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Habitat classification of the Khortytsia Island floodplain after the Kahovka catastrophe using the European Nature Information System (EUNIS)

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This study aimed to analyse, categorise, and interpret the habitat diversity of Khortytsia Island's floodplain in Ukraine. It employed the European Nature Information System Habitat Classification alongside an integrated approach that incorporated geobotanical, geomorphological, bioindication, and remote sensing methods. A total of 876 vegetation *relevés* from 2024–2025 were examined. Plant communities were initially grouped through Two-Way Indicator Species Analysis, with diagnostic species identified based on fidelity values and indicator analysis. These floristic groups were then assigned to habitat types by comparing them with the system's key navigation, factsheets, formal definitions, and official crosswalks. To understand the main factors driving habitat differentiation, analyses included geomorphological variables, ecological indicator values, plant strategy analysis, Multivariate Analysis of Variance, Canonical Correspondence Analysis, and Partial Canonical Correspondence Analysis. Habitat mapping using remote sensing was conducted to analyse spatial and temporal changes from 2022 to 2025. Ten terrestrial habitat types and two water-associated types were distinguished. The terrestrial habitats comprised pioneer sandy vegetation, drawdown-shore communities, riverine willow scrub, humid tall-herb assemblages, reed canary-grass beds, willow gallery forests, mixed poplar riparian forests, floodplain oak forests, and sandy steppes. Habitat differentiation was primarily influenced by geomorphology (especially elevation, topographic position, and wetness) distinguishing low alluvial depressions, wet floodplain zones, and elevated sandy terraces. Ecological indicator values revealed that edaphic moisture, air humidity, soil pH, and nitrogen levels were the strongest predictors of habitat differences. These gradients mainly reflected hydrological, trophic, and substrate-chemical variations, with plant strategies indicating distinct traits related to competition, stress tolerance, and disturbance adaptation. Spatial analysis showed a shift from a relatively stable floodplain pattern in 2022 to a highly dynamic mosaic in 2024–2025, driven by drainage, substrate exposure, and faster succession. The findings demonstrate that the European Nature Information System offers a robust framework for interpreting habitat changes after disturbances, supports comparable biodiversity assessments globally, and provides vital information for conservation planning in the former Kahovka floodplain. The study underscores the conservation potential of this area amidst ongoing ecological reorganisation.

Keywords: nature protection; innovative projects; monitoring; bioindication; environmental impact assessment; geographic information systems; remote sensing data.

Introduction

The European Nature Information System (EUNIS) Habitat Classification plays an important role in biodiversity research because it provides a standardised, hierarchical framework for describing, identifying, and harmonising the recording of habitat types across Europe (Chytrý et al., 2020). It covers all major habitat categories, from natural to artificial and from terrestrial to freshwater and marine ecosystems, and is linked within the broader European Nature Information System to data on species and protected sites (Si-Moussi et al., 2025). In this way, EUNIS enables local ecological and floristic studies to be translated into a common nomenclatural system that supports comparability, habitat mapping, biodiversity monitoring, conservation assessment, and environmental reporting at broader spatial scales (Galparsoro et al., 2012). Its practical importance is especially high in studies of dynamic or transformed landscapes, where locally observed community types need to be interpreted within widely recognised habitat concepts (Tomaselli et al., 2023). Phytosociological vegetation types play a central role in the classification of terrestrial habitats because they provide floristically delimited and ecologically interpretable units that link local plant communities with broader habitat concepts (Chhetri et al., 2024). In the recent development of the EUNIS Habitat Classification, habitat assignment has been based primarily on species composition and geographic criteria, while corresponding syntaxa and statistically derived characteristic species combinations have been compiled for individual habitat types (Rendón et al., 2025). In this sense, phytosociological units form an essential scientific basis for terrestrial habitat classification rather than serving merely as auxiliary descriptive categories (Chytrý et al., 2024). At the same time, their relationship to habitat types is not always one-to-one, because policy-related habitat typologies such as EUNIS and the Habitats Directive often integrate several syntaxa within broader habitat concepts (Xystrakis et al., 2022). Therefore, crosswalks between syntaxonomic systems and habitat classifications are crucial for ensuring both floristic precision and practical applicability in biodiversity assessment, habitat mapping, monitoring, and conservation reporting.

