








ORIGINAL PAPER

Vascular plant diversity in the former Kakhovka Reservoir area: two years after the dam breach

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ABSTRACT

Question: What is the composition of vascular plants in the territory of the former Kakhovka Reservoir in the early stages of its overgrowth, and what are the trends for the further development of this ecosystem?

Location: Area of the former Kakhovka Reservoir, Kherson, Zaporizhzhia, Dnipropetrovsk oblasts, Ukraine.

Methods: The study involved field surveys conducted during seven research trips between June 2023 and October 2025. Structural comparative analysis and phytoindicative assessment were performed to evaluate floristic changes. Data processing, including Pearson's criterion and Kruskal–Wallis tests, was conducted in the R software environment.

Nomenclature: Vascular plants species – POWO, families, traits – FloraVeg.EU

Results: The vascular plant richness showed a rapid exponential increase, rising from 11 species in June 2023 to 343 species by October 2025. The taxonomic structure stabilized quickly, with *Compositae*, *Poaceae*, and *Brassicaceae* becoming the dominant families already in the first year. A significant shift in life forms and dispersal mode was observed: while the initial stages were dominated by annuals and anemochorous species (e.g., *Salix* spp., *Populus nigra*), subsequent years saw an increase in perennial herbs and species with zoochorous and autochorous dispersal. Phytoindicative analysis revealed a gradual transition from hygrophytic communities to mesophytic ones as the substrate stabilized, although willow-poplar forests continue to form the structural backbone of the new landscape. Notably, the proportion of alien species (neophytes) peaked at the very first period of observations and then declined, suggesting high resilience of the emerging native communities. The presence of rare species, such as *Carex secalina*, further underscores the rapid formation of ecosystems with high conservation value.

Conclusions: The studied flora is undergoing rapid development, increasingly resembling natural floodplain ecosystems of the Lower Dnieper. The main structural changes occurred within the first three months after the dam breach, followed by a period of stabilization in the proportions of major plant groups.

KEYWORDS

biodiversity, recovery, floodplain ecosystems, functional traits, phytoindication, succession, Ukraine, vascular plants

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INTRODUCTION

The destruction of the Kakhovka Reservoir dam on June 6, 2023, was one of the most significant acts of ecocide committed by Russian troops during the current Russian-Ukrainian war. It resulted in severe environmental and humanitarian consequences in the region. Populations of many rare plant and animal species, whose range was limited to the Lower Dnieper, suffered significant losses within the flooded area, the real extent of which will only become clear when the territory is de-occupied and becomes accessible for research by Ukrainian scientists. The northwestern part of the Black Sea also underwent significant changes as a result of the influx of large volumes of fresh water, which accumulated significant amounts of pollutants and materials from flooded cities, villages, and fields (Shumilova *et al.* 2025). As for the reservoir itself, after the dam was blown up, its bed quickly became exposed. Immediately, many predictions about the future of this territory appeared within expert circles. In particular, it was predicted that desertification would occur, and it was assumed that this territory could become a source of dust storms and phytoinvasions (e.g. Naddaf 2023). However, none of this happened. Soon after, the former bed began to recover its natural vegetation and habitats, and research into this process was initiated almost simultaneously. The results of this research have already been published in a number of publications (Didukh *et al.* 2024, Vasylyuk *et al.* 2024, 2025a, b, Kuzemko *et al.* 2025, Lisovets *et al.* 2025a, Pichura *et al.* 2025, Tutova *et al.* 2025).

Most studies focus on restoration processes at the level of habitat types or natural ecosystems. The primary types identified include floodplain willow-poplar forests, marsh vegetation along reservoir banks and watercourses, and silty, sandy, or shell deposits with sparse vegetation (Kuzemko *et al.* 2025). At the same time, in the two years since the Kakhovka Hydroelectric Power Plant dam was blown up, continuous monitoring has been conducted in this area, not only at the level of vegetation and habitats, but also at the level of flora. The species richness on the exposed bed of the former reservoir continues to rise rapidly, with its composition reflecting the unique ecological processes occurring within this area. The sudden disappearance of a 70-year-old reservoir and the subsequent spontaneous revegetation of such an immense territory represent unprecedented ecological phenomena. The characteristics of the floristic composition of this territory and changes in the proportion of different plant groups over time can help predict scenarios and trends for the further plant cover development. This study aims to document the vascular plant diversity during the early stages of revegetation in the former reservoir area, provide a comparative structural analysis of the forming flora, and determine the key vectors of its future ecological development.

MATERIAL AND METHODS

The boundaries of the study area were determined by the waterline of the former reservoir. Thus, the floristic list included all species recorded in the area that was under water until June 6, 2023, and became exposed after the Kakhovka dam was blown up by Russian troops. The materials for the study were collected during seven research trips (FIGURE 1), as well as through ongoing monitoring studies by some authors. The main localities for the data collection are the National Nature Park “Kamianska Sich” and the town of Novovorontsovka (Kherson oblast), the National Reserve “Khortytsia” (Zaporizhzhia city), the vicinity of the villages of Kanivske, Lysogirka, and Malokaterynivka (Zaporizhzhia oblast), and the villages of Mariinske and Hrushivka (Dnipropetrovsk oblast) (FIGURE 1).

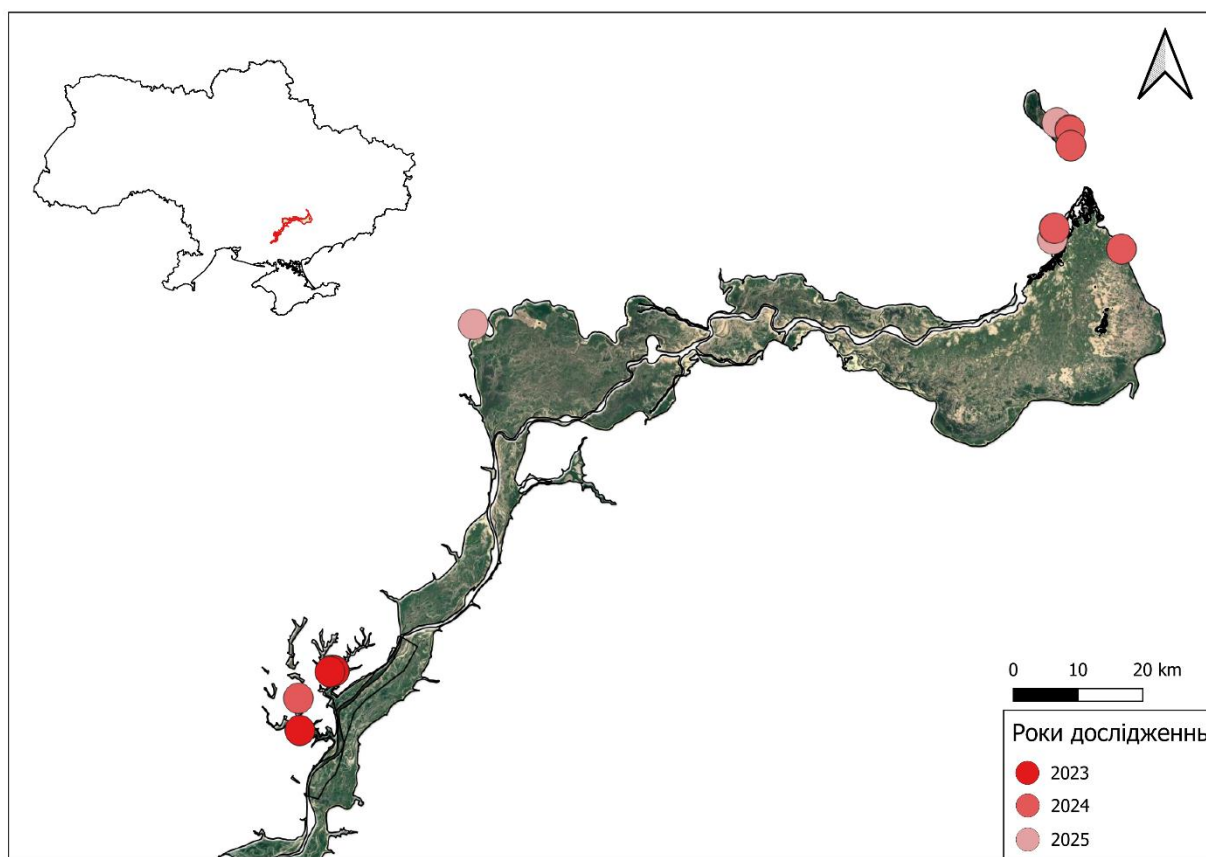


FIGURE 1. Map of surveyed localities. Country borders downloaded from OpenStreetMap (openstreetmap.org).

In addition, to supplement the list of species, we created and critically analyzed a project on the iNaturalist electronic resource <https://www.inaturalist.org/projects/flora-of-the-former-kakhovka-reservoir?tab=stats>, which mainly contains observations from the above-mentioned localities (FIGURE 2), most of which were made by the authors of this paper, as well as two datasets on GBIF representing data from the vicinity of Novovorontsovka village in the Kherson oblast (Chusova *et al.* 2024) and Khortytsia Island in Zaporizhzhia (Lisovets *et al.* 2025b). It is quite obvious that it is currently impossible to survey the entire exposed bed of the former reservoir for safety reasons, but the surveyed localities generally represent the territory quite fully, which makes it possible to understand the trends in changes in its floristic composition over time.

