wasteland ecosystems were negligible or zero.

3.2. Ecological scale and variability among soil factor gradations

To analyse vegetation colonisation patterns across varying degrees of desiccation along the Aral Sea shoreline, an ecological scale was developed based on the dominance patterns of the 30 identified plant species. This scale aimed to capture gradients in soil conditions and their influence on species distribution, incorporating the synergistic interactions among key abiotic factors. In this study, the ecological scale was conceptualised as a hierarchically structured gradient of environmental parameters, including soil mechanical composition, salinity level, and groundwater depth. These factors defined the ecological suitability of habitats for different plant species and served as the foundation for identifying and classifying ecotopes.

Ecotopes were defined as elementary habitat units, each characterised by a unique combination of these three soil-related variables. These units represented the spatial expression of synergism, interpreted not merely as the sum of individual factor effects but as the interactive influence of multiple factors that either enhance or constrain the colonisation potential of specific locations.

The final ecological scale comprised 65 ecotope classes (Appendix B), each reflecting a specific combination of the three soil-related factors. The scale was organised across three hierarchical levels. First level – MC: soil texture classes were differentiated based on clay content as follows: MC1: >45 % clay (heavy loams); MC2: 20–45 % clay (medium and light loams); MC3: 10–20 % clay (sandy loams); MC4: <10 % clay (cohesive and loose sands). These categories were statistically distinct and reflected variations in water retention capacity and soil structure (Table 2).

Second level –salinity levels were defined based on dry residue concentrations: soil salinity 1 and soil salinity 5 ranged from slightly saline soils (average 0.2 g/%) to solonchaks (up to 4.0 g/%); soil salinity 4 represented moderate salinity (0.7 ± 0.3 g/%); soil salinity 2 and soil salinity 3 indicated higher salinity levels (4.0–7.0 g/% and > 7.0 g/%, respectively), corresponding to hydromorphic solonchak subtypes typical of coastal zones.

Third level –groundwater level: each MC–soil salinity combination was further categorised into five groundwater depth intervals (groundwater level 1–5), reflecting the hydrological regime of the soil profile. groundwater level 1 (0.3 ± 0.3 m) exhibited high variability, attributed to shoreline dynamics during the initial 1–2 years following sea retreat and to seasonal fluctuations. This overlap of this range with groundwater level 2 did not warrant its exclusion, as it reflected ecologically meaningful variability.

Through this hierarchical approach, the ecological scale facilitated the identification of species groups prone to coexistence within shared ecotopes, as well as those more likely to compete under specific combinations of soil parameters. This framework enabled a nuanced understanding of successional dynamics and community assembly processes under conditions of extreme aridity and salinisation.

Table 1
Sørensen similarity index between vegetations of the ecosystem.

Ecosystems	EEs	NEs	PEs	REs	WEs
EEs	1.0				
NEs	41.4	1.0			
PEs	9.1	54.1	1.0		
REs	0.0	21.4	19.1	1.0	
WEs	0.0	16.7	11.8	0.0	1.0

3.3. Vegetative cover activity within soil gradations

Across the gradients of soil parameter, MA(Fg) ranged from 60.3 ± 43.5 to 261.7 ± 178.8. An increase in vegetation cover was observed with a decrease in physical clay content and a corresponding increase in sand content (from MC1 to MC4). Analysis of standard deviation (SD) showed significant outliers, indicating uneven species dominance with similar activity within the soil mechanical composition (Table 2).

A trend of increasing vegetation activity was also observed with decreasing soil salinity. The highest MA(Fg) activity (497.7 ± 108.7) was found in the soil salinity 4 gradation, where the dry residue content was less than 1 %. Conversely, the lowest vegetation cover was characteristic of hydromorphic solonchaks (soil salinity 2, soil salinity 3). Despite the lack of statistically significant differences between soil salinity 1 and soil salinity 5, vegetative cover in the soil salinity 5 gradation (352.3 ± 124.3) was significantly higher and exhibited fewer outliers (lower SD) compared to soil salinity 1 (206.5 ± 129.6).

Variations in groundwater level did not show a linear influence on MA(Fg). The highest vegetation activity was characteristic of groundwater level 2 (279.0 ± 143.0). In groundwater level 1, where the groundwater level was less than 1 m, the lowest vegetation activity was observed (103.7 ± 39.0) (Table 2).

3.4. Species activity within soil gradations

Within the MC gradations, the highest RA(Fg) values (32.1 ± 24.9) were observed in sandy soils (MC4). Similar RA(Fg) values were found in soil salinity 4 (32.8 ± 23.9) and soil salinity 5 (34.4 ± 24.9). No significant differences in Mean ± SD and median (Md) values of RA(Fg) were found among the groundwater level gradations. However, low Md values for species relative activity are characteristic of heavy soils (MC1, Md = 8.0) and hydromorphic solonchaks (soil salinity 3, Md = 5.5) (Table 2).

Heavy soil (MC1) and sandy soils (MC4), and areas with groundwater levels between 1.0–1.5 m exhibited distinct RA(Fg) patterns not replicated in other gradations. Salinity gradations soil salinity 4- soil salinity 5, as well as groundwater levels groundwater level 1, groundwater level 3, and groundwater level 5, grouped into comparable categories based on their RA(Fg) values (Fig. 2).

3.5. Biodiversity index among independent soil gradations

MC4 (1.4 ± 0.8) exhibited the highest mean Shannon index value and showed a strong correlation (MI ± SD = 0.73). MC1 (0.9 ± 0.4) had a lower mean Shannon index value but also demonstrated a moderate correlation (0.54).

Stronger correlations with the Shannon index were observed. Particularly high mean Shannon index values were found in soil salinity 4 areas (2.3 ± 0.4), which also showed a strong correlation (0.87). soil salinity 1 (1.8 ± 0.5) and soil salinity 5 (2.0 ± 0.4) also exhibited notable Shannon index values and correlations.

Groundwater level 2 (1.6 ± 0.6) stood out with a higher mean Shannon index value and a moderate correlation (0.71). GL1 (0.8 ± 0.4) had a lower mean value but also showed a moderate correlation (0.59) (Table 2).

3.6. Interrelationships between soil factor conditions, species composition, and ecosystem types

The interrelationships between soil factor conditions, species composition, and ecosystem types are presented in Table 3 and Fig. 3. Analysis of soil structure and properties revealed that out of 14 soil gradation types, 8 significantly influenced the activity patterns within the corresponding ecosystems. The gradations explaining the most variance in the analysis included MC1, MC4, groundwater level 1,

Table 2
Variability among soil factor gradations and vegetation indicators.