The European Union biodiversity targets are aimed at putting nature on a path to recovery by 2030 through the protection of at least 30% of land and sea, the restoration of degraded ecosystems, and the implementation of legally binding restoration measures, with the broader long-term vision that by 2050, ecosystems should be restored, resilient, and adequately protected (Chapman et al., 2025). The EUNIS Habitat Classification is particularly important because achieving European Union biodiversity targets requires a consistent framework for identifying, mapping, monitoring, and assessing habitat types, particularly to protect biodiversity-rich areas and restore degraded ecosystems (Valentini et al., 2015). Habitat classification in Ukraine has developed in parallel with broader European approaches and has a distinctly conservation-oriented character (Onyshchenko, 2016). Unlike vegetation classification (which is based primarily on data on vascular plants and bryophytes and requires substantial botanical expertise), habitat classifications were created as a practical tool for describing terrestrial and aquatic areas in terms of their suitability for biodiversity conservation. In the contemporary Ukrainian context,

the main general framework is the EUNIS Habitat Classification, used for habitat identification and linking Ukrainian habitats to the broader European nature information system (Chusova et al., 2022). The importance of habitat classification in Ukraine is further strengthened by its direct connection with practical conservation tasks, particularly the development of the Emerald Network (Shumilo et al., 2023). One of the criteria for designating Emerald Network sites is the presence of valuable habitats listed in Resolution 4 of the Standing Committee of the Bern Convention. Since 2010, the EUNIS classification has been used for this purpose. Thus, habitat classification in Ukraine is not only a scientific tool for describing ecological diversity, but also a basis for conservation planning, international reporting, and the designation of areas of special importance for biodiversity conservation. Alongside the broader European system, national habitat classifications have also been developed in Ukraine, particularly for the forest and forest-steppe zones and for the Mountain Crimea. Such classifications are better adapted to smaller territories and more closely reflect the national tradition of vegetation classification. At the same time, the adaptation of EUNIS to Ukrainian conditions remains necessary, because some habitats in the official materials may be described based on material that is not fully representative of Ukraine, and some diagnostic criteria require local refinement. For this reason, Ukrainian reference works based on EUNIS place particular emphasis on the most diagnostic features and on the distinction between similar habitat types to ensure correct identification under national conditions.

The destruction of the Kahovka Dam during Russia's war against Ukraine triggered one of the gravest environmental catastrophes in Eastern Europe in recent decades (Pichura et al., 2025). Its consequences extended far beyond the immediate flood pulse. They included the collapse of aquatic and riparian ecosystems, widespread contamination, biodiversity loss, deterioration of water quality, disruption of water supply and irrigation infrastructure, and long-term risks to human health and environmental safety (Kuzemko et al., 2025). The rapid drawdown of the reservoir also exposed extensive areas of the former reservoir bed, initiating a cascade of long-term transformations in hydrology, soil conditions, shoreline morphology, and habitat structure (Hryhorczuk et al., 2024). As a result, the Dnipro floodplain entered a phase of rapid ecological reorganisation marked by drainage, substrate exposure, spontaneous succession, and the formation of new and unstable habitat complexes (Gleick et al., 2023). Studying the repercussions of the Kahovka catastrophe may provide insights to some less known environmental impacts of dam destruction, as well as to the reestablishment of damaged ecosystems (Shumilova et al., 2025). The classification of habitats affected by catastrophic impacts is important for the scientific description of ecosystem change and for communicating to the international community the scale of environmental destruction caused by the Russian occupation and military aggression (Pichura & Potravka, 2025). It enables the translation of locally recorded consequences of the catastrophe (including the loss of aquatic ecosystems, transformation of floodplains, exposure of new substrates, destruction of riparian and terrestrial habitats, and the emergence of post-catastrophic successional complexes) into a standardised, internationally understandable habitat-based language. In this way, the event can be interpreted not merely as "damage to vegetation" or "landscape change", but as the loss, degradation, or replacement of specific habitat types that can be compared with broader European conservation categories (Pichura et al., 2025). Such an approach strengthens the evidential value of ecological studies, makes the consequences of the catastrophe internationally comparable, and provides a scientific basis for environmental damage assessment, conservation reporting, restoration planning, and communication of the ecological consequences of Russian aggression in Ukraine at the global level. It highlights not only a period of massive environmental destruction, but also the onset of a prolonged post-catastrophic reconfiguration of landscape and biotic diversity (Pichura et al., 2024). The dynamic character of habitat change represents a substantial challenge for habitat identification (Kvach et al., 2025). For this reason, the present study applied an integrated approach combining geobotanical, geomorphological, and bioindication methods. In addition, habitat classification based on remote sensing was used to monitor spatial and temporal changes. This combination of approaches enabled improved habitat interpretation under post-catastrophic conditions and the tracing of the ongoing reorganisation of habitat structure. This study aimed to identify and classify the floodplain habitat types of Khortytsia Island under the conditions of post-catastrophic transformation following the destruction of the Kahovka Reservoir, using an integrated approach combining geobotanical, geomorphological, and bioindication methods, along with remote-sensing-based habitat mapping to analyse the spatial and temporal changes.