Information on the presence of vascular plant species in the former reservoir area was obtained during field studies and from all analyzed sources, compiled into an Excel table (Electronic appendix), and supplemented with data on their traits, in particular biomorphological characteristics – life span (Dřevojan *et al.* 2023a), life form (Dřevojan *et al.* 2023b), dispersal modes and distances (Lososová *et al.* 2023), origin in Europe (Axmanová 2022a), ecological groups (Axmanová 2022b, c, d, e) obtained from the electronic resource FloraVeg.EU (Chytrý *et al.* 2024), as well as the values of ecofactors according to the ecological scales of Y.P. Didukh (2011). Given the specific focus of this article, we introduced additional categories to the classification systems used.

For instance, we added “perennial woody” as a separate category to the life-span system. To enable statistical processing, traits assigned to multiple categories were simplified by selecting only the primary (first-listed) one. For instance, for a species characterized as both a “Phanerophyte” and a “Tree”, it was coded as a “Phanerophyte”, and for combined dispersal types like “Anemochory, Anthropochory”, only the former was included in the analysis.

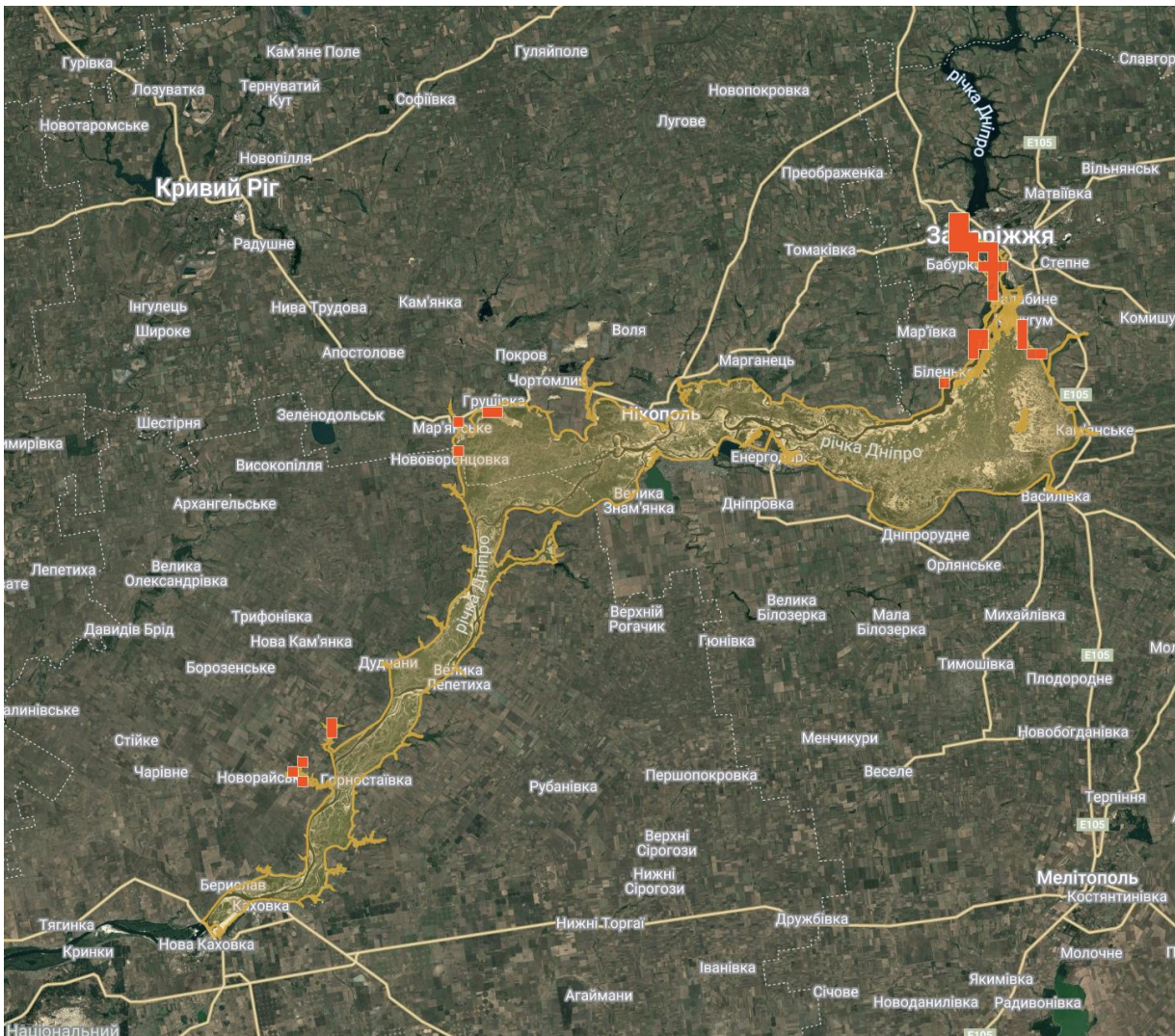


FIGURE 2. Location of observations collected as part of the Flora of the former Kakhovka Reservoir project on the iNaturalist electronic resource.

However, in the case of herbaceous and woody lianas, which could simultaneously belong to the phanerophytes, hemicryptophytes, or therophytes, we specifically noted their classification as lianas, since these life forms clearly reflect the characteristics of floodplain forests, which are the predominant ecosystem type on the former bed of the reservoir.

Data processing and diagram construction were performed in the R software environment (version 4.4.2). The visualization code was developed and optimized using the Gemini artificial intelligence model (Google 2025). The *readr* (Wickham et al. 2024b), *dplyr* (Wickham et al. 2024a), *tidyr* (Wickham & Girlich 2024), *ggplot2* (Wickham 2016), *ggalluvial* (Brunson & Read 2023), *scales* (Wickham & Seidel 2024), *stringr* (Wickham 2024), *patchwork* (Pedersen 2022), and *grid* (Murrell 2024) packages were used. The statistical significance of differences in flora structures between successive observation periods was assessed using Pearson's chi-squared test. To ensure accuracy when comparing small groups of categories, the p-value was calculated using the Monte Carlo simulation method with 2000 repetitions. To compare the changes of ecological indicators values on the Didukh's scales during the study period, the nonparametric Kruskal–Wallis test was used (Sokal & Rohlf 2012, Agresti 2013).

The QGIS3.38 software package (QGIS Development Team 2025) was used to generate the map. Satellite images from Google Earth were used as the cartographic base via the XYZ Tiles protocol in the WGS 84 / Pseudo-Mercator coordinate system (EPSG:3857).

The nomenclature of vascular plant species is given according to POWO (2025), and family affiliation is assigned according to FloraVeg.EU (Chytrý *et al.* 2024) both aligned with the APG IV system (The Angiosperm Phylogeny Group 2016). The exceptions are three species that we consider according to M.M. Fedoronchuk – *Cerastium pseudobulgaricum* (Fedoronchuk 2023) and *Salix × rubens* (Fedoronchuk 2025), or we reference them according to the journal's rules – *Taraxacum officinale* F.H.Wigg.

RESULTS

Taxonomic structure

Studies have shown that the number of species of vascular plants in the studied areas of the former Kakhovka Reservoir increased from 11 species in June 2023 to 343 species by October 2025. The number of genera increased from 11 to 212, and the number of families from 8 to 60 (FIGURE 3).

Analysis of the leading families (TABLE 1) revealed that while *Compositae*, *Poaceae*, and *Salicaceae* initially shared the first position in the summer of 2023 (with 2 species each), the taxonomic structure has since significantly shifted. Currently, the top positions are occupied by *Compositae* (55 species), *Poaceae* (45 species), and *Brassicaceae* (28 species). Notably, *Salicaceae*, which was a co-leader at the onset of flora formation, has now shifted to the 12th position, which it shares with *Malvaceae*. On the other hand, the contribution of species of the *Brassicaceae*, which was absent among the flora in the summer of 2023, is gradually increasing from ninth place in the autumn of 2023 to third place in the autumn of 2025.

During the formation of the flora, there was a gradual increase in the positions of the *Polygonaceae* and *Rosaceae* and a decrease in the positions of the *Fabaceae*, *Chenopodiaceae*, *Salicaceae*, *Malvaceae*, *Onagraceae*, *Ranunculaceae*, *Convolvulaceae*, *Juncaceae*, and *Ulmaceae*. The positions of the remaining families maintained stable during the two-year observations. Particularly interesting in this context is the stability of the position of the *Cyperaceae* family, the number of species of which increased from six in the autumn of 2023 to 19 in the autumn of 2025, while the position of this family increased only from fifth place in the autumn of 2023 to fourth during the following periods. We consider 18 genera, comprising 10 to 4 species, as leading genera of the studied flora (TABLE 2). The genus *Carex* occupies the first position, the second is shared by the genera *Poa* and *Veronica*, the third by *Rumex*, the fourth by *Bromus* and *Persicaria*, and the rest of the genera in the spectrum share the fifth position. It is noteworthy that none of the genera currently dominating the spectrum were present during the initial colonization phase in the summer of 2023.

At that time, each of the 11 genera was represented by one species recorded in this territory. The genus *Carex* appeared in the flora only in spring 2024, and by autumn 2025 it had already topped the spectrum, while the genus *Poa*, which held the leading position throughout 2024, moved to second place, sharing it with the genus *Veronica*, whose rank has gradually increased, while the position of the genus *Rumex*, which ranked first in the autumn of 2023, is gradually declining.