Soil factors				*MA(Fg)*	*RA(Fg)*		*H´*	
factors	gradations	gradients	*M* ± *SD*	*M* ± *SD*	*M* ± *SD*	*Md*	M_I ± *SD*	*ρ*
MC^1	MC1	>45	54.1 ± 5.4	60.3 ± 43.5	14.7 ± 19.6	8.0	0.9 ± 0.4	0.54
	MC2	20–45	29.2 ± 6.1	115.5 ± 86.5	18.4 ± 16.2	14.0	1.2 ± 0.7	0.64
	MC3	10–20	15.2 ± 2.2	169.4 ± 134.5	22.2 ± 20.5	15.0	1.2 ± 0.8	0.69
	MC4	<10	4.9 ± 1.9	261.7 ± 178.8	32.1 ± 24.9	24.0	1.4 ± 0.8	0.73
SS^2	SS1^a	0.2–4.0	1.9 ± 1.2	206.5 ± 129.6	20.8 ± 18.7	15.0	1.8 ± 0.5	0.68
	SS2	4.0–7.0	5.4 ± 1.1	94.7 ± 71.9	19.2 ± 20.2	12.0	0.9 ± 0.6	0.59
	SS3	>7.0	11.4 ± 2.4	43.9 ± 37.7	17.7 ± 24.1	5.5	0.5 ± 0.3	0.61
	SS4	<1	0.7 ± 0.3	497.7 ± 108.7	32.8 ± 23.9	25.0	2.3 ± 0.4	0.87
	SS5^a	1.0–4.0	2.6 ± 1.3	352.3 ± 124.3	34.4 ± 24.9	24.0	2.0 ± 0.4	0.81
GL^3	GL1^b	<1.0	0.3 ± 0.3	103.7 ± 39.0	23.1 ± 21.5	15.5	0.8 ± 0.4	0.59
	GL2^b	1.0–1.5	1.1 ± 0.2	279.0 ± 143.0	26.7 ± 23.4	15.5	1.6 ± 0.6	0.71
	GL3	1.5–2.0	1.9 ± 0.1	195.8 ± 154.4	23.2 ± 21.3	15.0	1.4 ± 0.8	0.65
	GL4	2.0–3.0	2.8 ± 0.4	135.3 ± 127.6	21.2 ± 20.8	15.0	1.0 ± 0.8	0.61
	GL5	>3.0	4.0 ± 0.4	124.0 ± 120.3	24.1 ± 24.5	15.0	1.0 ± 0.7	0.61

Data with similar letters do not differ significantly at $p < 0.05$. MC^1 – % mechanical composition of marine soils by physical clay; SS^2 – weighted average % of salts in the 0–20 cm horizon; GL^3 – groundwater level in meters. Data with different letters are not significantly different at $p < 0.05$. *MA(Fg)* – mean activity (*M* ± *SD*) of vegetation within soil gradations. *RA(Fg)* – relative activity of species (*M* ± *SD*) and its median (*Md*) within soil gradations. *H´* – Shannon-Wiener Index (M_I ± *SD*) and results of correlation analysis (*ρ*) between soil gradations.

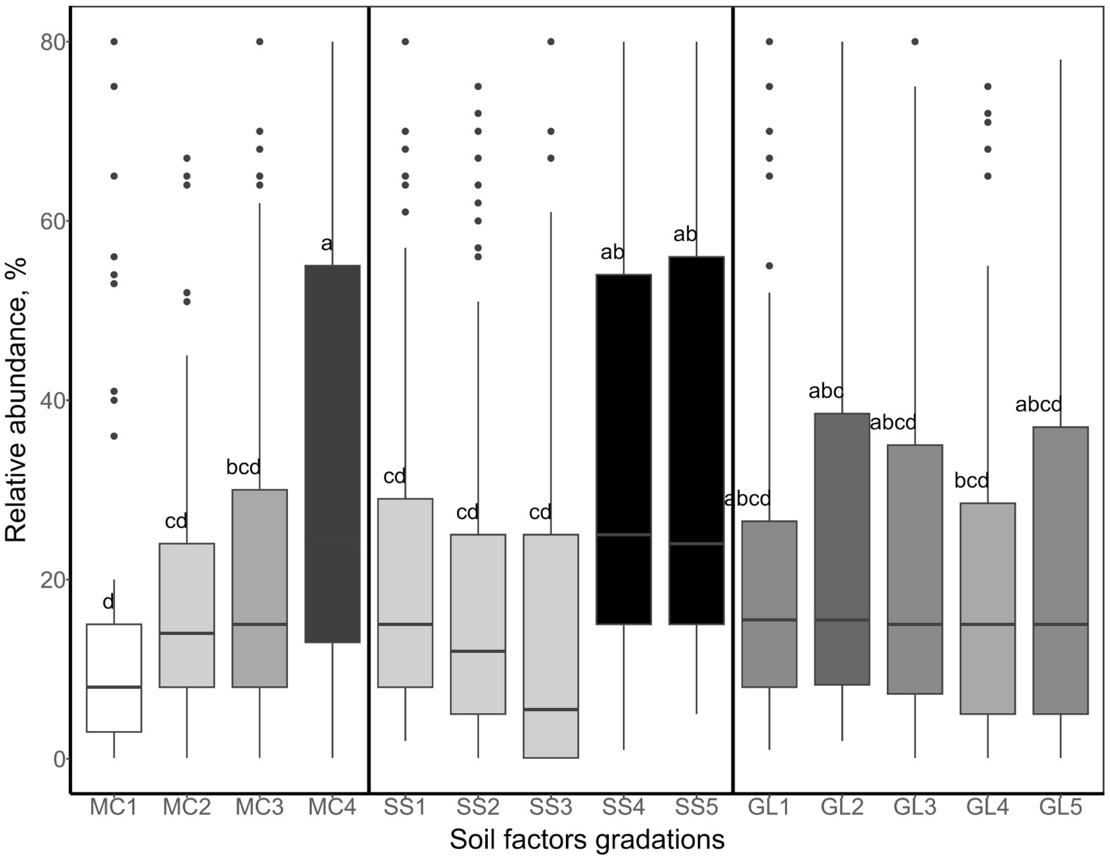

Fig. 2. Relative activity of species across different soil gradations, based on Tukey's Honest Significant Difference (HSD) analysis. Soil texture categories by physical clay content: MC1 (>45 %), MC2 (20–45 %), MC3 (10–20 %), MC4 (<10 %). Soil salinity categories by dry residue: SS1 (0.2–4.0 %), SS2 (4.0–7.0 %), SS3 (>7.0 %), SS4 (<1%), SS5 (1.0–4.0). Groundwater level categories: GL1 (<1.0 m), GL2 (1.0–1.5 m), GL3 (1.5–2.0 m), GL4 (2.0–3.0 m), GL5 (>3.0 m). Box colors correspond to factor groups; shades are used to highlight statistically similar or distinct distributions of species' relative activity, as identified by the HSD test ($p < 0.05$). Different letters above boxes indicate significant differences among groups.

groundwater level 5, and groundwater level 2 all significant at ($p < 0.001$).

Stepwise regression results indicated that the variables groundwater level 4 demonstrated an adjusted R^2 (0.261) and Akaike Information Criterion (AIC) (438.83) compared to other variables with high significance ($p < 0.05$).

Canonical Correspondence Analysis identified four ecosystem types whose vegetation composition correlated closely with specific soil

Table 3

Results of stepwise regression correlation analysis of canonical variables (CCA).

