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Latitudinal transformation of tugai forests in the Lower Amu Darya River reflects the degradation of floodplain vegetation

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Abstract

Tugai ecosystems, including poplar forests, are among the most threatened under conditions of global environmental change. Based on the analysis of 312 geobotanical descriptions representing the Tugai forests of the Lower Amu Darya River, the current state of vegetation was evaluated across four segments of the river valley. In the continental part of the river delta, there is an intensification of salinization processes and degradation of poplar communities. Due to the absence of hydraulic structures in the upper part of the study area, vegetation changes are minimal; here, valley ecosystems remain under natural floodplain conditions, and plant communities exhibit low levels of transformation. Vegetation in the two middle sections, located in areas with regulated water flow, shows significantly less degradation compared to the delta. However, a negative trend in the dynamics of Tugai forests is predicted for these areas, associated with the progressive aridization of the climate. The transformation is reflected in the floristic composition of the vegetation across different valley segments. The highest number of differentiating species is observed in the delta part of the Amu Darya River, which is explained by the

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formation of halophytic shrub and herbaceous communities, as well as ruderal assemblages of annual plants that replace forest communities. The southern section is characterized by a distinct species composition, where indigenous and long-persisting poplar forests dominate the valley complexes. An analysis of species constancy in Tugai communities indicates a consistent increase in vegetation heterogeneity toward the Amu Darya River delta.

Keywords
Tugai forests, Amu Darya River, floodplain ecosystem, riparian forests, salinization, vegetation degradation, aridization

Introduction

Arid Central Asia faces a variety of environmental and socioeconomic challenges. The Amu Darya River, once a lifeline that sustains rich riparian ecosystems and traditional livelihoods, now flows only in fragments downstream, its waters diverted largely for agriculture. As a result, the iconic Tugai forests, dominated by *Populus euphratica* and associated shrubs, are undergoing widespread degradation and loss. These ecosystems do not just support biodiversity; they provide essential services including flood regulation, soil stabilization, fuelwood, feed, and medicinal plants for millions of people living in one of the driest regions.

The intensification of desertification processes in arid and semi-arid regions of Asia is a major driver of negative ecosystem transformations (Orsenigo et al. 2022, 2025, 2026; Fenu et al. 2022, 2023, 2024, 2025; Beshko et al. 2025; Khabibullaev et al. 2026). Alongside the progressive aridization of the climate, the escalating anthropogenic pressure manifested primarily in overgrazing and extensive regulation of river flow has led to severe degradation of vegetation within major river valleys. As a critical hydrological lifeline in Central Asia, the Amu Darya River spans approximately 2,540 km, originating in the Pamir-Alai mountains and traversing the vast Kyzylkum and Karakum deserts before flowing through the Aral-Caspian lowlands.

However, the water resources are under immense stress. The water from its main tributaries is largely diverted for irrigation to sustain the densely populated basin of around 25 million people (Asarin et al. 2010; Yildiz 2015; Dukhovny et al. 2018; Xi et al. 2019). The agricultural economies of Turkmenistan and Uzbekistan rely heavily on this irrigation for cotton and rice production. Consequently, massive water extraction – nearly 697,000 acres currently irrigated in the lower reaches alone (Adenbaev 2014) has drastically reduced downstream environmental flows.

A vital ecological component of the Amu Darya valley is the Tugai floodplain ecosystems dominated by riparian woody and shrub vegetation (Korolyuk et al. 2024, 2025, 2026). Driven by hydrological regulation and climate change, the Lower Amu Darya has experienced a drastic ecological regime change, resulting in fundamental environmental transformations and severe degradation of Tugai vegetation. Historical data indicate that by 1990, the area of Tugai forests in the lower reaches

had already declined by approximately 40% (Kuzmina and Treshkin 2012), accompanied by catastrophic reductions in reed beds and Glycyrrhiza glabra stands. Of the 600,000 hectares of reedbeds recorded in the mid-20th century, only about 60,000 hectares remained by the early 2000s (Gerasimov et al. 1983; Bakhiev et al. 2012; Sariabaeva et al. 2025). Consequently, these vegetation complexes are losing their essential landscape stabilizing and hydrological buffering functions, accelerating desertification in the valley and adjacent arid lands.