Biomorphological structure

Analysis of the biomorphological structure of the flora based on life span (FIGURE 4A) showed that at the early stages, the exposed bed of the former reservoir was populated mainly by woody plants (*Acer negundo*, *Amorpha fruticosa*, *Fraxinus pennsylvanica*, *Gleditsia triacanthos*, *Populus nigra*, *Salix × rubens*), which at that time accounted for more than half of all species found. As expected, the proportion of annual plants was significant.

However, in the autumn of 2023, 3.5 months after the dam was destroyed and the bed of the reservoir was drained, many herbaceous perennials appeared, the number of which continues to increase, and the predominance of annuals is gradually decreasing, although it remains quite high.

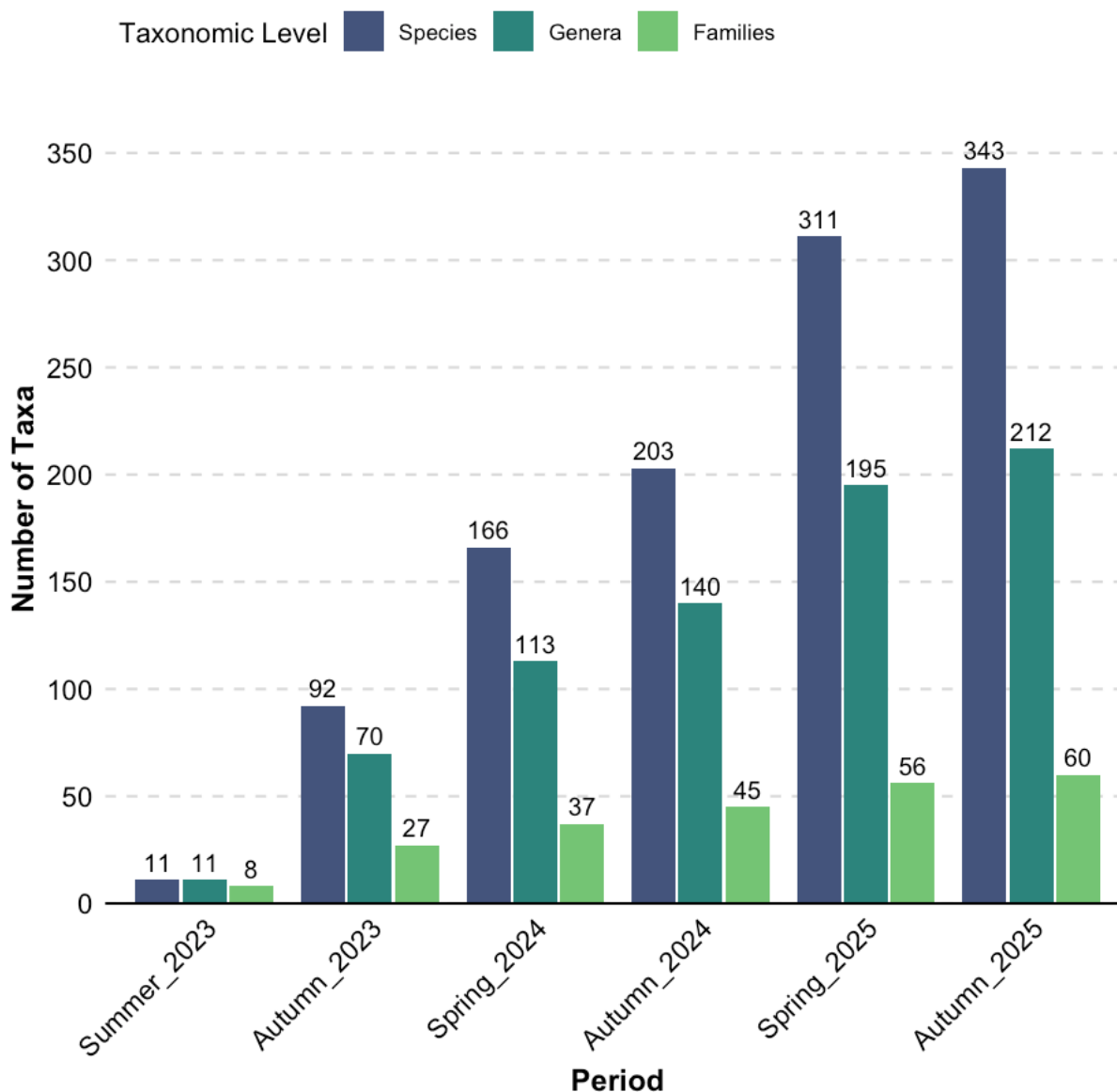


FIGURE 3. Changes in the number of vascular plant taxa at the exposed bed of the former Kakhovka Reservoir over two years after its breach.

The proportion of short-lived plants that became part of the flora in the autumn of 2023 also remains stable. In contrast, the proportion of woody perennials in the autumn of 2023 remains low. Thus, as of the end of autumn 2025, approximately half of the biormorphs in the spectrum are perennials, and the same number are species with a short life cycle.

Similar trends are characteristic of the biomorphological spectrum in terms of life form (FIGURE 4B), although it has its own peculiarities. Thus, the proportion of phanerophytes is low and has remained relatively stable, while there has been some increase in the role of therophytes from summer to autumn of 2023. The gradual decline in the proportion of hydrophytes is expected, as is the growth in the role of hemicryptophytes, which were recorded starting in the autumn of 2023 and then their contribution gradually increased.

The number of geophytes has stayed nearly constant since autumn 2023, with their declining share in the spectrum being driven by the growth of the total flora. The rest of the life forms play an insignificant role in the composition of the studied flora, and their contribution is consistently low, with the exception of chamaephytes, which were first recorded in the spring of 2024 and have been gradually increasing their role since then.

TABLE 1. Dynamics of the leading families of vascular plant species at the exposed bed of the former Kakhovka Reservoir over two years after its breach. Families are listed in descending order of species number as of the end of autumn 2025

Family	Summer 2023			Autumn 2023			Spring 2024			Autumn 2024			Spring 2025			Autumn 2025		
	Count	%	Position	Count	%	Position	Count	%	Position	Count	%	Position	Count	%	Position	Count	%	Position
<i>Compositae</i>	2	18.18	1	14	15.22	1	26	15.66	2	33	16.26	2	50	16.08	1	55	16.03	1
<i>Poaceae</i>	1	9.09	2	11	11.96	3	33	19.88	1	35	17.44	1	42	13.01	2	45	13.12	2
<i>Brassicaceae</i>	0	0		1	1.09	9	4	2.41	8	9	4.43	6	25	8.01	3	28	8.16	3
<i>Cyperaceae</i>	0	0		6	6.52	5	10	6.26	4	11	5.42	4	19	6.01	4	19	5.54	4
<i>Fabaceae</i>	2	18.18	1	13	14.13	2	15	9.04	3	15	7.39	3	16	5.14	5	18	5.25	4
<i>Chenopodiaceae</i>	0	0		7	6.61	4	8	4.82	5	10	4.93	5	11	3.54	7	14	4.08	6
<i>Plantaginaceae</i>	0	0		1	1.09	9	6	3.61	6	7	5.45	7	12	3.86	6	14	4.08	6
<i>Polygonaceae</i>	0	0		7	6.61	4	10	6.02	4	10	4.93	5	10	3.22	8	14	4.08	6
<i>Rosaceae</i>	0	0		2	2.17	8	3	1.81	9	5	2.46	9	12	3.86	6	12	3.05	7
<i>Lamiaceae</i>	0	0		4	4.35	6	4	2.41	8	4	1.97	10	9	2.89	9	10	2.92	8
<i>Caryophyllaceae</i>	0	0		0	0		2	1.02	10	3	1.48	11	9	2.89	9	9	2.62	9
<i>Apiaceae</i>	0	0		0	0		2	1.02	10	4	1.97	10	8	2.57	10	8	2.33	10
<i>Boraginaceae</i>	0	0		0	0		1	0.6	11	2	0.99	12	7	2.25	11	7	2.04	11
<i>Salicaceae</i>	2	18.18	1	2	2.17	8	3	1.81	9	4	1.97	10	6	1.93	12	6	1.75	12
<i>Malvaceae</i>	0	0		3	3.26	7	5	3.01	7	6	2.96	8	6	1.93	12	6	1.75	12
<i>Onagraceae</i>	0	0		2	2.17	8	2	1.02	10	3	1.48	11	4	1.29	14	5	1.46	13
<i>Ranunculaceae</i>	0	0		2	2.17	8	2	1.02	10	2	0.99	12	5	1.61	13	5	1.46	13
<i>Convolvulaceae</i>	0	0		2	2.17	8	3	1.81	9	3	1.48	11	3	0.96	15	4	1.17	14
<i>Juncaceae</i>	0	0		2	2.17	8	3	1.81	9	3	1.48	11	3	0.96	15	4	1.17	14
<i>Ulmaceae</i>	0	0		0	0		3	1.81	9	4	1.97	10	4	1.29	14	4	1.17	14

For both analyzed spectra, the changes were statistically significant only for summer and autumn 2023.