Stepwise regression	R^2 adjusted[1]	*AIC*[2]	*F*	*Pr (>F)*
All variables	0.3236972			
GL1	0.0713920	448.14	5.9130	0.001
GL1 + GL5	0.1310601	444.81	5.2911	0.001
GL1 + GL5 + MC4	0.1764460	442.26	4.4245	0.001
GL1 + GL5 + MC4 + GL2	0.2103792	440.48	3.5907	0.001
GL1 + GL5 + MC4 + GL2 + MC1	0.2279995	439.94	2.3547	0.025
GL1 + GL5 + MC4 + GL2 + MC1 + SS3	0.2445253	439.47	2.2428	0.024
GL1 + GL5 + MC4 + GL2 + MC1 + SS3 + GL3	0.2610774	438.95	2.2527	0.017
GL1 + GL5 + MC4 + GL2 + MC1 + SS3 + GL3 + GL4	0.2610774	438.83	1.8641	0.062

[1] Stepwise regression of the adjusted coefficient of determination for factors in the CCA model;

[2] Akaike Information Criterion.

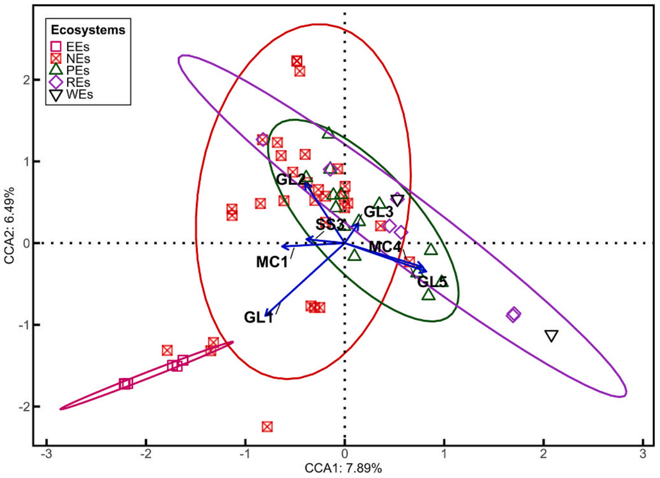

Fig. 3. Canonical Correspondence Analysis (CCA) illustrating the relationships between significantly correlated soil factors ($p < 0.05$) and ecosystem types. Soil texture by physical clay content: MC1 (>45 %), MC4 (<10 %). Soil salinity by dry residue: SS3 (>7.0 %). Groundwater level: GL1 (<1.0 m), GL2 (1.0–1.5 m), GL3 (1.5–2.0 m), GL4 (2.0–3.0 m), GL5 (>3.0 m).

gradations: MC1, MC4, soil salinity 3, groundwater level 1–5. Vegetation formation in ephemeral ecosystems and post-ecosystems exhibited distinct patterns of conservatism. The formation of ephemeral ecosystems was particularly influenced by the groundwater level 1 gradation, while post-ecosystems was significantly associated with MC4, soil salinity 3, groundwater level 2–5.

The greatest variability in vegetation characteristics was observed in neo-ecosystems and remnant ecosystems. Correlation analysis results suggested that the formation of neo-ecosystems was similar to that of ephemeral ecosystems, while the emergence of remnant ecosystems was often associated with post-ecosystems vegetation, a finding corroborated by the Sorensen index values between ecosystem vegetation (Table 1).

3.7. *Regression model of plant colonization*

A Gradient Boosting Model for plant colonization in the desiccated part of the Aral Sea area yielded a mean squared error (MSE) of 49.64 and a coefficient of determination (R^2) of 0.72 (Fig. 4). Among the predictor variables, MC exhibited the highest mean gain (0.61). The year of colonization also demonstrated high importance, as indicated by its cover values (0.69) and usage frequency in model splits (0.7680).

SHAP values further corroborated these findings. MC was identified as the most influential variable (mean SHAP value = 8.204), consistent with its high gain-based importance (0.61). soil salinity, groundwater level, and H' displayed considerably lower mean SHAP values (1.415, 0.202, and 0.024, respectively), supporting their relatively minor roles as suggested by the initial gain and frequency metrics. This consistency between traditional model importance measures and SHAP-based interpretations provides robust evidence for the primary role of MC in driving plant colonization dynamics on the desiccated Aral Sea bed (Appendix C).

The accuracy and robustness of the Gradient Boosting Model, assessed through five-fold cross-validation, demonstrated strong predictive performance. The model's suitability for prediction: the RMSE was 6.79, and the approximate coefficient of determination (R^2) reached 0.754. This is further supported by a plot of observed versus predicted values, which shows a high degree of agreement between the model output and the actual data (Appendix D).

3.8. *Dynamics of ecosystems*

The dynamics of the five ecosystem types from 1980 to 2030 are illustrated in Fig. 5. TELCC changes were based on multi-temporal data from five periods (1980–1985, 1990–1995, 2000–2005, 2010–2015, and 2016–2022), with all classification validation Kappa values exceeding 60 %. The analysis revealed significant transformations among the TELCC. Notably, the water level of the Aral Sea consistently declined throughout the observation period. While there was a general trend of increasing areas for neo-ecosystems, post-ecosystems, wasteland ecosystems, and remnant ecosystems, a reduction in ephemeral ecosystems areas was observed up to the 2010–2015 period. From 2016 to 2022, coinciding with the extensive desiccation of the Large Aral Sea, the areas of wasteland ecosystems and post-ecosystems markedly increased.

4. Discussion

4.1. *Species diversity, floristic similarity, and vegetation dynamics across soil conditions of desiccated part of the Aral Sea*

Analysis of independent vegetation activity and biodiversity reveals interconnected dynamics across different soil gradations. It is well established that improved soil conditions generally foster more robust vegetation during succession, a trend confirmed by our findings. In many ecological contexts, such as vegetation regrowth on fallow lands and spoil heaps (Suleymanov et al., 2021; Zhuikova et al., 2022), community species diversity often exhibits conservatism compared to overall species coverage or biomass. However, in our study of the desiccated part of the Aral Sea area, the primary colonization strategy appears to involve concurrent increases in both phytomass and species richness across all observed successional stages (Table 2). We posit that under the unique conditions of the desiccated Aral Sea bed, the formation of phytomass does not substantially alter the structural and chemical properties of the soil, primarily because the development of a significant organic layer is impeded. A distinctive feature of soil formation processes in the desiccated part of the Aral Sea is the profound influence of active aeolian processes, coupled with hyper-arid