Although numerous studies have documented this ecological collapse within the Amu Darya delta (Treshkin 2001; Kuzmina and Treshkin 2001; Kuzmina and Treshkin 2012; Aimbetov et al. 2017; Zan et al. 2022), transformations in the middle reaches remain less pronounced and understudied. Previous delta-focused research has not addressed broader valley-wide gradients, leaving a significant gap in our understanding of how vegetation transitions from the middle to the lower reaches. To date, no formalized comparative analysis has been performed in the different latitudinal segments of the valley within Uzbekistan.

Addressing this knowledge gap, we hypothesize a distinct latitudinal trend in vegetation degradation moving from south to north, that is, from the less disturbed upper/middle reaches toward the delta. Specifically, we postulate that proximity to the delta correlates with: (1) intensified salinization and a functional shift toward halophytic dominance; (2) reduced constancy of core Tugai forest species; and (3) increased vegetation heterogeneity (beta diversity) driven by the encroachment of ruderal and desert plants. The primary objective of this study is to analyze spatial patterns in the floristic composition and structural transformation of Tugai plant communities along this latitudinal degradation gradient. By comparing degraded and relatively undisturbed communities, our objective is to identify specific indicators of structural change, providing a vital scientific foundation for developing targeted monitoring programs and ecological restoration strategies in arid riparian zones.

Materials and methods

Study area characteristics

The Lower Amu Darya River Basin lies between western Uzbekistan and northern Turkmenistan, bordered to the north by remnants of the Aral Sea (currently represented by Lake Sudochie in the northwest and Lake Zhyltirbas in the northeast). The study area covers approximately 31,000 km², the majority of which comprises the river delta. The plains of the delta are composed of Cretaceous, Paleogene, and Neogene sandstones, clays, and marls. Pliocene sandstones, subjected to weathering and aeolian processes, from the Kyzylkum and Zaunduz Karakum deserts. Due to harsh climatic conditions, soils exhibit varying degrees of salinity (Rachkovskaya and Khramtsov 2003; Dukhovny 2018; Zan et al. 2022).

Located deep within the Eurasian continent, far from oceanic influences, the Amu Darya basin experiences a typically continental desert climate with high thermal amplitudes. Annual precipitation ranges below 200 mm, dropping below 100 mm in certain lower reaches, while potential evaporation reaches approximately 1,800 mm annually. The near-total absence of rainfall during peak summer induces seasonal biological dormancy in vegetation, the mean annual temperatures range from 10.6 °C to 13.4 °C, the sum of active temperatures (total annual positive temperatures) is approximately 5,000–5,500 °C, reaching up to 6,000 °C in the extreme south and adjacent desert areas (White et al. 2014; Dukhovny 2018). Primary economic activities include livestock farming and agriculture, with major crops such as cotton, wheat, rice, maize, and alfalfa (Zan et al. 2022).

Field data collection and geobotanical analysis

Based on fieldwork conducted in 2022 and 2023, we compile a dataset of 312 geobotanical surveys that represent the current phytocoenotic diversity of the Tugai vegetation in the Lower Amu Darya. Data were managed using the database 'Plant Communities of Tugai' within the IBIS 7.2 software package (Zverev 2007). Vegetation surveys were conducted on standard 25 × 25 m plots (Lavrenko and Korchagina 1964), a size appropriate for woody communities. High resolution satellite imagery was used to identify intact Tugai forests, and the number of survey plots established within each patch was proportional to its size. Plant taxonomy and nomenclature followed Plants of the World Online (POWO 2024).