Dispersal structure

The distribution of species by seed dispersal mechanisms (FIGURE 5A) showed that wind-dispersed seeds dominated in the early stages of flora formation. Species with endozoochorous seed dispersal also comprised a significant proportion. However, from June to October 2023, anemochorous species lost their leading position to species with local non-specific seed dispersal, the number of which although fluctuating somewhat, remains fairly stable at around 60%. Analysis of other groups showed that during the formation of the flora, the role of species whose seeds are dispersed by animals, in particular endozoochorous, epizoochorous, and myrmecochorous species, gradually increased.

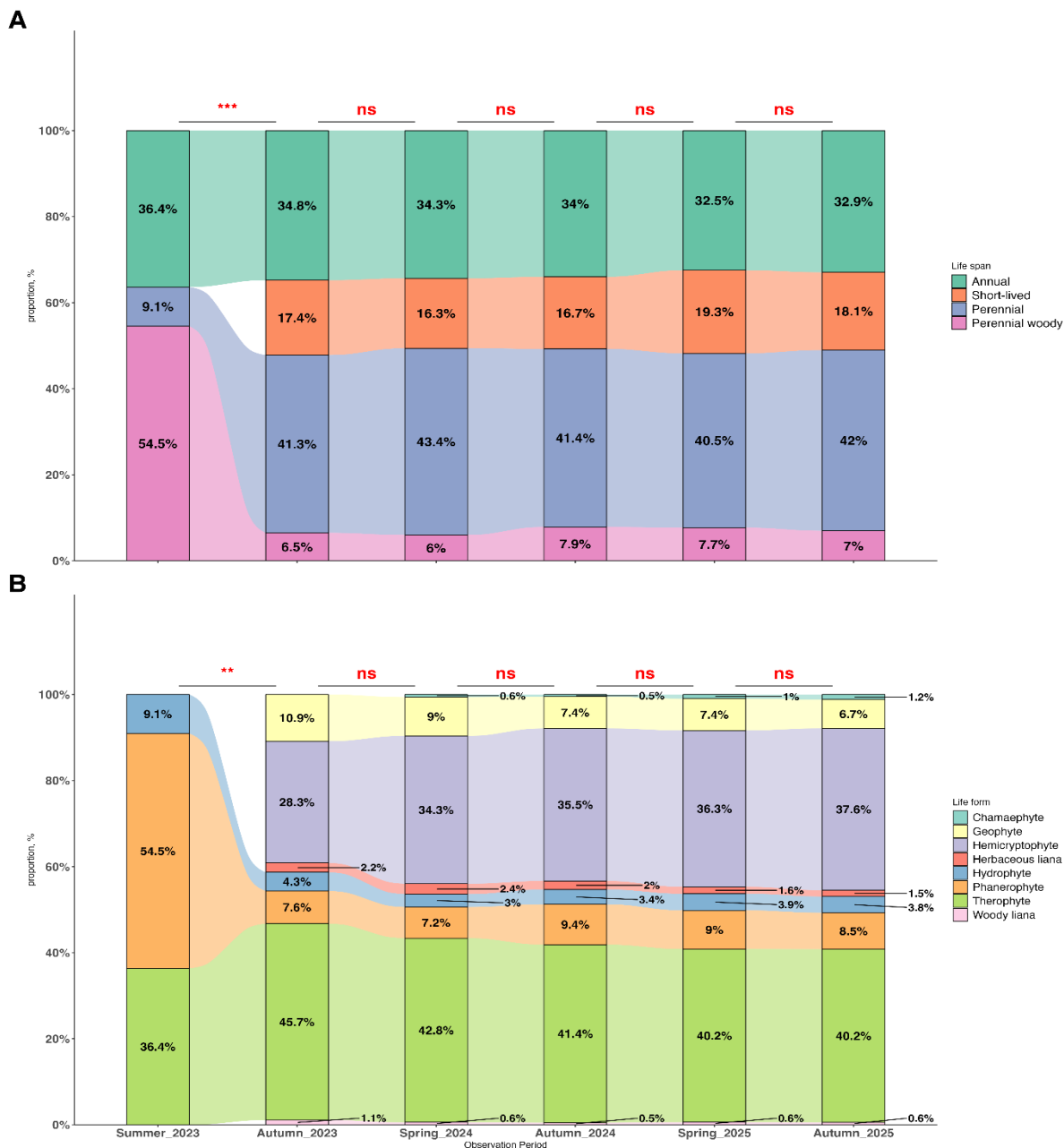


FIGURE 4. Dynamics of the relative proportions of biomorphological groups of species at the exposed bed of the former Kakhovka Reservoir over two years after its breach, by life span (A) and life form (B). Here and in Figures 5–7, asterisks (*) denote levels of statistical significance based on the Kruskal-Wallis test, while 'ns' indicates no significant difference.

Also, during the initial colonization of the exposed bed of the former reservoir, plants that spread seeds over long distances (from 10 to 1500 m) using special features for wind (class 5) or animal (class 6) dispersal had an advantage (FIGURE 5B), but at the next stage, the proportion of plants characterized by short seed dispersal distances increased significantly. By the end of autumn 2025, species without special features for seed dispersal with average distances of 1–5 m (class 2) predominated in the studied flora (FIGURE 5B).

Only the changes between summer and autumn 2023 were statistically significant. After that, although the participation of the analyzed groups fluctuated slightly, the differences were not statistically significant.

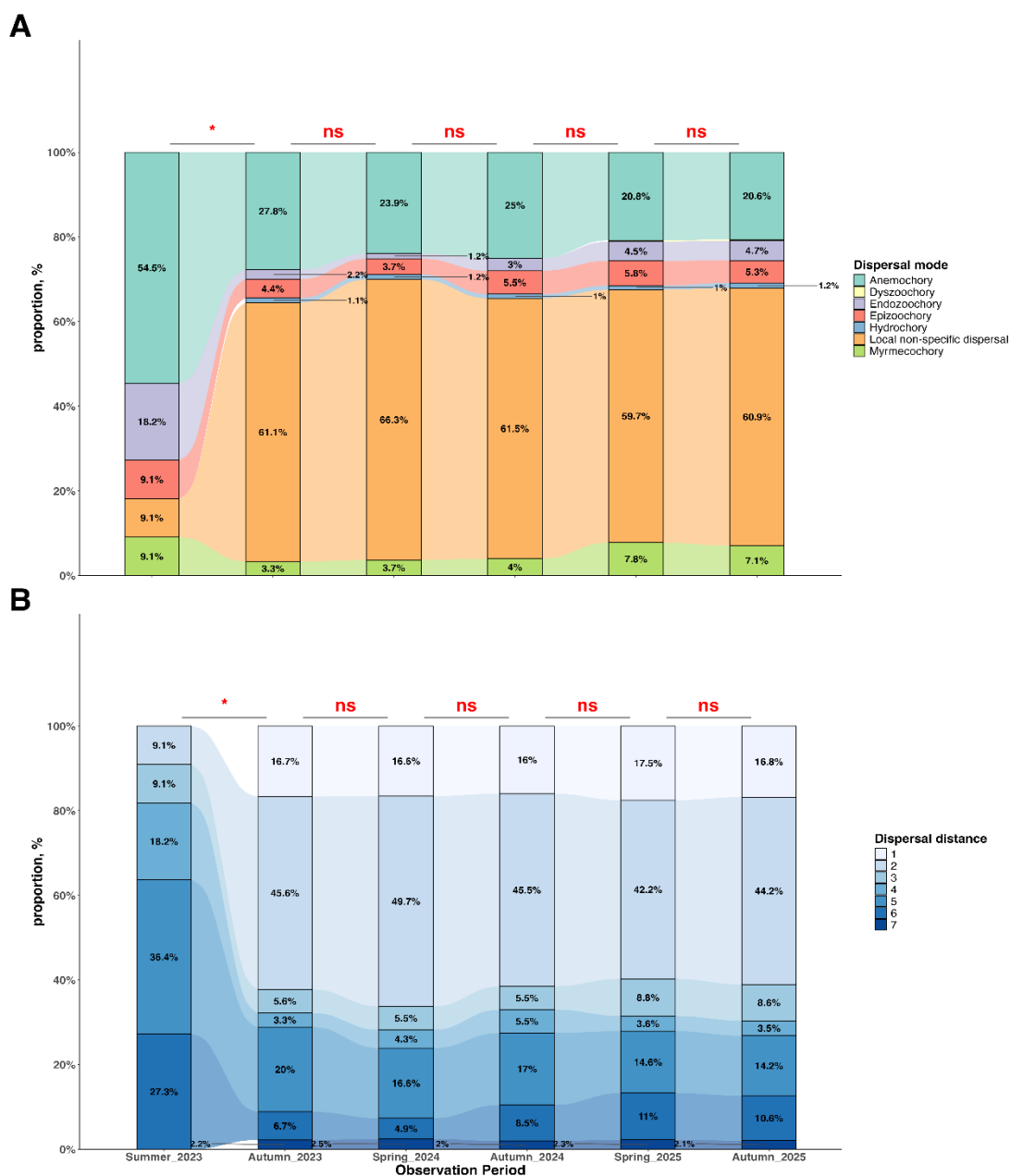


FIGURE 5. Dynamics of the relative proportions of functional group species at the exposed bed of the former Kakhovka Reservoir over two years after its breach according to seed dispersal modes (A) and distances (B): Class 1. Small plants without any specific dispersal features. Mean dispersal distance: 0.1–1 m; Class 2. Tall plants without any specific dispersal features. Mean dispersal distance: 1–5 m; Class 3. Wind-dispersed plants of forest understorey and ant-dispersed plants. Mean dispersal distance: 2–15 m; Class 4. Tumbleweed and wind dispersed trees and shrubs without trichomes. Mean dispersal distance: 40–150 m; Class 5. Wind dispersed trees and shrubs with trichomes and wind dispersal plants of open habitats. Mean dispersal distance: 10–500 m; Class 6. Animal dispersed plants. Mean dispersal distance: 400–1500 m; Class 7. Human dispersed plants. Mean dispersal distance: 500–5000 m.