Material and methods

The study focused on the floodplain ecosystems of Khortytsia Island, which experienced significant restructuring following the destruction of the Kahovka Reservoir in 2023. Khortytsia Island in Ukraine was selected as a model site to analyse land-cover changes following the disaster (Lisovets et al., 2025). Khortytsia is the largest island in the Dnipro River, located near Zaporizhzhia, downstream of the Dnipro Hydropower Plant (DniproHES). It stretches roughly 12 km northwest to southeast and measures between 1.6 and 2.7 km in width, covering about 2,359 hectares before the Kahovka Dam collapse. Situated within the northern part of the former Kahovka Reservoir and its floodplain, Khortytsia was surveyed in 2024–2025. On 6 June 2023, an explosion destroyed the Kahovka Dam, triggering rapid reservoir drainage and lowering water levels across the Dnipro. Observations at the Nikopol gauge indicated the river level dropped by roughly eight meters (Gleick et al., 2023). This event initiated a series of long-term changes in the floodplain's hydrological regime, shoreline shape, and soil moisture patterns. These changes subsequently influenced the vegetation structure and the spatial arrangement of the habitats. On Khortytsia Island, the disaster mainly caused a quick reorganisation of river channels and floodplain ecosystems, including the disconnection of some water bodies from the main river, gradual shallowing and substrate exposure, the development of new sandy shores and shoals, and the rapid colonisation of the newly exposed areas by pioneer and aquatic vegetation (Lisovets et al., 2025). Changes in the higher areas of the floodplain tend to occur more slowly. However, they remain ecologically significant because changes in root-zone moisture increase stress on woody vegetation, particularly in summer. Overall, these processes have created a mosaic of new and unstable surface types, resulting in novel spectral features. This is a key factor when choosing remote sensing methods to identify land-cover classes that were previously unknown or unexpected (Lisovets et al., 2025; Tutova et al., 2025, 2026).

The openly available dataset provides detailed descriptions of the methods used for vegetation sampling, phytosociological data processing, and the compilation of the Prodromus of vegetation (Lisovets et al., 2025). A total of 876 *relevé* plots were recorded. Plant lifeforms are classified following Raunkiaer (1937). Pollenochores are groups of plants defined by their pollination method; for spore-producing plants, this depends on the type of gamete transfer. These groups are classified according to how male gametes reach the female reproductive organs. In this study, two types were included: anemophily (Anph), or wind pollination, and entomophily (Ent), or insect pollination. Diasporochores, also called ecobiochores, are plant groups characterised by their dispersal mechanisms. The types observed were autochory (Ach), anemochory (Anch), ballochory (Bal), barochory (Bar), endozoochory (EndZ), epizoochory (EpZ), hydrochory (Hdch), myrmecochory (Myrm), tumbleweed dispersal (Perv), and synzoochory (SynZ) (Zhukov et al., 2023). Pollenochores and diasporochores are defined according to Tarasov (Tarasov, 2012). The Shannon index was calculated to assess plant cover diversity.