The fieldwork focused on key sites containing large and well-preserved fragments of natural Tugai vegetation, strictly avoiding areas affected by direct agricultural impacts such as logging, plowing, or artificial irrigation. The sample plots were strategically placed to capture the complete typological diversity and spatial distribution of the plant communities on an approximately 700-kilometer stretch of the lower reaches and delta. To analyze latitudinal differentiation in forest communities, the study region was divided into four roughly equal segments (Fig. 1). Geobotanical surveys were grouped accordingly for each segment.

These segment-specific datasets were synthesized into summary descriptions, comprising aggregated species lists, occurrence frequencies, and cover-abundance values. In the field, the cover of species was recorded using the Braun-Blanquet scale, later converted to percentage estimates; mean projective cover was calculated as the arithmetic mean across all plots per segment.

Constancy classes followed standard phytosociological practices, grouping species into five classes based on their frequency of occurrence in the plots (I: <20%; II: 20–40%; III: 41–60%; IV: 61–80%; V: 81–100%).

Differentiating species were identified on inter-segment comparisons. Following European botanical approaches (Dengler et al. 2005; Michl et al. 2010), a species was classified as differentiating if its frequency in one or more segments was at least twice that in others. This method relies on absolute thresholds rather than formal statistical tests.

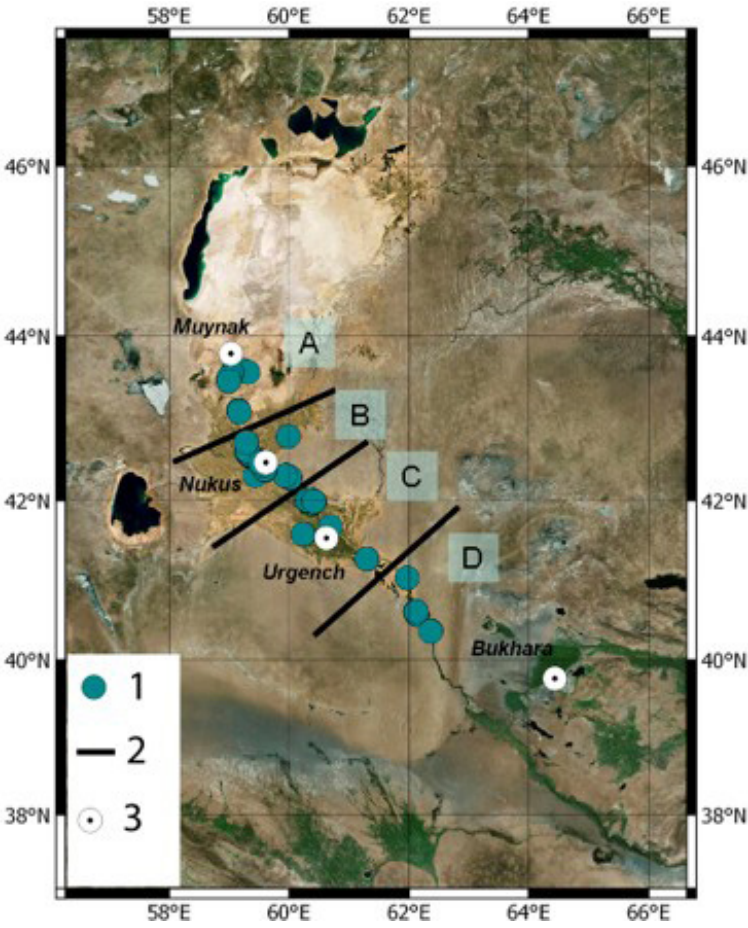


Figure 1. The study area. **1** – localities of geobotanical descriptions, **2** – river valley segments, 3 – cities (Generated from QGIS 3.30).

Results

A comparative analysis revealed distinct latitudinal patterns. Segment A represents the continental delta, where negative processes of ecosystem degradation, driven by global desertification and climate aridization, are most pronounced. These manifest themselves as reduced river water availability, increased soil salinization, and severe degradation of tugai vegetation.

Segment D, located in the upper valley within Uzbekistan, remains largely unregulated hydraulically. Here, natural flood regimes persist, supporting spontaneous regeneration of Tugai forests. These ecosystems function with minimal anthropogenic disruption and exhibit very low levels of structural transformation. Intact forests and shrublands, such as those in the Kyzylkum Nature Reserve group, serve as essential reference sites for natural Tugai vegetation (Fig. 2).