Origin structure

In the summer of 2023 neophytes accounted for 60% of all species recorded by us in this area, but by autumn 2023 their proportion had decreased significantly and remains low (FIGURE 6). For *Salix × rubens*, which is the most widespread species in the former reservoir area since the earliest stages of overgrowth, its distribution in Europe has not been determined, as this species is a hybrid of a native species *S. alba* and an alien species *S. fragilis*.

TABLE 2. Dynamics of the leading genera of vascular plant species at the exposed bed of the former Kakhovka Reservoir over two years after its breach. Genera are listed by descending species count, then alphabetically for tied ranks

Genus	Summer 2023			Autumn 2023			Spring 2024			Autumn 2024			Spring 2025			Autumn 2025		
	Count	%	Position	Count	%	Position	Count	%	Position	Count	%	Position	Count	%	Position	Count	%	Position
<i>Carex</i>	0	0	0	0	0	0	4	2.41	3	4	1.97	3	10	3.22	1	10	2.92	1
<i>Poa</i>	0	0	0	1	1.09	4	6	3.61	1	6	2.96	1	8	2.57	2	8	2.33	2
<i>Veronica</i>	0	0	0	0	0	0	2	1.02	5	2	0.99	5	7	2.25	3	8	2.33	2
<i>Rumex</i>	0	0	0	4	4.35	1	5	3.01	2	5	1.46	2	5	1.61	4	6	1.75	3
<i>Bromus</i>	0	0	0	0	0	0	3	1.81	4	3	1.48	4	5	1.61	4	5	1.46	4
<i>Persicaria</i>	0	0	0	2	2.17	3	3	1.81	4	3	1.48	4	3	0.96	6	5	1.46	4
<i>Achillea</i>	0	0	0	0	0	0	3	1.81	4	3	1.48	4	4	1.29	5	4	1.17	5
<i>Atriplex</i>	0	0	0	2	2.17	3	2	1.02	5	2	0.99	5	2	0.64	7	4	1.17	5
<i>Carduus</i>	0	0	0	1	1.09	4	1	0.6	6	2	0.99	5	4	1.29	5	4	1.17	5
<i>Cirsium</i>	0	0	0	2	2.17	3	2	1.02	5	2	0.99	5	3	0.96	6	4	1.17	5
<i>Crepis</i>	0	0	0	0	0	0	3	1.81	4	3	1.48	4	4	1.29	5	4	1.17	5
<i>Juncus</i>	0	0	0	2	2.17	3	3	1.81	4	3	1.48	4	3	0.96	6	4	1.17	5
<i>Medicago</i>	0	0	0	3	3.26	2	3	1.81	4	3	1.48	4	3	0.96	6	4	1.17	5
<i>Myosotis</i>	0	0	0	0	0	0	1	0.6	6	1	0.49	6	4	1.29	5	4	1.17	5
<i>Plantago</i>	0	0	0	1	1.09	4	4	2.41	3	4	1.97	3	4	1.29	5	4	1.17	5
<i>Potentilla</i>	0	0	0	1	1.09	4	1	0.6	6	1	0.49	6	4	1.29	5	4	1.17	5
<i>Sisymbrium</i>	0	0	0	0	0	0	1	0.6	6	1	0.49	6	4	1.29	5	4	1.17	5
<i>Trifolium</i>	0	0	0	2	2.17	3	3	1.81	4	3	1.48	4	4	1.29	5	4	1.17	5

Ecological structure

Analysis of the participation of ecological groups of species and their changes during the flora development showed that in relation to substrate moisture (FIGURE 7A), there was an increase in the role of species that prefer dry conditions and, accordingly, a decrease in species that thrive in waterlogged conditions. The proportion of species associated with mesic conditions decreases only from summer to autumn 2023 and then remains relatively stable. In relation to substrate pH (FIGURE 7B), there was a significant decrease in the proportion of species that prefer alkaline soil conditions from summer 2023 to spring 2024, which was then followed by a slight increase. At the same time, there was an increase in the proportion of species characteristic of slightly acidic and neutral conditions, which stabilized starting in spring 2024. Species that prefer acidic substrates appeared in the flora in spring 2024, and their proportion, although still very low, has been gradually increasing since then. In terms of nutrient content in the substrate (FIGURE 7C), eutrophic species have prevailed throughout the two-year study period, but their contribution has been gradually decreasing. The role of species characteristic

of mesotrophic conditions almost doubled from summer to autumn 2023, but by spring 2024 it had stabilized at 27–28%. In contrast, the proportion of oligotrophic species, which were first recorded in autumn 2023, continues to grow. The proportions of hypertrophic and dystrophic species are very small, but the first group is showing a slight decline, while the second is rising. The dynamics of the spectrum of species groups in relation to substrate salinity is quite interesting (FIGURE 7D). Throughout the study period, species characteristic of non-saline conditions predominated. However, from summer to autumn 2023, there was a significant increase in the proportion of species that prefer slightly saline or brackish habitats, with the simultaneous appearance of species characteristic of saline conditions. After that, the proportion of species characteristic of both saline and brackish conditions gradually decreased and stabilized in 2025. In all cases, the changes were statistically insignificant.

Analysis of the dynamics of edaphic factors based on Y.P. Didukh's ecological scales (FIGURE 8) revealed a certain decrease in soil moisture and nitrogen content, accompanied by a slight increase in pH, salinity, and carbonate content. However, for almost all these factors, such changes were noticeable only when comparing the summer and autumn of 2023, after which the median values remained approximately at the same level.

Only for soil moisture changes were noticeable until the spring of 2025 and for nitrogen content from spring 2024. Changes in salinity indicators generally corresponded to those observed in the previous analysis, with salinity slightly increasing from summer to autumn 2023 and then marginally decreasing. In all cases, an increase in the range of the indicators was observed. It should be emphasized that for all six factors, the changes were statistically insignificant. As for substrate aeration, as well as a number of climatic indicators, they remained almost unchanged throughout the observation period (FIGURE 9). However, substantial and statistically significant changes were recorded for the thermal and ombroclimatic regimes. The former decreased, while the latter increased. Changes in lighting were also statistically significant, with indicators increasing in the early stages and then gradually decreasing.

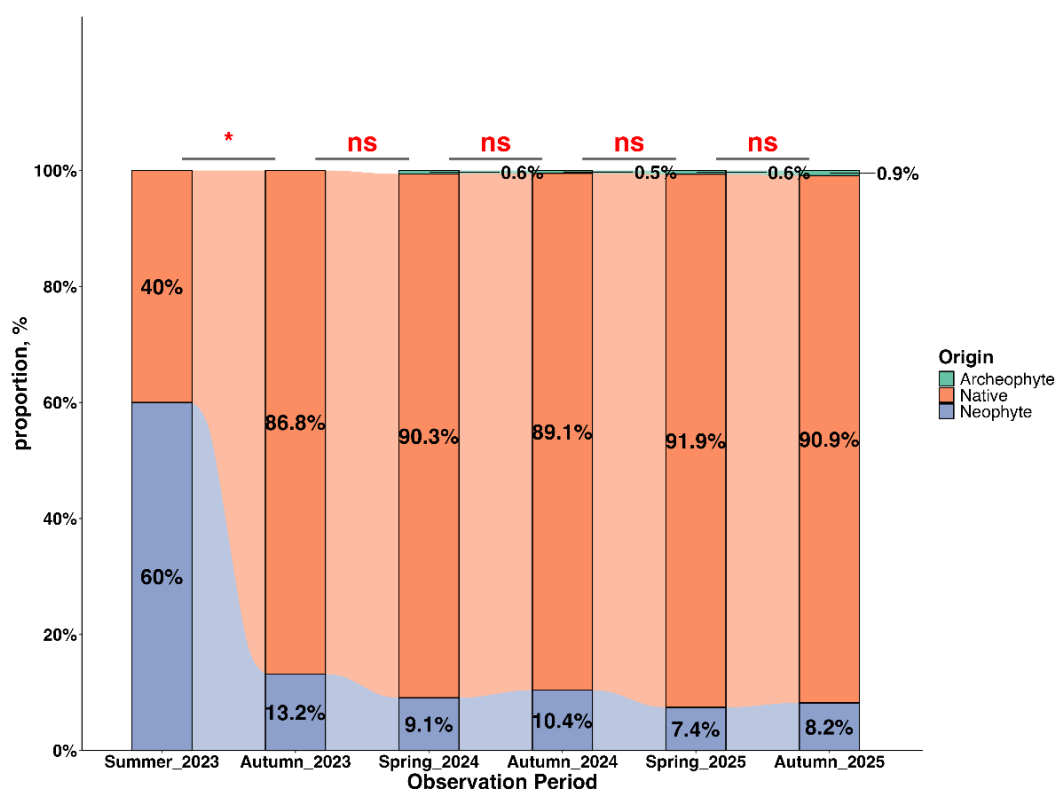


FIGURE 6. The dynamics of the relative proportions of species groups according to their origin in Europe, at the exposed bed of the former Kakhovka Reservoir over two years after its breach.