Didukh indicator values serve as ecological indicators that describe plant species across key environmental gradients (Didukh, 2011). In this study, the variables included edaphic moisture (Hd), air humidity (fH), soil pH (Rc), soil salinity (Sl), carbonates (Ca), nitrogen/fertility (Nt), substrate aeration (Ae), temperature (Tm), and ombroregime, which reflects climatic moisture (Om). Ellenberg-type ecological indicator values were employed to assess the environmen-

tal needs of plant species, focusing on moisture (W), soil pH (R), temperature (T), light (L), and continentality (K) (Dengler et al., 2023). Ecological indicators provide many benefits, including enabling a comprehensive evaluation of environmental conditions, integrating data over long periods, avoiding costly and lengthy instrumental measurements, and reflecting human impacts. Similar to abiotic factors, naturalness and degradation form a continuum from artificial (degraded) to 'natural' states. Different species respond uniquely to human disturbance; some are found mainly in natural or near-natural habitats, while others tolerate, benefit from, or depend on human influences. This variability allows for assessing a site's naturalness or degradation according to its species composition. To assist this, two indicator systems have been created: naturalness and hemeroby. Hemeroby quantifies the degree of ecosystem change due to human activity, whereas naturalness measures how closely an ecosystem resembles the minimally disturbed natural reference state (Erdős et al., 2022). The projected area of herbaceous plant species was used as a weight in calculating the hemeroby assessment:

$$Hem = \frac{\sum_{i=1}^{n} H\text{-score}_i \times Pr_i}{\sum_{i=1}^{n} Pr_i},$$

where *H-score*$_i$ is the hemeroby indicator score of the *i*-th species, and Pri is the projective cover of the *i*-th species in the *relevé*. Plant hemeroby scores are provided according to Frank & Klotz (1990) with adaptations for regional conditions by Goncharenko (2017). The naturalness values of the plant species are based on those of Borhidi (1995) with our adaptations reflecting the conservation status of the species and the potential for the spread of adventitious species in the region. The Borhidi category of naturalness is assessed based on social behaviour types and their associated naturalness values. These social behaviour types are derived from the C–S–R strategic model of competitor, stress tolerator, and ruderal species, as proposed by Grime (1974). The following social behaviour types (SBT) were used: competitors (C, with a naturalness value of +5), stress-tolerant species adapted to narrow ecological conditions, including specialists (S, +6), and stress-tolerant species adapted to broader ecological conditions, including generalists (G, +4). Ruderals (R) include the following categories: natural pioneers (NP, +3), disturbance-tolerant plants of natural habitats (DT, +2), native weed species (W, +1), introduced alien species (I, –1), adventitious species (A, –1), ruderal competitors (RC, –2), and aggressive invaders such as alien competitors (AC, –3). The estimated cover of herbaceous plants served as a weight in calculating the naturalness assessment:

$$Nat = \frac{\sum_{i=1}^{n} Nat\text{-score}_i \times Pr_i}{\sum_{i=1}^{n} Pr_i},$$

where *Nat-score*$_i$ is the SBT scores of the *i*-th species, and *Pr*$_i$ is the projective cover of the *i*-th species in the *relevé*.

The competitor, stress-tolerator, and ruderal values of plant species (Pierce et al., 2017), expressed as proportions summing to one, were subjected to a weighted mean procedure based on plant percentage cover. These estimates were subsequently normalised to sum to unity for each vegetation *relevé*. The isometric log-ratio (ilr) transformation was applied to obtain orthonormal coordinates (Egozcue et al., 2003). The first ILR axis is created by comparing the proportion of competitors with the geometric mean of stress-tolerators and ruderals, serving as an indicator of the competitive adversity gradient:

$$\text{Competitive adversity} = \sqrt{\frac{2}{3}} \ln\left(\frac{C}{\sqrt{SR}}\right).$$

The second *ilr* axis contrasts stress-tolerators and ruderals, and was interpreted as an indicator of environmental adversity gradient:

$$Environmental\ adversity = \sqrt{\frac{1}{2}}\, ln\left(\frac{S}{R}\right).$$

Disturbance indicators are variables that describe the intensity, frequency, and specific forms of disturbance affecting vegetation and the soil surface (Midolo et al., 2023). In the present study, they were represented by disturbance severity in the herb layer, disturbance frequency in the herb layer, mowing frequency, grazing pressure, and soil disturbance.