Figure 2. Well-preserved tree forest (tugai) in the Kyzylkum Nature Reserve located on the right bank of the Amu Darya River (Photo by B. Khabibullaev, 2022).

Segments B and C occupy intermediate positions. Both have undergone long-term flow regulation following the construction of the Tuyamuyun Hydroelectric Complex in the 20th century. Although the degradation of the Tugai ecosystems in these middle segments is currently less severe than in the delta, the ongoing aridization of the climate threatens similar successional trends, particularly in segment B. Segment C harbors some of the largest remaining poplar forest stands in Uzbekistan, protected within the Lower Amu Darya State Biosphere Reserve (Fig. 3).

The floral composition reflects these environmental gradients (Table 1). Only 12 species occur ubiquitously across all segments, primarily dominant woody taxa: *Populus euphratica*, *Populus pruinosa*, *Tamarix ramosissima*, *Caragana halodendron*, *Elaeagnus angustifolia*, and *Halostachys caspica*.

A larger group consists of 17 differentiating species. The most pronounced differences occur between the extremes (segments A and D). The delta (Segment A) hosts the highest number (10). A clear latitudinal shift in dominance is evident: in Segments D and C, both poplar species co-dominate the canopy, but moving northward, *P. pruinosa* declines markedly due to salt intolerance, leaving *P. euphratica* as the sole dominant.

Simultaneously, halotolerant species such as *Caragana halodendron* and *Aeluropus littoralis* increase significantly in the delta, dominating shrub and herbaceous

layers, respectively. Segment D shows high floristic uniqueness; five of its six differentiating species are exclusive to it, reflecting the integrity maintained under natural flow regimes.



Figure 3. Poplar forests protected within the Lower Amu Darya Biosphere Reserve (Photo by B. Khabibullaev, 2022).

Table 1. The species constancies in river valley segments

Species/parameter	Segment A	Segment B	Segment C	Segment D
n (Number of vegetation relevés)	47	127	103	35
Differential species				
Acroptilon repens	19	2	-	-
Sphaerophysa salsula	15	3	-	-
Descurainia sophia	13	2	2	-
Zygophyllum oxianum	56	45	14	6
Suaeda altissima	51	44	9	6
Leymus multicaulis	22	36	6	3
Caroxylon scleranthum sclerantha	13	8	-	-
Salsola tragus	10	14	3	3
Tamarix hispida	30	15	26	3
Karelinia caspia	17	15	13	6

Species/parameter	Segment A	Segment B	Segment C	Segment D
Lycium ruthenicum	7	4	14	-
Asparagus brachyphyllus	-	-	31	17
Tripidium ravennae	-	-	7	15
Calamagrostis pseudophragmites	11	4	8	52
Apocynum venetum subsp. *lancifolium*	-	8	8	55
Salix songarica	-	-	-	17
Cistanche mongolica	-	-	1	12
Common species				
Populus euphratica	81	78	65	77
Tamarix ramosissima	77	64	71	89
Phragmites australis	53	52	52	83
Glycyrrhiza glabra	45	66	32	63
Populus pruinosa	22	42	63	63
Cynanchum sibiricum	51			
Caragana halodendron	56	40	58	17
Aeluropus littoralis	41	54	61	15
Elaeagnus angustifolia	32	45	21	60
Alhagi pseudalhagi	32	35	48	18
Halostachys caspica	11	25	32	32
Limonium otolepis	26	15	21	15

Note: Values represent species constancy (%). Shaded cells indicate the river valley segment where the species is classified as differential (characteristic). Unshaded cells in the same row indicate the constancy of that species in the remaining segments. n = number of vegetation relevés.