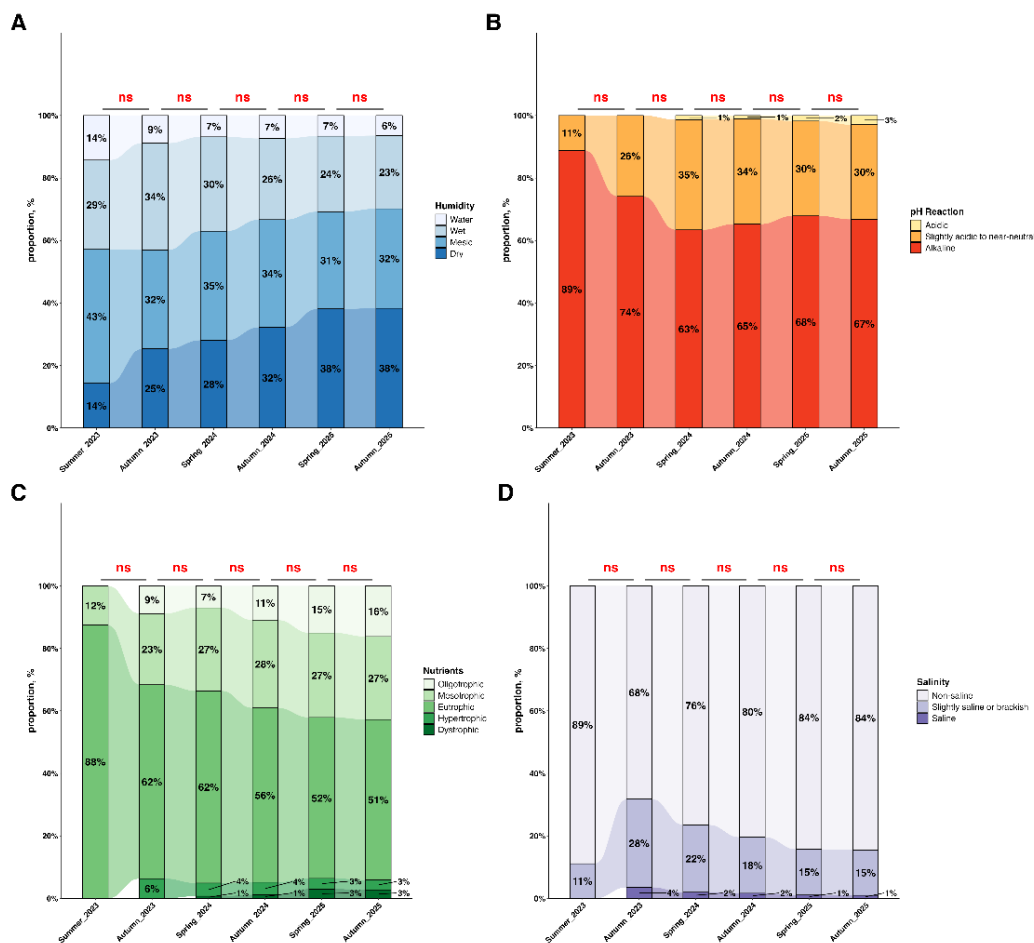


FIGURE 7. Dynamics of the relative proportions of ecological groups of species at the exposed bed of the former Kakhovka Reservoir over two years after its breach according to substrate moisture (A), substrate pH (B), nutrient content in the substrate (C), and substrate salinity (D).

DISCUSSION

Inventory studies of vascular plant flora on the lands of the former Kakhovka Reservoir, conducted approximately every six months for two years after the destruction of the reservoir dam, showed that the flora is still in the process of development, as evidenced by the rapid growth in the number of species recorded in this area, according to the data for each research period. The main changes in the composition of this flora apparently occurred during the first three months of its formation, from June to October 2023. During this period, the number of recorded species increased 8.3 times, while from autumn 2023 to autumn 2025, this number increased only 3.7 times. It is also noteworthy that over the two years from autumn 2023 to autumn 2025, the ratio of different species groups, defined by their main structures, has not changed significantly. This is evidence of a certain stabilization in the floristic composition of the newly formed ecosystem. These findings also indicate a rather high level of data representativeness, since the addition of new localities where field research was conducted and, accordingly, new species, did not significantly change the relative proportions of different structural and ecological groups. Even if they did change slightly, these changes were not statistically significant. So it can be emphasized that already in the autumn of 2023, the flora acquired its characteristic features.

At the same time, during the two years following the destruction of the Kakhovka Hydroelectric Power Plant dam, clear trends in vegetation development emerged, which were also reflected in changes in the structure of vascular plant flora. Thus, the spectrum of leading plant families gradually acquired characteristics typical of floodplain ecosystems in southern regions.

It is very similar to the spectrum of leading families of the Lower Dnieper floodplain (Dubyna & Shelyag-Sosonko 1989) – the geographically closest natural floodplain ecosystem, which indicates the high rate of restoration of intrazonal floodplain flora at the bottom of the former Kakhovka Reservoir. The leading positions of the genera *Carex*, *Poa*, and *Veronica* in the spectrum of leading genera indicate the predominance of species characteristic of grassland habitats in the flora. In general, compared to the zonal steppe flora (Krytska 1985, Moysiienko 2011, 2013), the taxonomic structure of the leading families and genera on the former Kakhovka Reservoir bed exhibits patterns that reflect both the intrazonal character of the developing flora and the significant influence of synanthropization. The significant species richness of graminoids is noteworthy (FIGURE 10), although the high ranking of *Cyperaceae* and, to an extent, *Poaceae* is atypical for zonal natural floras (Krytska 1985, Moysiienko 2011, 2013) and is attributable to the intrazonal character of the studied flora. At the genus level, this is reflected in the high position of various ecologically different genera: predominantly moisture-associated species within *Carex*, *Juncus*, mostly xerophilous representatives of *Veronica*, and diverse *Poa* and *Rumex*. On the other hand, the transformation of the spectrum due to the synanthropization of the flora is manifested in the high position in the spectrum of the leading families *Brassicaceae* and *Chenopodiaceae* and the genera *Bromus*, *Atriplex*, *Cirsium*, and *Sisymbrium*.

The biomorphological spectrum shows a clear predominance of herbaceous perennials and hemicryptophytes. However, the proportion of biormorphs with a short life cycle and therophytes remains high, which is quite obvious, since it was these species that played a major role in the formation of pioneer vegetation on the former reservoir bed immediately after its release from water. It should be noted that most short-lived plants are synanthropic. Thus, a significant percentage of annuals and short-lived species indicate a high level of synanthropization of the flora (Krytska 1985, Dubyna & Shelyag-Sosonko 1989, Moysiienko 2011).

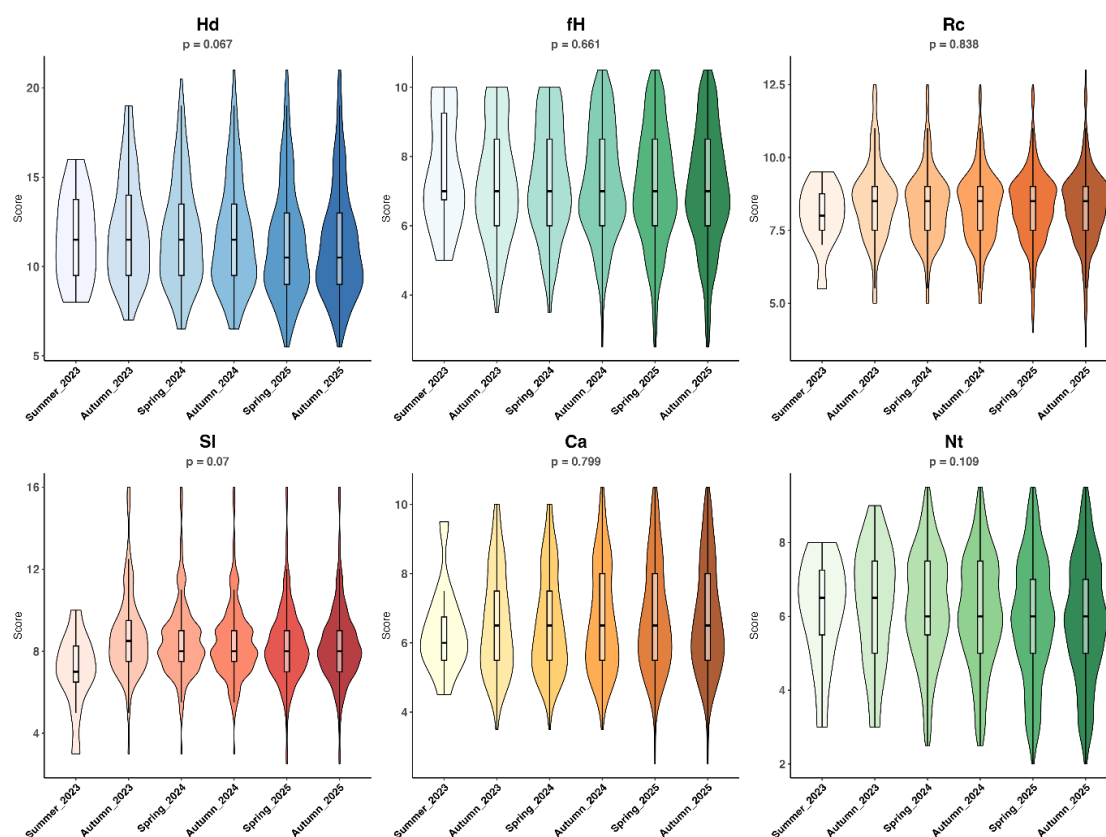


FIGURE 8. Dynamics of edaphic (except for soil aeration) ecological indicators of vascular plant species according to Y.P. Didukh's ecological scales at the exposed bed of the former Kakhovka Reservoir over two years after its breach: Hd – soil moisture, fH – soil moisture variability, Rc – soil pH, SI – soil salinity, Ca – carbonate content in soil, Nt – nitrogen content in soil.