A digital elevation model (DEM) in the UTM zone 36N projection (EPSG:32636) was used to evaluate the topographic control of the spatial variability of the studied indicators. Terrain-derivative layers were generated in the R environment using the terra and whitebox (WhiteboxTools) packages (Lindsay, 2016). Using terra, slope in degrees, aspect, local topographic position index (TPI), terrain ruggedness index (TRI), and surface roughness were calculated for each DEM cell based on an eight-neighbour scheme. In addition, a multiscale TPI was calculated within an 11 × 11 moving window as the difference between the elevation of the central cell and the mean elevation within the window. Hydrologically derived variables were computed using the whitebox package, which provides access to WhiteboxTools algorithms. Before these calculations, the DEM was hydrologically corrected by filling depressions, and flat areas were also resolved. Based on the corrected elevation model, the specific catchment area (SCA) was calculated using the D-infinity algorithm, and the topographic wetness index (TWI) was derived accordingly. The slope for this stage was also calculated in WhiteboxTools. Thus, the final set of topographic predictors included absolute elevation, slope, TWI, multiscale TPI, surface roughness, and the sine and cosine components of aspect, which were used to account for its circular nature. For the regression analysis of vegetation characteristics, the initial set of topographic predictors included absolute elevation, slope, topographic wetness index (TWI), multiscale topographic position index (11 × 11 window), surface roughness, and the sine and cosine transformations of aspect. Separate models were fitted for each vegetation variable, and predictor selection was carried out independently in each case using stepwise AIC-based model selection. As a result, the composition of final predictors varied among response variables.

Vegetation plots were classified using the TWINSPAN method to identify operational floristic groups. For each group, diagnostic species were determined based on fidelity values (the φ-coefficient) and the statistical significance of the indicator analysis. The resulting synoptic tables were used as a local species-based diagnostic framework for assigning vegetation plots to EUNIS habitat types. The final assignment was completed by matching local diagnostic species combinations to the EUNIS key navigation, factsheets, formal definitions, and official crosswalks. Geomorphological position and morphometric terrain variables were used solely as additional location-based criteria when floristic characteristics did not allow unambiguous discrimination among candidate habitat types. A detailed synoptic table and a full description of the classification procedure are provided in the accompanying openly available dataset (Tutova et al., 2026).

The one-way Multivariate Analysis of Variance (MANOVA) was employed to evaluate the overall effect of vegetation classification on ecological indicators, with plant association as the independent variable and ecological indicators as the response variables. The multivariate significance was determined using Pillai's trace, known for its robustness and conservatism, especially when group sizes vary or the assumptions of multivariate normality are not fully met. The analysis was carried out in R (R Core Team, 2025) using the manova() function from the stats package. To identify the most suitable ordination method for analysing species–environment interactions, a Detrended Correspondence Analysis (DCA) was initially performed on the species composition matrix using the decorana() function from the vegan package. The first DCA axis had a length of 8.64 standard deviation units, suggesting a lengthy ecological gradient and mainly unimodal species responses. Based on standard criteria (Ter Braak and Prentice, 1988; Ter Braak and Prentice, 2004), gradient lengths exceeding 3 standard deviation units justify the use of Canonical Correspondence Analysis (CCA). Therefore, CCA was utilised to explore the relationships between species composition and the environmental variables examined. To determine the unique impact of each predictor on species composition, Partial Canonical Correspondence Analysis (Partial CCA) was used. This technique evaluates the effect of a specific explanatory variable while accounting for the influence of other predictors. In each model, the species composition matrix served as the response matrix. A single variable of interest (such as association type, an individual Didukh ecological indicator, naturalness, or hemeroby) was included as the constrained variable. All other predictors were incorporated as covariates via the condition() term. This approach isolated the effect of the focal variable from the variation explained by other ecological gradients. The anal-

yses were conducted with the cca() function in the vegan package. Model significance was tested through permutation tests with 999 permutations under the reduced model, and adjusted R^2 values were computed using RsquareAdj() to provide a penalised estimate of the proportion of inertia uniquely attributable to each predictor.