The exceptionally high number of differentiating species in segment A is driven by the severe fragmentation and transformation of the baseline forest and shrub communities, which historically possessed a unified floristic composition. These intact communities are increasingly being replaced by encroaching nonforest vegetation types, primarily halophytic shrub-herbaceous communities and ruderal annual assemblages that rapidly colonize degraded woody remnants. A primary driver of this shift is widespread salinization of the soil. Intensive agricultural irrigation exacerbates the evaporative regime, causing salts to accumulate on the upper soil horizons. At the same time, the cessation of natural seasonal floods (due to upstream flow regulation) prevents vital leaching of readily soluble salts from the floodplain. Furthermore, localized areas of active sand movement are emerging and colonized by psammophytes typical of sandy deserts (eg, *Caroxylon scleranthum*). Consequently, the degraded Tugai flora becomes artificially 'enriched' with halophytes and of halotolerant species (*Acroptilon repens*, *Karelinia caspia*, *Sphaerophysa*

salsula, *Suaeda altissima*, *Tamarix hispida*, and *Zygophyllum oxianum*), psammophytes (*Caroxylon scleranthum*) and ruderal therophytes (*Descurainia sophia*, *Salsola tragus*). Canopy destruction creates large gaps with sparse herbaceous cover, facilitating the rapid expansion of aggressive long rhizome species such as *Acroptilon repens*, *Leymus multicaulis*, and *Sphaerophysa salsula*. These interacting degradation factors result in a seemingly paradoxical phenomenon: the overall richness of species increases within the valley landscape as the native forest vegetation becomes increasingly fragmented and structurally degraded.

Therefore, the richness of species alone cannot serve as a reliable metric to assess the conservation value of Tugai communities. A more ecologically meaningful criterion is the spatial extent and structural integrity of the remaining forests and shrubland stands; large, unfragmented tracts undoubtedly represent the highest conservation priorities.

The analysis of species constancy across the four segments reveals a clear latitudinal increase in vegetation heterogeneity toward the delta. A traditional phytosociological measure of community heterogeneity is the ratio of species with high constancy classes to those with low constancy. This ratio is highest in segment D (Table 2), indicating a high degree of homogeneity and stability. In stark contrast, the delta (Segment A) exhibits the lowest ratio, and consequently the highest spatial heterogeneity

Table 2. Species diversity and richness metrics of vegetation across river valley segments

Parameter	Segment A	Segment B	Segment C	Segment D
n (Number of vegetation relevés)	47	127	103	35
Total species richness, S	54	67	65	31
Number of species in constancy classes IV–V	2	3	4	6
Number of species in constancy classes II–III	15	12	9	4
Number of species in constancy classes II–V	17	15	13	10
Ratio of species in constancy classes IV–V to II–III	0.1	0.3	0.4	1.5
Margalef richness index	14.5	17.8	15.7	6.8
Odum diversity index	14.8	18.0	16.0	7.0
Menhinick's richness index	7.5	8.9	8.5	3.4
Chao's diversity index (Chao1)	1521.0	622.5	821.3	284.0

This trend is further corroborated by the size of the constant floristic core (defined here using a 20% constancy threshold). The use of this threshold is particularly robust when the number of geobotanical surveys varies substantially between sites; in this study, the number of surveys between Segments B and D differed by more

than threefold. While species richness is heavily influenced by sample size, the size of the floristic core remains remarkably stable, typically stabilizing once the sample size reaches several dozen geobotanical surveys. Our data demonstrate an almost linear decline in this metric and a corresponding decrease in overall vegetation heterogeneity from Segment A (the delta) to Segment D (the upper reaches). A parallel trend is observed in various biodiversity indices, all of which record their lowest values in segment D, where the Amu Darya's flow remains natural and unregulated.