Although floodplain willow and poplar forests occupy the largest area of this territory, the proportion of tree species in the flora is low, although in quantitative terms, *Salix alba* and its hybrid *S. × rubens* are undoubtedly the most numerous plants at the exposed bed of the former reservoir. At the same time, other tree species are also present in this territory (FIGURE 11). The leading role of species whose seeds were dispersed by the wind over considerable distances is also quite obvious. It was precisely these species that played a key role in the earliest stages of colonizing the former bed. These species have gradually been replaced by species that do not have special features for wind dispersal and are only capable of dispersing their seeds over short distances. It is worth emphasizing the growing role of species whose seeds are spread by animals, which indicates the formation of a fully functioning ecosystem in this territory, inhabited by numerous representatives of fauna.

Despite concerns about the possible role of the former reservoir area as a source of invasive species, the proportion of such species is currently low, but some of them (*Amorpha fruticosa*, *Erigeron canadensis*, etc.) are quite numerous and require control over their spread (FIGURE 12). However, the implementation of any control measures is currently precluded by the ongoing security situation.

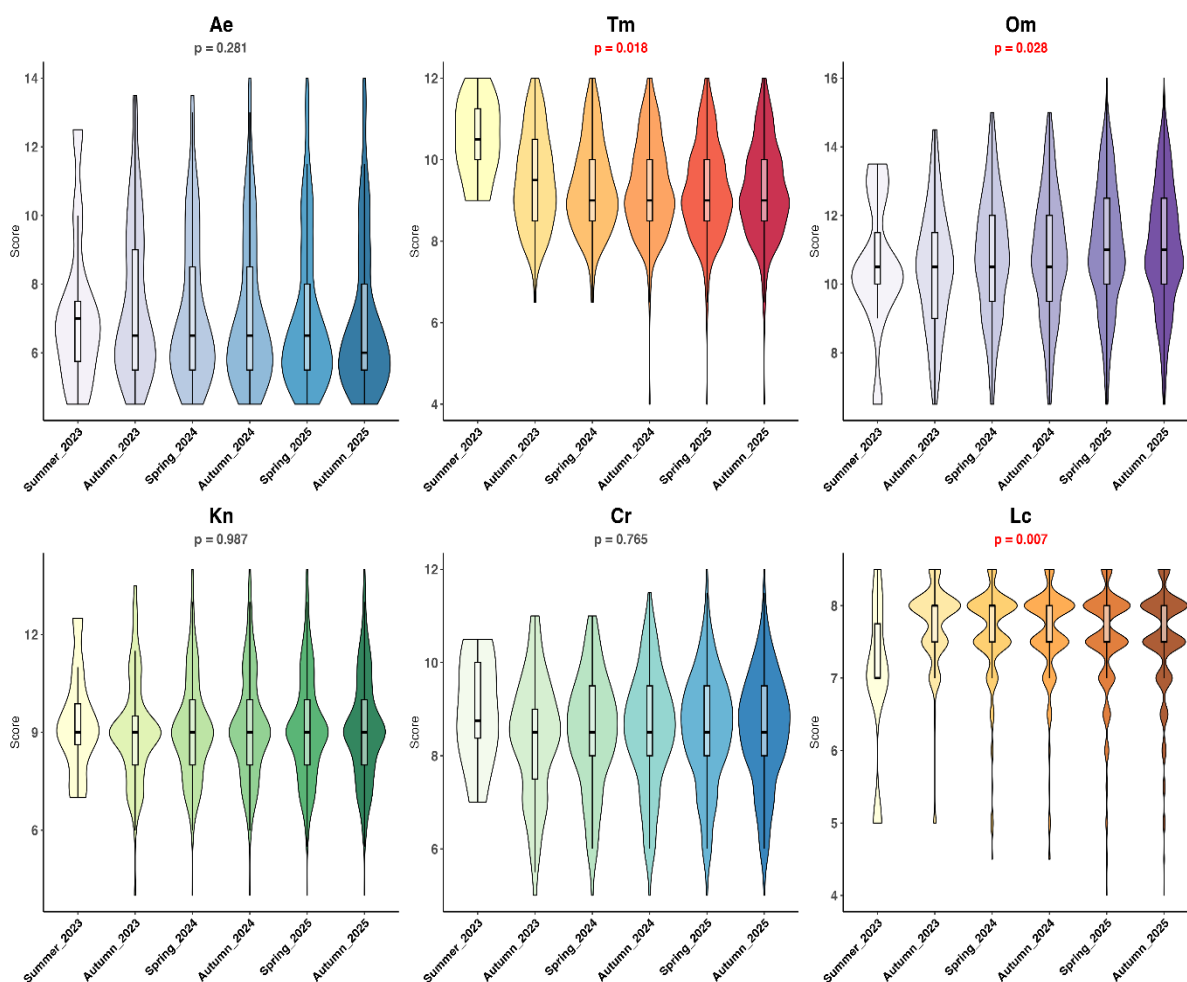


FIGURE 9. Dynamics of soil aeration and climatic ecological indicators of vascular plant species according to Y.P. Didukh's ecological scales at the exposed bed of the former Kakhovka Reservoir over two years after its breach: Ae – soil aeration, Tm – thermoclimate, Om – ombroregime of climate, Kn – continentality of climate, Cr – cryoregime of climate, Lc – light.



FIGURE 10. Some grasses and sedges observed at the exposed bed of the former Kakhovka Reservoir during research: a – *Bolboschoenus maritimus*, b – *Carex otrubae*, c – *Carex hirta*, d – *Carex secalina*, e – *Agrostis stolonifera*, f – *Bromus sterilis*, g – *Alopecurus aequalis*, h – *Poa pratensis*, i – *Poa bulbosa*, j – *Koeleria glauca*. Photo by: M. Mulyenko (a), A. Kuzemko (b–f, h– j), I. Moysiienko (g).