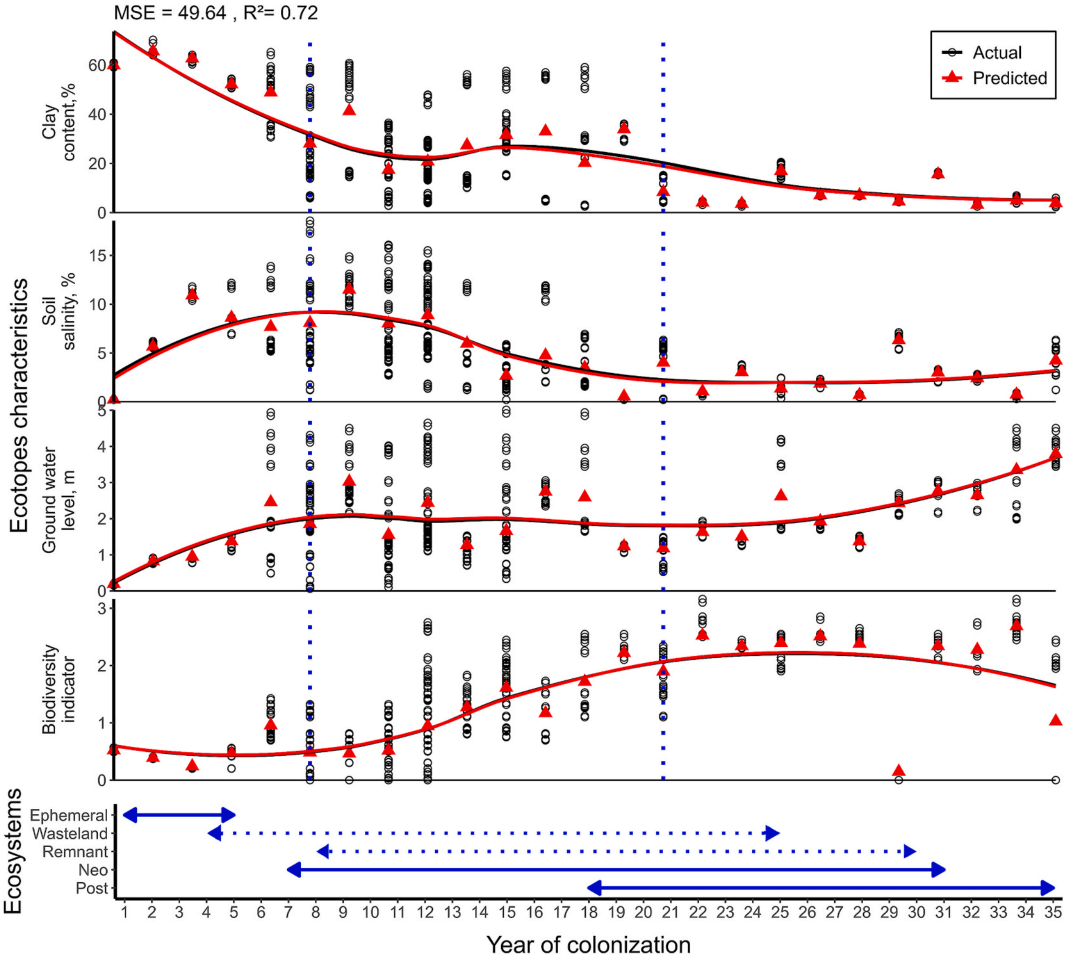

Fig. 4. Actual and predicted (Gradient Boosting) regression model (MSE = 49.64, R^2 = 0.72) of the species colosization process in the desiccated part of the Aral Sea area and the formation of different ecosystem types based on the biodiversity indicator (Shannon-Wiener index) from 1986 to 2021. The analysis included all observed gradients of clay content (MC, %), soil salinity (SS, %), and groundwater level (GL, m). The intervals of vertical lines indicate periods of "biodiversity spikes" during the colonization process.

conditions and high salinity, which collectively limit humus accumulation (Stulina and Sektimenko, 2004), despite gradual improvements in other physicochemical soil properties over time.

This pattern of fragmented and site-specific development is also reflected in the Sørensen similarity index values (Table 1), which quantify the degree of floristic overlap between ecosystem types. Overall, the results indicate low floristic similarity among the identified ecosystem types, suggesting the absence of uniform, linear successional trajectories across the exposed Aral Sea bed. Particularly low similarity values (0.0 %) between ephemeral ecosystems and intermediate types, such as remnant ecosystems and wasteland ecosystems, highlight a high degree of species turnover and underscore the fragmented nature of succession. Such fragmentation is likely driven by spatial heterogeneity in soil salinity, mechanical composition, and groundwater depth, which collectively create localized microsites with varying suitability for plant colonization (González-Alcaraz et al., 2014).

Moderate similarity values between ephemeral ecosystems and neo-ecosystems (41.4 %), as well as between neo-ecosystems and post-ecosystems (54.1 %), suggest the presence of some transitional species and indicate a partial, albeit uneven, progression of plant communities along certain successional gradients. These findings imply that while stable successional trajectories may be possible under specific edaphic and hydrological conditions, they are frequently disrupted or fragmented in other areas.

The complete lack of shared species between ephemeral ecosystems and intermediate stages such as wasteland ecosystems, as well as between remnant ecosystems and other types, points to the likely role of external abiotic barriers in hindering a smooth, sequential progression through successional stages. Under conditions of high spatial variability in landscape features and heterogeneity in abiotic factors—such as salinity, soil texture, and groundwater depth—succession tends to follow a mosaic and unstable pattern. In such environments, ecological and geomorphological barriers can limit species continuity and the formation of coherent, predictable successional sequences (Rietkerk et al., 2002; Prach & Walker, 2011).

4.2. *Soil mechanical composition*

Soil texture is widely recognized an indicator of the degree of soil formation and its capacity to support vegetation development (El-Ghani, 2003; Su et al., 2015; Prodhan et al., 2018; Juhos et al., 2019; Li et al., 2022). In arid regions, reduced soil compaction and the development of lighter-textured soils typically favor pioneer species during plant colonization (Su et al., 2015; Fan et al., 2018). The desiccating Aral Sea bed exhibits a complex lithological-morphological composition that, under rapidly changing hydrogeological conditions, transforms into various types and subtypes. Frequent desiccation cycles lead to soil disintegration and increase in sand content (Stulina and Sektimenko, 2004). This process of soil breakdown and sand emergence is pivotal in the forming new sandy landscapes, characteristic of post-ecosystems, and is driven by a decrease in clay content and an increase in the proportion of sandy fractions (Table 2).