Results

Based on the geobotanical *relevés*, geomorphological features, and vegetation physiognomy, we distinguished ten terrestrial habitat types. In addition, two water-associated habitat types were identified: C3.6 Unvegetated or sparsely vegetated shores with soft or mobile sediments and C2.3 Permanent non-tidal, smooth-flowing watercourses.

R1BA11 *Corispermum* pioneer swards represent open pioneer sand vegetation within R1BA1 Pannonic sand pioneer swards. In the EUNIS classification, this habitat is defined as pioneer sand swards of the southern Pannonic basin, particularly the Deliblato sands, dominated by *Corispermum nitidum* and *Polygonum arenarium*. In the studied floodplain, its local expression is represented by sparse annual vegetation developing on recently exposed or weakly stabilised sandy alluvium. The floristic core of this unit is formed by *Corispermum nitidum*, *C. hyssopifolium*, *Xanthium strumarium*, *Portulaca oleracea*, *Chenopodium strictum*, *Amaranthus albus,* and *Echinochloa crus-galli*, together with other short-lived therophytic and ruderal species. According to the synoptic table, Cluster 1 is primarily distinguished by high fidelity values for *Xanthium strumarium* ($\varphi = 0.67$), *Corispermum nitidum* ($\varphi = 0.66$), *Corispermum hyssopifolium* ($\varphi = 0.60$), *Portulaca oleracea* ($\varphi = 0.54$), *Chenopodium strictum* ($\varphi = 0.54$), and *Amaranthus albus* ($\varphi = 0.46$). Ecologically, these stands occupy low-elevation but relatively well-drained sandy microsites within the floodplain, in periodically disturbed substrates that dry rapidly after exposure. In this sense, the recorded stands are best interpreted as a local floodplain expression of R1BA12, rather than as a textbook core form of the habitat, because alongside *Corispermum* they contain a pronounced admixture of nitrophilous annuals, while *Polygonum arenarium* is not among the principal diagnostic species in the analysed dataset.

Q61 Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation comprises periodically exposed margins of rivers, drying oxbows, lakes, fishponds and similar eutrophic wetland habitats with muddy or sandy-muddy sediments enriched by natural sedimentation or anthropogenic nutrient input. In the studied floodplain, this habitat is represented by ephemeral drawdown vegetation developing after water-level recession in exposed fine alluvium. Its local floristic expression is characterised by high representation of *Persicaria lapathifolia*, *Epilobium hirsutum*, *Typha angustifolia*, *Epilobium tetragonum*, *Rumex maritimus*, *Bidens frondosa*, *Atriplex prostrata*, *Rorippa palustris*, *Nuphar lutea*, *Typha latifolia,* and *Alisma plantago-aquatica*. The cluster is best interpreted as a eutrophic drawdown-shore community rather than an aquatic *Nuphar* bed, because pioneer and ephemeral mud-shore species form its floristic core. At the same time, *Nuphar lutea* occurs here only as a residual terrestrial form after water retreat. This interpretation is consistent with the EUNIS concept of Q61, which emphasises periodically exposed eutrophic shores with pioneer vegetation dominated mainly by annual herbs of the genera *Bidens*, *Chenopodium* and *Persicaria*, and lists *Rumex maritimus*, *Rorippa palustris*, *Oenanthe aquatica*, *Ranunculus sceleratus*, *Alopecurus aequalis*, *Oxybasis rubra,* and *Echinochloa crus-galli* among its diagnostic species.

Q62 Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation comprises periodically exposed margins of rivers, oxbows, ponds and other shallow freshwater bodies with stable, mesotrophic muddy to sandy-muddy sediments, supporting low-growing, weakly competitive pioneer vegetation after water-level recession. In the studied floodplain, this habitat is represented by open drawdown communities developing on exposed mesotrophic sediments after flooding. Its local floristic expression is characterised by *Cyperus glomeratus*, *Cyperus fuscus*, *Oxybasis rubra*, *Cyperus michelianus*, *Lythrum salicaria*, *Rumex hydrolapathum*, *Leersia oryzoides*, *Juncus compressus*, *Oenanthe aquatica*, *Ranunculus sceleratus,* and *Alopecurus aequalis*. *Phragmites australis* is also present, but it is interpreted here as a local structural admixture rather than a primary diagnostic element of the habitat. This cluster is therefore best understood as a mesotrophic ephemeral drawdown-shore community rather than a reed bed, because small annual and amphibious mud-shore species form its floristic core. This interpretation is consistent with the EUNIS concept of Q62, which emphasises exposed mesotrophic sediments with low-growing, competitively weak pioneer vegetation. At the same time, the expansion of taller and more nutrient-demanding species is regarded as successional development towards Q61.