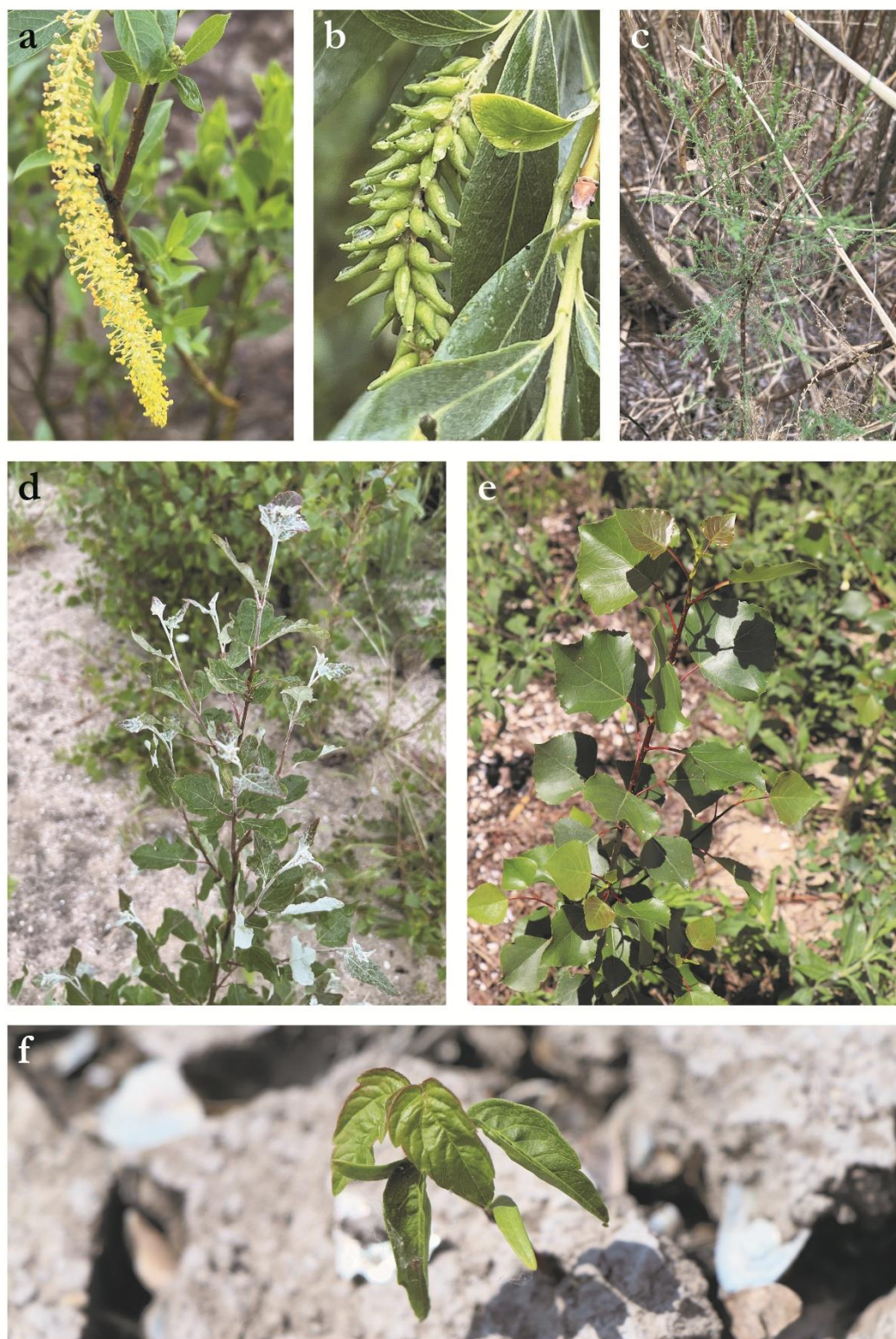


FIGURE 11. Some species of trees and shrubs observed at the exposed bed of the former Kakhovka Reservoir during research: a – *Salix × rubens*, staminate flowers, b – *Salix × rubens*, pistillate flowers, c – *Tamarix ramosissima*, d – *Populus alba*, e – *Populus nigra*, f – *Acer negundo*. Photo by A. Kuzemko.



FIGURE 12. Some alien species observed at the exposed bed of the former Kakhovka Reservoir during research: a – *Ipomoea purpurea*, b – *Ailanthus altissima*, c – *Erigeron canadensis*, d – *Xanthium orientale*, e – *Bidens frondosa*, f – *Amorpha fruticosa*, g – *Robinia pseudoacacia*. Photo by: M. Mulenko (a, e), I. Moysiienko (b, g), A. Kuzemko (c, d, f).



FIGURE 13. Some aquatic species observed at the exposed bed of the former Kakhovka Reservoir during research: a – *Myriophyllum spicatum*, b – *Myriophyllum spicatum*, terrestrial form, c – *Lemna minor*, d – *Nuphar lutea*, terrestrial form. Photo by: M. Mulenko (a), A. Kuzemko (b–d).

Changes in the ecological spectrum of flora are quite predictable, manifested in the gradual increase in species characteristic of drier habitats and a decrease in the number of hygrophilous species after the drainage of the former reservoir area. Although some aquatic species still occur in the studied area, forming terrestrial forms (FIGURE 13), the stability of mesophytic species indicates that this area has sufficient moisture. On the drained slopes of ravines and river valleys, plants characteristic of true (*Achillea pannonica*, *A. nobilis*, *A. setacea*, *Carex melanostachya*, *Coronilla varia*, *Koeleria macrantha*, *Medicago falcata*, *Potentilla recta* subsp. *recta*, *Scabiosa ochroleuca*, *Sisymbrium polymorphum*, *Taraxacum erythrospermum*, *Thalictrum minus*), sandy (*Alyssum minutum*, *Arabidopsis arenosa*, *Carex colchica*, *Cerastium schmalhauseni*, *Filago arvensis*, *Koeleria glauca*, *Linaria genistifolia*, *Pilosella officinarum*, *Secale sylvestre*) and rocky (*Cota tinctoria*, *Erysimum diffusum*, *Polygala comosa*, *Sanguisorba minor*) steppes are present. The significant presence of eutrophic species in the flora is quite logical, given the high nutrient content of the dried mud at the bottom of the former reservoir, while the high proportion of species that prefer alkaline substrates is obviously related to the high carbonate content in the soils of this area, as well as the presence of limestone outcrops along the shores of the reservoir, especially in its southern part. At the same time, the relative proportion of these species is gradually declining as the flora continues to develop. The dynamics of participation of groups distinguished by their relationship to substrate salinity is interesting. A certain increase in the role of saline habitat species immediately after the drying up of the former reservoir is probably related to the intense evaporation of moisture from the exposed bed, which contributed to the formation of salt crystals on the surface and their pulling up from deeper horizons. In particular, a number of species characteristic of saline soils were identified, e.g. *Oxybasis glauca*, *O. rubra*, *Puccinellia gigantea*, *Suaeda altissima*, *Tripolium pannonicum*. It is hypothesized that the formation of a stable vegetation layer suppressed surface evaporation, which, along with the extensive spring flooding of 2024, may have contributed to a shift toward lower substrate salinity. There was a noticeable decrease in thermal regime and, conversely, an increase in climate humidity (ombroregime), which may be related to the climate-regulating properties of floodplain ecosystems, primarily the willow and poplar forests that is rapidly forming on the exposed reservoir bed. The variable dynamics of ecological indicators suggest that fluctuational processes currently prevail. Consequently, it is premature to make definitive predictions regarding the long-term future of the flora, although certain developmental trends are already discernible at this initial stage.

The special environmental significance of the studied territory is evidenced by the discovery of some protected species of vascular plants as *Carex secalina*, listed in the Red Book of Ukraine (Nakaz 2021), and regionally rare species: *Polygala comosa* in the Kherson oblast, *Astragalus contortuplicatus* in the Dnipropetrovsk oblast, and *Butomus umbellatus*, *Cerastium pseudobulgaricum*, and *Iris pseudacorus* in the Zaporizhzhia oblast (FIGURE 13) (Kolomiychuk 2017).

CONCLUSIONS

The study demonstrates that in the two years following the destruction of the Kakhovka Dam, a vascular plant flora has established on the exposed reservoir bed, closely resembling the floodplain ecosystems of southern Ukraine and the Lower Dnieper in particular. The study of vascular plant diversity dynamics revealed that the most significant structural shifts proceeded during the initial months of the flora formation. Subsequent changes, although characterized by fluctuations in the main structures of the flora, were statistically insignificant. These patterns reflect the relative stability of the studied flora; provided there are no catastrophic shifts in vegetation, such developmental trends are likely to persist in the future.

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ADDITIONAL INFORMATION

Conflict of Interest

The authors declare that they have no conflicts of interest.

Ethical Statement

The authors declare that no ethical standards were violated during the research.

Use of AI

During the preparation of this work the author used Gemini in order to develop R scripts for statistical analysis and biodiversity visualization. After using this tool, the author reviewed and edited the code as needed and take full responsibility for the content of the publication.

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Author Contributions

A.K.: Conceptualization, Investigation, Formal Analysis, Visualization, Writing – original draft; **L.B.:** Investigation, Writing – review & editing; **Y.D.:** Investigation, Writing – review & editing; **V.M.:** Investigation, Writing – review & editing; **M.M.:** Investigation, Resources, Writing – review & editing; **N.S.:** Investigation, the Map preparation, Writing – review & editing; **O.Ch.:** Investigation, Visualization, Writing – review & editing; **I.M.:** Conceptualization, Data Curation, Investigation, Writing – original draft. All authors have read and agreed to the published version of the manuscript.

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Data Availability

All data supporting the findings of this study are available in:

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РЕЗЮМЕ

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У статті представлено результати вивчення складу судинних рослин, що були зафіксовані на території колишнього Каховського водосховища на початкових етапах його заростання. Матеріали для дослідження були отримані під час семи дослідницьких поїздок на територію колишнього водосховища у межах Херсонської, Запорізької та Дніпропетровської областей у період з червня 2023 року по жовтень 2025 року. Для оцінки флористичних змін були проведені структурно-порівняльний аналіз та фітоіндикаційна оцінка списку вищих судинних рослин, зафіксованих на території, що звільнилася з-під води. Різноманітність судинних рослин показала стрімке експоненціальне зростання, збільшившись із 11 видів у червні 2023 року до 343 видів у жовтні 2025 року. Таксономічна структура швидко стабілізувалася, і вже в перший рік домінуючими родинами стали Compositae, Poaceae та Brassicaceae. Було відмічено значну зміну у співвідношенні груп видів за життєвими формами і способом поширення насіння: якщо на початкових етапах переважали однорічні види та види, які характеризуються поширенням насіння за допомогою вітру (наприклад, види роду *Salix*, *Populus nigra*), то в наступні роки спостерігалось збільшення кількості багаторічних трав та видів із зоохорним і автохорним розповсюдженням. Розподіл видів на екологічні групи відповідно до їхніх фітоіндикаційних характеристик виявив поступовий перехід від гідрофітних угруповань до мезофітних у міру стабілізації субстрату, хоча вербово-тополеві ліси продовжують формувати структурну основу нового ландшафту. Примітно, що частка чужорідних видів (неофітів) досягла піку в найперший період спостережень, а потім зменшилася, що свідчить про високу стійкість нових аборигенних угруповань. Наявність рідкісних видів, таких як *Carex secalina*, ще більше підкреслює швидке формування екосистем з високою природоохоронною цінністю. Таким чином, доведено, що досліджувана флора швидко формується, все більше нагадуючи природні екосистеми заплави Нижнього Дніпра. Основні структурні зміни відбулися протягом перших трьох місяців після руйнування греблі, після чого настав період стабілізації пропорцій основних груп рослин.

Ключові слова: біорізноманіття, відновлення, заплавні екосистеми, судинні рослини, сукцесія, фітоіндикація, Україна, функціональні ознаки.