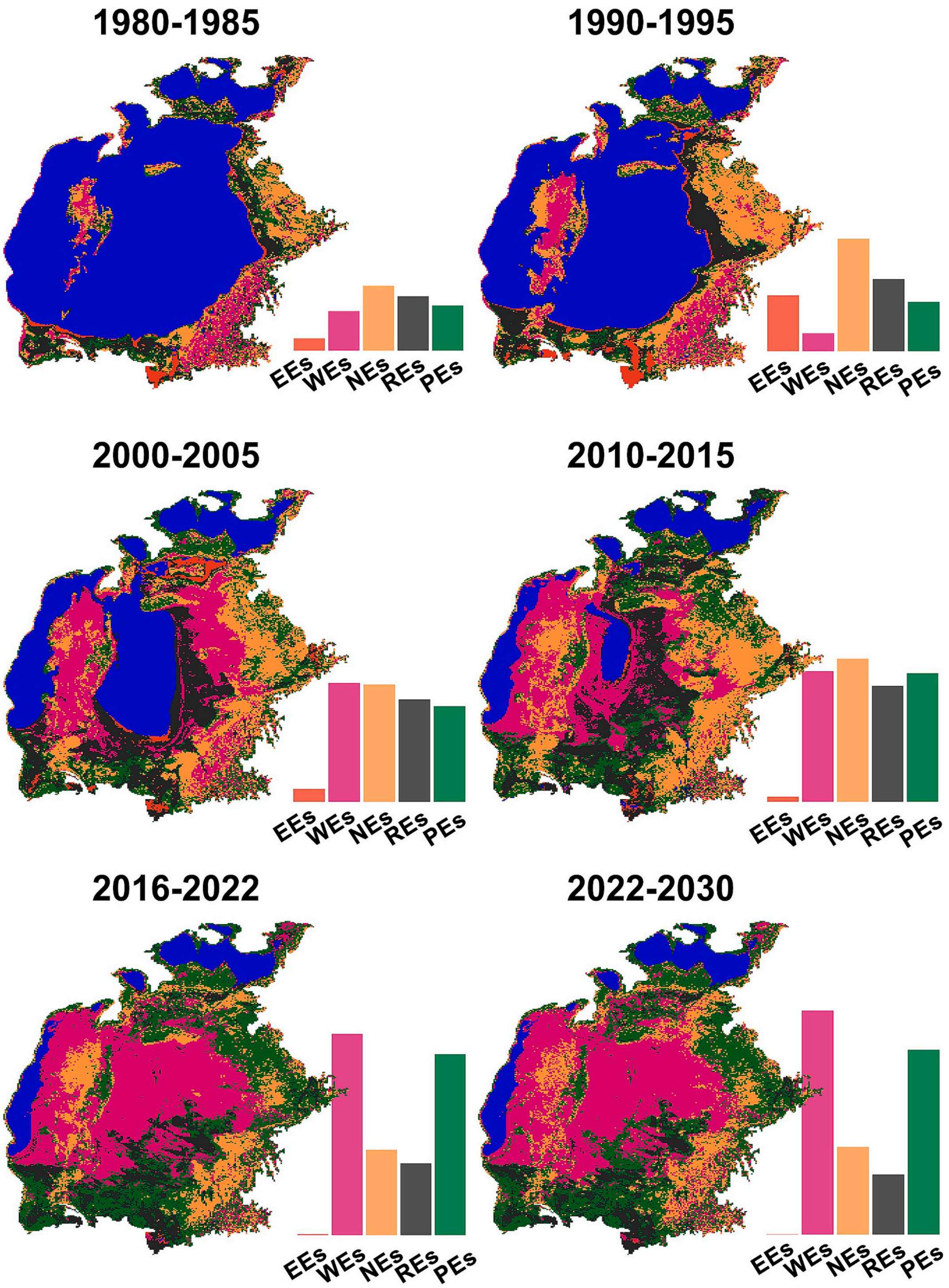

Fig. 5. The dynamics of temporal ecosystems land cover conditions (TELCC) for five distinct periods (1980–1985, 1990–1995, 2000–2005, 2010–2015, 2016–2022) and their predicted changes for 2022–2030. EEs – ephemeral ecosystems, WEs – wasteland ecosystems, NEs – neoecosystems, REs – remnant ecosystems, PEs – post-ecosystems.

In arid conditions, plant colonization and vegetation development on depleted lands are often sensitive to specific soil fractions. For instance, some studies highlight the importance of the silt fraction (Su et al., 2015) or heavy soil composition (Abdi and Afsharzadeh, 2016), while others emphasize the role of sand (Abdi and Afsharzadeh, 2016; Fan et al., 2018), with these factors often positively affect biomass and floristic composition (Dimeyeva, 2011). Our results align with the latter, indicating that with an increase in the sandy fraction, MA(Fg), RA(Fg), and H´ all tend to increase (Table 2). This contrasts with findings by Deng et al., (2022), who concluded that soils with a higher sandy fraction content have poor water retention, which can hinder vegetation growth. This discrepancy suggests that other factors, possibly related to specific adaptations of local flora or interactions with groundwater, might modulate the effects of soil texture in the desiccated part of the Aral Sea.

Results from the Tukey Honest test (HSD) indicated significant differences among soil texture gradients (Table 2). However, the most distinct differences in ecosystem colonization were associated with the extreme ends of the texture spectrum: MC1 and MC4. These soil types appear to define specific, relatively stable ecological niches or endpoints. The distinct ecological roles of MC1 and MC4 suggest that they are key determinants, or "initiators," for the development of ephemeral ecosystems within haloseric successional pathways and post-ecosystems within psammoseric successional pathways, respectively, during plant colonization.

According to Su et al., (2015), in some arid areas, high clay content can contribute to organic carbon reserves, thereby affecting plant productivity. However, in the Aral Sea bed, intense aeolian processes under hyper-arid conditions and high salinity prevent the constant accumulation of humus or organic carbon (Stulina and Sektimenko, 2004; Kharitonova et al., 2022). Consequently, ephemeral ecosystems, despite having higher clay content, are characterized by the lowest biomass and biological diversity (Table 2). This low biogenicity, the predominance of organic matter decomposition over accumulation, and the near-complete absence of humus development (Stulina and Sektimenko, 2004) contribute to the prevalence of monodominant communities with low biological diversity. Such conditions are particularly characteristic of vegetation in the arid regions of Central Asia, including the desiccated part of the Aral Sea (Adilov et al., 2021).

4.3. *Degree of soil salinity*

In the desiccated part of the Aral Sea region, our findings demonstrate that soil salinity is a principal limiting factor governing vegetation structure and species distribution. The analysis of the Shannon diversity index confirmed that plant colonisation is more sensitive to variations in salinity than to differences in soil mechanical composition or groundwater level (Table 2). Notably, colonisation was observed even within highly saline ecotopes (soil salinity 2 and soil salinity 3), suggesting that certain species possess tolerance thresholds enabling establishment under elevated salinity levels. These results align with remote sensing-based observations from other arid landscapes (e.g., Kim et al., 2020; Duan et al., 2022b), where vegetation can occur across a salinity gradient. However, our data further refine this understanding by demonstrating that colonisation in the desiccated part of the Aral Sea occurs not randomly but in accordance with structured salinity gradations, reflecting ecotope-specific responses. Thus, while salinity is a major constraint, it does not preclude colonisation altogether but rather defines ecological boundaries within which species assemblages can emerge.

According to V.V. Vukhrer (1990) and L.A. Dimeyeva, (2007), the development of halophytic vegetation, or the onset of autogenic succession in the desiccated part of the Aral Sea, is associated with fluctuations in groundwater levels and soil salinity. A decrease in groundwater depth and the development of solonetz processes are thought to initiate the halosere stage (Dimeyeva, 2011). However, the HSD test results indicated that species colonization and activity within the soil salinity 1–3 salinity gradations are similar to those observed in soils with mechanical composition MC2. This suggests that the initial formation of halophytic vegetation is closely related to early stages of soil formation characterized by an increase in sand fraction and more labile soil conditions (Fig. 2).

Plant colonization in the higher salinity gradients SS 4 and soil salinity 5 follows a generally similar trend in terms of plant response metrics. Despite statistically significant but minor differences in mean values between soil salinity 1 (1.9 ± 1.2) and soil salinity 5 (2.6 ± 1.3) ($p < 0.05$), overall values for MA(Fg), RA(Fg), and H′ tend to be higher within the soil salinity 5 gradation (Table 2). Considering that soil salinity 5 often occurs within MC4 (sandy soils), this highlights the importance of a sandy soil mechanical composition for successful plant colonization, even under conditions of high substrate salinity (Table 2; Appendix B).

The only salinity gradation that showed a consistent, distinct positive correlation with plant colonization patterns across different desiccated part of the Aral Sea ecosystems was soil salinity 3 (Fig. 3), irrespective of soil mechanical composition and groundwater level variations within other ecosystem types. This suggests that while plants might tolerate moderate to high salinity when other conditions (like sandy texture) are favorable, the extreme salinity represented by soil salinity 3 (where salinity often exceeds 7 %) acts as a severe limiting factor. Plants cannot successfully colonise habitats, even those with favourable sandy composition types of post-ecosystems, as seen in soil salinity 3, broadly restricts plant colonization in depleted areas. Therefore, when delineating potential habitats for plant species on salt flats, consideration of substrate salinity changes may be more critical than other edaphic factors (Moffett et al., 2010).