Discussion

The unexpectedly high number of differentiating species recorded in segment A does not indicate greater ecological value; it is a symptom of degradation. Fragmentation and transformation of the formerly unified low-diversity forest and shrub communities has opened the canopy to encroachment by halophytic shrub-herbaceous vegetation and ruderal annuals. Two processes appear to be responsible. First, intensive irrigation increases evaporative losses and promotes salt accumulation in the upper soil horizons, while loss of natural seasonal flooding, a consequence of upstream flow regulation, has removed the periodic leaching that once flushed these readily soluble salts from the floodplain. Second, localized sand mobilization has created new habitats for psammophytes such as *Caroxylon scleranthum*. Together, these processes have allowed halotolerant species (*Acroptilon repens*, *Karelinia caspia, Sphaerophysa salsula*, *Suaeda altissima*, *Tamarix hispida*, and *Zygophyllum oxianum*), psammophytes, and ruderal therophytes (*Descurainia sophia*, *Salsola tragus*) to establish in the gaps left by canopy loss. Once the shrub layer thins, aggressive long-rhizome species, notably *Acroptilon repens*, *Leymus multicaulis*, and *Sphaerophysa salsula*, spread rapidly across newly opened ground. The result is more species but a degraded forest, which is why species richness alone is a poor proxy of conservation value in Tugai communities: the extent and structural integrity of the remaining unfragmented stands is the more informative criterion, and these are the stands that should be prioritized for protection.

The pattern along the valley reflects two forces that are compounding each other rather than acting in isolation. Progressive aridization reduces the total discharge of the Amu Darya across the whole basin, but the ecological consequences of this decline are far from uniform: they intensify sharply toward the delta, where flow regulation and intensive irrigation withdraw nearly the entire river volume before it reaches the lowermost reaches. There, seasonal flooding has effectively stopped, and the resulting hydrological deficit accelerates soil salinization and drives the successional shift toward the salt-tolerant vegetation described above.

Comparable dynamics are documented in other dryland river systems. In Australia's Murray–Darling Basin, reduced flood frequency and rising groundwater salinity have caused widespread dieback of river red gum (*Eucalyptus camaldulensis*) (Mac Nally et al. 2011), closely paralleling the pattern observed in the Amu Darya

delta. Along the Colorado River in the Southwest United States, dam construction, prolonged drought, and the spread of invasive saltcedar (*Tamarix ramosissima*) have displaced native cottonwood (*Populus fremontii*) and willow (*Salix* spp.) galleries in much the same way (Busch and Smith 1995), echoing the shift toward *Tamarix* dominance documented here in Segment A.

This pattern is not unique to Amu Darya. Comparable "greening" has been reported across other degraded drylands, from the Aral Sea basin to California's Salton Sea, where rising apparent richness can mask underlying ecosystem disintegration rather than signal recovery. In this light, the Amu Darya Tugai is not only a regional conservation concern, but an illustrative case of how water scarcity, irrigation management and climate change jointly erode the ecosystem services that floodplain forests provide, a convergence that argues for more comprehensive water-ecosystem governance across dryland river basins.

Conclusion

The synergistic effects of progressive climate aridization and increasing anthropogenic pressure, primarily river flow regulation and intensive irrigation, are the main drivers of severe desertification within the ecosystems of the Amu Darya River valley in Uzbekistan. Consequently, the lower reaches of the river, particularly the delta, have already undergone catastrophic and likely irreversible ecological regime changes. Furthermore, as regional hydrological deficits persist, the imminent threat of complete degradation now extends to the currently intact Tugai complexes in the middle and upper sections of the valley. To effectively track and potentially mitigate these ongoing transformations, it is imperative to establish a dedicated long-term monitoring system for these riparian ecosystems. Because our findings demonstrate that vegetation degradation follows a distinct spatial and intensity gradient from south to north, we recommend structuring this monitoring effort as a continuous sublatitudinal transect. This transect-based network must integrate hydrological monitoring and floristic diversity assessments. The most critical candidates for these permanent observation plots are the remaining large and unfragmented tracts of natural Tugai forests, which will serve as vital reference baselines for evaluating future ecosystem dynamics. Specifically, we strongly advocate for the immediate establishment of a coordinated network of permanent monitoring sites anchored within the protected territories of the Kyzylkum Nature Reserve, the Lower Amu Darya State Biosphere Reserve, and the Khujayli Forest Tract.

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