4.4. *Groundwater level*

The floristic composition of the desiccated part of the Aral Sea vegetation primarily consists of drought-tolerant and salt-tolerant species (Akzhigitova, 1982), which emerge during successive ecological stages (Dimeeva, 2007; Shomurodov et al., 2021). Each successional trajectory or habitat type may feature distinct indicator species of halophytes (Dimeyeva, 2007), which can differ in their relationship to soil mechanical composition or their mode of groundwater utilization (Akzhigitova, 1982).

According to Duan et al., (2022a), groundwater level fluctuations within the range of approximately 7–8 m can have either positive or negative effects on the desiccated part of the Aral Sea vegetation development, depending on the concurrent salt content. We acknowledge the role of groundwater salinity as a significant source of soil salinity in the desiccated part of the Aral Sea (Stulina and Sektimenko, 2004; Duan et al., 2022b). During evapotranspiration, salt accumulation on the soil surface can lead to surface soil salinity levels that exceed those of the underlying groundwater (Stulina and Sektimenko, 2004; Andrulionis et al., 2021). Furthermore, extensive salt flats (Vukhrer, 1990; Kim et al., 2020; Issanova et al., 2022) and saline dust storms (Ge et al., 2016; Banks et al., 2022; Duan et al., 2022b) are recognized as additional negative factors affecting vegetation development in the desiccated part of the Aral Sea.

Atmospheric precipitation and other surficial freshwater inputs cannot be considered primary water sources for sustaining desiccated part of the Aral Sea vegetation development, contrary to suggestions by Duan et al., (2022a). This is because such freshwater sources rapidly lose their efficacy upon contact with saline soil particles (Evans and Levin, 1969; Fuentes-Yaco et al., 2001), leading to osmotic stress (Redfield and Zwiazek, 2002; Zhao et al., 2021) and direct toxic effects on plants (Koźmińska et al., 2019; Sharmin et al., 2021; Redfield and Zwiazek, 2002). Given that the desiccated part of the Aral Sea vegetation is mainly composed of shrubs and trees (Kabulov, 1990; Sherimbetov et al., 2015) with root zones typically extending below 30 cm, these plants predominantly utilise groundwater as phreatophytes (Bakhiev et al., 1987; Kabulov, 1990). In this context, particularly with annual precipitation totals often below 100 mm (Gaybullaev et al., 2012), the role of direct precipitation in supporting significant the desiccated part of the Aral Sea vegetation formation remains questionable.

Despite the adaptation of halophytic species to these saline areas, they often experience water deficits under high salinity conditions (González-Orenga et al., 2020), which can suppress their morphophysiological functions (Kachout et al., 2021). Several studies (e.g., Page, 1995; García-Caparrós et al., 2017; Karasińska et al., 2021) highlight the positive effect of accessible groundwater or supplemental water intake for halophytes experiencing water deficit, noting improvements in biomass, the yield of aboveground and underground organs, and their spatial spread. Supporting this view, our results demonstrate higher relative vegetation activity, species activity, and Shannon diversity index values at intermediate groundwater levels. Notably, sharp positive differences in these metrics are observed when groundwater levels are between 1.0–1.5 m, significantly benefiting halophyte colonization in saline habitats compared to other groundwater depths (Table 2, Fig. 2).

A close correlation between plant colonization patterns in different ecosystems and all five defined groundwater level gradients (Fig. 3), suggesting that groundwater depth acts as an indicator or a differentiating factor for each successional stage or ecosystem type. Different soil types, varying in mechanical composition and salinity, can be found across the spectrum of groundwater levels. However, very low groundwater levels do not invariably create optimal conditions for plant colonization. According to our results, excessively deep groundwater levels can decrease or even halt the colonization process, as evidenced by lower Shannon index (Table 2). This phenomenon, as suggested by Li et al., (2012), may be related to advanced stages of vegetation change where communities shift towards a dominance of shrub species with pronounced xerophytic characteristics, adapted to more profound water scarcity.

4.5. The desiccated part of the Aral Sea ecosystems of the Aral sea during colonisation

Landscapes are inherently heterogeneous territories composed of groups of interacting ecosystems that recur in similar forms throughout a given area (Forman and Godron, 1986). Many studies on the desiccated part of the Aral Sea land cover have focused on classifying different landscape categories (Löw et al., 2013, 2021; Kim et al., 2020; Shomurodov et al., 2021; Issanova et al., 2022) and assessing their predictive significance for vegetation patterns (Löw et al., 2021), often based on satellite data. For instance, Löw et al., (2021) identified 10 different landscape categories, of which four correspond to vegetated areas: “Sandy soils with sparse vegetation,” “Meadow,” and “Shrubland.” In an earlier study, Löw et al., (2013) also proposed categories such as “Reed” and “Shrubland.” Kim et al., (2020) suggested a broader category of “Potential vegetation establishment areas,” which encompasses all vegetation types subject to various unstable environmental factors. However, the process of colonization, understood as a dynamic interaction between biotic and abiotic environments (Magnússon et al., 2014; Setyawan, 2004), fundamentally occurs not at the broad landscape scale but at the ecosystem level. Ecosystems are defined as interacting systems formed by living organisms and their specific abiotic environment (Ellenberg, 1973).

In the desiccated part of the Aral Sea, the general successional trajectory is considered to progress from a halosere to psammosere (Dimeyeva, 2007; 2011), This implies that colonization typically begins with the migration and establishment of halophytes and culminates in the formation of communities dominated by psammophytic species. Many different plant life forms participate in this succession (Appendix A). Broad landscape classifications that define categories such as “Meadow,” “Shrubland,” and “Reed” (Löw et al., 2013, 2021) may not fully reflect how successfully plants have colonised particular habitats or the precise successional stage of a given area. Since successful colonization in depleted or newly available areas is ultimately determined by the development of stable ecosystems (Magnússon et al., 2009; Issanova et al., 2022) that are representative of the prevailing local conditions (Prach and Rachlewicz, 2012), an ecosystem-focused approach is crucial.

According to Dimeyeva (2007), the degree of landscape disturbance and heterogeneity in the desiccated part of the Aral Sea ecosystems is often so significant that it can be challenging to delineate a clear, universally applicable successional sequence. In our study, we have proposed ecosystem types that aim to represent the synergism between landscape-level development processes and the specifics of plant colonization. This approach considers the establishment and subsequent development of relatively stable ecosystems, irrespective of the dominant plant life forms initially present, as the key indicators of successional progression.

4.6. Landscape interference as a factor in the formation of various ecosystem types and plant colonization

The vegetation of the Aralkum exists in various stages of development, primarily on sandy and saline substrates, as well as in areas influenced by groundwater. This allows these areas to be considered pedobiomes, distinct from the surrounding zonal vegetation mosaic (Breckle et al., 2012). The desiccated part of the Aral Sea represents not a single, uniform newly formed area but rather a complex of different landscape units where plant species colonize depending on the availability of optimal conditions. Consequently, the plant diversity of the desiccated seabed should be assessed based on distinct ecosystem types, the formation of which is determined by these landscape units and their specific lithological, hydrological, and halological conditions.

Despite the identification of 65 ecotopes in our study, many of them represent intermediate or transitional ecological conditions for plant colonization, highlighting the boundaries and effects of landscape interference. The degree of intermixing or blurring of ecotope boundaries influences whether initial colonization leads to subsequent successional stages with a more stable character or to regressive stages characterized by vegetation destabilization.

Primary stages of colonization often occur in ephemeral ecosystems, which are characterized by transience and low predictability, or even unpredictability. These conditions do not initially ensure stable, long-term plant colonization (Fig. 4), particularly on hydromorphic marsh solonchaks. The halosere succession at the stage dominated by annual saltwort plants (Dimeyeva, 2007; Breckle et al., 2012; Shomurodov et al., 2021) includes dominant species of annual halophytes such as *Salicornia europaea*, *Suaeda acuminata*, *Suaeda salsa*, *Caroxylon scleranthum*, *Petrosimonia triandra*, and *Climacoptera aralensis* (Appendix A). Depending on salinity gradients, the frequency and duration of flooding, soil texture, and the amount of organic matter, various vegetation structures and levels of habitat productivity may develop across different bioclimatic zones (Pennings and Callaway, 1992; Mucina et al., 2003; Mahdavi et al., 2017).

The formation of vegetation in ephemeral ecosystems is largely controlled by shallow groundwater levels, typically less than 1.0 m deep. A decrease in groundwater to 1.5–2.0 m sharply limits vegetation formation in ephemeral ecosystems and often indicates the emergence of other ecosystem types, depending on the prevailing soil mechanical composition or degree of soil salinity. Even a high level of salinity is not necessarily a critical limiting factor for initial plant colonization in ephemeral ecosystems, provided that groundwater levels remain very shallow. Under such conditions, typical ephemeral ecosystem representatives like *Salicornia europaea* and *Suaeda acuminata* can dominate. In these situations, species representative of various ecosystems and different life forms can become associated, often leading to temporary increases, or “spikes” in biodiversity indices.

These “Biodiversity spikes” represent a phenomenon where the precise direction of succession becomes difficult to determine. The landscape composition is so diverse and patchy that habitat suitability becomes highly labile, allowing for the opportunistic establishment of various plant species. In neo-ecosystems, where the integrity of distinct landscape patches and the extent of homogeneous areas change sharply, the probability of arrival and establishment for a wide array of plant species increases (Sloan et al., 2016).

During succession, changes in ecological mechanisms related to biodiversity can occur, which turn contribute to ecosystem functioning (Poorter et al., 2024). According to Lohbeck et al., (2020), many ecosystem processes are determined more by the quantity of vegetation (biomass) than by its qualitative aspects (e.g., species richness alone), as biomass is a primary factor in ecosystem energy exchange. Our results confirm the importance of both diversity and phytomass along the observed soil gradients (Table 2), indicating that both are key factors in the formation and characterization of the desiccated part of the Aral Sea ecosystem types.

As seen in Fig. 4, starting from approximately the sixth year of colonization, the biodiversity index changes sharply, peaking between the 12th and 15th years and remaining elevated until around the 22nd year. During this period, representatives from what will become distinct ecosystems can form a mixed species pool. The convergence or co-occurrence of various soil factor gradients in close proximity facilitates active soil colonization by diverse ecological groups of plants, forming varied vegetation assemblages across different incipient ecosystems. Annuals typical of ephemeral ecosystems, regardless of the physical clay content or soil salinity, can dominate in parts of neo-ecosystems where groundwater levels are below 1.0 m. Also prominent during this phase are species characteristic of wasteland ecosystems (e.g., *Kalidium capsicum*, *Halocnemum strobilaceum*, *Halostachys capsica*), riparian vegetation of remnant ecosystems (*Tamarix hispida*, *Tamarix laxa*, *Tamarix elongata*), and psammophilous vegetation of post-ecosystems (e.g., *Salsola paulsenii*, *Stipagrostis pennata*, *Eremosparton aphyllum*, *Astragalus villosissimus*, *Calligonum caput-medusae*) (Appendix A).

In neo-ecosystems, the landscape characteristics inherited from, or transitional towards, wasteland ecosystems and remnant ecosystems play a significant role. These ecosystems themselves can vary in their duration of existence, typically from 8 to 20 years. wasteland ecosystems represent an ecosystem stage where shallow groundwater levels (below 1.0 m) lose their primary significance as a distinguishing factor. Instead, the crucial factors become heavy soils (high mechanical composition, with physical clay content exceeding 45 %) and high salinity (above 7.0 %). This is often the most conservative stage of the halosere, where perennial super-halophytes, such as *Kalidium capsicum* and *Halocnemum strobilaceum* begin to colonize the desiccated part of the Aral Sea (Appendix A). The soil of wasteland ecosystems often represents automorphic solonchaks (Stulina and Sektimenko, 2004), and their formation process may eventually lead to the development of desert-sandy soils. In wasteland ecosystems, perennial super-halophytes play a vital dust-trapping role, contributing to the accumulation of sand particles. The duration of WE existence can be unpredictable or predictable (up to around 20 years), depending on the extent of their seed bank dispersal in newly exposed areas and the rate of sand particles accumulation in the soil, which ultimately steers succession towards neo-ecosystems and then post-ecosystems.

Despite the phenomenon of “biodiversity spikes” in neo-ecosystems, the process of progressive succession, particularly within chronosequences on developing sandy dunes, continues. This progression involves changes in the physicochemical composition of soils, moving them towards a more zonal type (Warming, 1895). After approximately 20 years of colonization within the broader neo-ecosystems phase, plant species assemblages tend to form in a more predictable manner. Future dominant species, despite potentially low stability in these dynamic environments, become characterized by more reliable regeneration patterns, reflecting the ongoing process towards a subsequent major successional stage—the psammosere.

The final stage of plant colonization, occurring in post-ecosystems, resulting in the formation of true psammophilous vegetation. The development of post-ecosystem vegetation is primarily associated with sandy soils (MC4) and groundwater levels within 2.0–3.0 m range, and especially at depths below 3.0 m. Post-ecosystems are characterized by stability or relative stability and include dominant species typical of the Kyzylkum desert—true psammophytes, and glycophytes—such as *Carex physodes*, *Astragalus villosissimus*, *Calligonum microcarpum*, *Ephedra strobilacea*, and *Haloxylon persicum* (Appendix A).

Currently, post-ecosystems with stable vegetation are well-represented in the EGD1 area, where the vegetation of the North-Western Kyzylkum is fully reflected as an integral part of the South Turanian floristic province (Rachkovskaya, 2003). At present, the main expanse of the drained Aral Sea bed lies in an area where the formation of desert-sandy soils is actively taking place (Vukhrer and Brekle, 2003; Toderich and Adilov, 2024). Therefore, despite the initial predominance of species colonizing from various eco-regions, such as the Amudarya Delta and the Ustyurt Plateau, at different early to intermediate stages of succession, the colonization process in the desiccated part of the Aral Sea area ultimately culminates in the establishment and dominance of vegetation characteristic of the North-Western Kyzylkum, driven by ongoing aeolian sand deposition and dune formation.

Despite the prolonged duration of the final successional stages, soil mechanical composition emerged as the most influential factor determining both the rate of plant colonization and the completion of these stages. This finding is supported by the results of the predictive model developed using a Gradient Boosting algorithm. As the proportion of sandy fractions increases and dunes form—reaching heights of 2–3 m—the influence of groundwater level and salinity gradually diminishes. Their effect tends to persist primarily in interdunal depressions, where the specific hydrosaline regime can favor the continued existence of plant species from different, earlier-stage ecosystems. These microsites can serve as localized hotspots of biodiversity, particularly evident between the 12th to 22nd years of colonization, enabling the coexistence of species with varying ecological requirements and functional strategies.

Thus, in the hyper-arid and heavily transformed environment of the desiccated Aral Sea bed—where large areas are initially dominated by solonchaks and sandy-clay substrates—the mechanical properties of the soil constitute the primary limiting factor. These properties largely determine site suitability for plant establishment and the potential for sustainable development of phytocoenoses (plant communities). Accordingly, soil texture should be considered a priority variable in planning vegetation restoration strategies and long-term ecosystem management for the Aralkum region.

These observations indicate that transitions between ecosystem types within the desiccated part of the Aral Sea do not consistently follow a strictly linear trajectory. Instead, they often reflect a complex pattern of regressive, cyclical, or fragmented succession. This is particularly evident in areas characterized by unstable groundwater dynamics, fluctuating salinity gradients, or significant aeolian sand redistribution. In such zones, succession frequently follows pulsed or reversible dynamics, where temporarily stabilized communities may degrade or revert, leading to co-occurrence of early- and late-successional species (Walker & del Moral, 2003; Rietkerk et al., 2002).

Of special significance are the so-called landscape interference zones. In these areas, overlapping features of multiple ecotopes create intricate habitat mosaics that obscure the predictability of successional direction. These heterogeneous zones frequently host a coexisting mix of ephemeral, halophytic, and psammophytic species, thereby complicating the delineation of clear successional stages based on classical models (Luken, 1990; Vítovcová et al., 2021). Moreover, these interference zones are often particularly susceptible to external disturbances such as episodic heavy precipitation, pronounced groundwater fluctuations, or grazing pressure, all of which contribute to deviations from expected, more linear successional pathways (D’Odorico et al., 2019; Vítovcová et al., 2021).

Therefore, vegetation succession across the dried Aral Sea bed should not be interpreted as a purely deterministic or unidirectional process. Rather, it is better understood as a dynamic system of self-organization that simultaneously exhibits elements of progressive, regressive, and cyclical development. This highlights the importance of integrating not only chronosequential approaches but also landscape-scale and spatially explicit analyses. Such multi-faceted approaches are necessary to capture the recursive, overlapping, and often non-linear trajectories of vegetation assembly in these challenging arid saline ecosystems.

4.7. Predictive indicators of ecosystem development

Traditionally, the study of vegetation succession has often focused primarily on the process of species replacement over time (Pickett et al., 1987). However, differences in the performance and ecological strategies of various species drive vegetation succession across multiple organizational levels, which in turn leads to significant changes in overall ecosystem structure and function (Poorter et al., 2024).

In the context of a recovering or developing ecosystem such as the desiccated part of the Aral Sea, the formation of stable vegetation, especially the mature psammophytic communities of post-ecosystems, is of primary interest for long-term ecological restoration. According to our results (Fig. 5), the spatial pattern of PE formation appears to occur from east to west, as well as bidirectionally from south to north and from north to south across the landscape. During the earlier stages leading up to this, plant colonization within wasteland ecosystems can be dominant in certain areas. The precise duration of these wasteland ecosystem stages can be uncertain, particularly due to the formation of extensive saline crusts and masses following significant declines in local water levels observed since approximately 2016. To accelerate the transition towards and emergence of neo-ecosystems and subsequently post-ecosystems, active measures for sand accumulation and reforestation are being implemented. These include the sowing of seeds and the planting of seedlings of super-halophytes (such as *Kalidium capsicum*, *Halocnemum strobilaceum*) directly into areas classified as wasteland ecosystems (Bakirov et al., 2020, 2022).

The predicted that remnant ecosystems will become a predominant ecosystem type in certain parts of the desiccated part of the Aral Sea is particularly noteworthy. As previously mentioned, remnant ecosystems often initially represent relatively small patches within the broader neo-ecosystems, typically populated by a mix of herbaceous and shrubby tugai vegetation. The anticipated increase in the total area occupied by remnant ecosystems is largely associated with extensive design and survey work aimed at creating artificial reservoirs and water bodies, around which tugai flora is expected to form or expand. As a result of water conservation policies and efforts to retain existing water resources, various dams, water outlets, and spillway hydraulic structures have been constructed. This has led to the creation of numerous artificial lakes (e,g., Kungard, Sudochye, Mezhdurechye, Karadjar, Toguztur, Daukempyr, Kazakhdarya, Dautkol, Atrek, Zhylturbas), covering a combined total area of 99,000 ha (Kurbanbaev et al., 2010; United Nations Environment Programme, 2011). These developments are, in turn, resulting in the emergence and spread of, at least initially, potentially unstable or rapidly changing tugai flora in these newly created or modified riparian zones.

5. Conclusion

This 35-year Aral Sea study identified five ecosystem types from vegetation colonisation on its desiccated bed. Crucially, soil mechanical composition, more than salinity, groundwater, or biodiversity, dictates vegetation dynamics, a finding confirmed by Gradient Boosting and SHAP analysis. Sandy and moderately textured soils with intermediate groundwater fostered greater species richness and phytomass; conversely, heavy, saline soils supported low biodiversity and mono-dominant halophytes. Succession is non-linear and mosaic-like, with regressive and cyclical pathways. Low floristic similarity (Sørensen values) between ecosystem types indicates spatial heterogeneity. Canonical Correspondence Analysis linked early (ephemeral) and late (post-) successional stages to specific edaphic gradients, while intermediate (neo-, remnant) types showed more environmental variability. Projections (1980–2030) suggest expanding neo- and post-ecosystems, declining ephemeral ecosystems, and increasing remnant ecosystems, partly via artificial water bodies fostering tugai vegetation. Despite extreme aridity and salinity, stable vegetation forms where critical soil and water availability thresholds are met. This research significantly advances understanding of saline ecosystem succession, offering a scientific basis for restoration and sustainable land management in the Aralkum Desert and similar arid regions. However, generalisation to other arid environments warrants caution and further comparative studies.

CRediT authorship contribution statement

Bekhzod Adilov: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Khabibullo Shomurodov:** Writing – review & editing, Writing – original draft, Project administration, Conceptualization. **Tashkhanum Rakhimova:** Writing – original draft, Investigation. **Azamat Sultamuratov:** Writing – original draft, Investigation. **Farrukh Polvonov:** Writing – original draft, Investigation. **Gulnora Begjanova:** Writing – original draft, Investigation. **Zafarjon Jabbarov:** Writing – original draft, Investigation. **Lei Wang:** Writing – review & editing, Writing – original draft. **Zhenyong Zhao:** Writing – review & editing, Funding acquisition.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113789.

Data availability

Data will be made available on request.

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