F9.12 Lowland and collinar riverine *Salix* scrub comprises linear shrubby willow formations along river banks in plains, hills, and low mountains, developing in alluvial substrates subject to periodic flooding and fluvial disturbance. In the studied floodplain, this habitat is represented by riparian scrub with a woody layer characterised by *Salix rubens* and *Populus nigra*, with a strong admixture of *Amorpha fruticosa*. By contrast, the herb layer includes hygrophilous floodplain species such as *Carex riparia*, *Carex pseudocyperus,* and *Calystegia sepium*, as well as disturbance-tolerant species such as *Apera spica-venti*, *Achillea millefolium*, and *Ailanthus altissima*. These stands are best interpreted as a shrubby riparian willow habitat rather than as a fully arborescent poplar-willow forest, because their physiognomy is dominated by scrub. Meanwhile, the abundance of *Amorpha fruticosa* is treated here as an invasive and disturbance-related component rather than as the primary habitat-defining feature. In the current revised EUNIS hierarchy, this habitat corresponds to S912 Lowland and collinar riverine *Salix* scrub, which is equivalent to the earlier code F9.12.

R5523 Continental tall-herb communities of humid meadows comprise river-bank and freshwater humid-depression tall-herb vegetation of the continental steppe zone. In the studied floodplain, this habitat is represented by tall, moisture-demanding herbaceous stands developing in periodically wet, nutrient-rich soils in depressions, abandoned wet meadows, and river-margin habitats. *Cirsium arvense*, *Calamagrostis epigejos*, *Cirsium vulgare*, *Urtica dioica*, *Lycopus europaeus*, *Persicaria minor*, *Persicaria hydropiper*, *Glyceria maxima,* and *Solanum dulcamara* characterise its local floristic expression. These stands are best interpreted as humid tall-herb communities rather than as true helophyte beds, because mixed tall forbs and mesohygrophilous species of wet floodplain habitats form their floristic core. By contrast, the presence of reed-like or fringe species reflects local wetness and disturbance rather than dominance by a single emergent graminoid. This interpretation is consistent with the EUNIS concept of R5523, defined as river-bank and freshwater humid-depression tall-herb communities of the continental steppe zones, within the broader unit R55, which includes tall-herb-dominated vegetation of moist, sometimes flooded, nutrient-rich soils in floodplains and other wet lowland environments.

Q516 *Phalaris arundinacea* beds comprise vegetation of the margins of lakes, rivers, brooks, and swamps dominated by *Phalaris arundinacea*, either in relatively pure stands or mixed with other tall wetland species. In the studied floodplain, this habitat is represented by disturbed water-margin and shallow floodplain stands in which *Phalaris arundinacea* forms the ecological core of the community. However, the vegetation is strongly enriched by ruderal and neophytic species. Its local floristic expression is characterised by *Erigeron canadensis*, *Erigeron annuus*, *Lactuca tatarica*, *Phalaris arundinacea*, *Persicaria maculosa,* and *Festuca rupicola*. These stands are best interpreted as a ruderalised floodplain variant of reed canary-grass beds rather than as tall-herb fringes or purely anthropogenic herbaceous vegetation, because the habitat remains linked to wet alluvial margins and to the persistence of *Phalaris arundinacea* as the principal wetland structural element. This interpretation is consistent with the EUNIS concept of Q516, which emphasises *Phalaris arundinacea*-dominated communities of lake, river and swamp margins that are highly tolerant of drying, pollution, and disturbance, may form the landward belt of reedbeds, and are often characteristic of degraded systems.

T111223 Eastern Ponto-Sarmatic steppe willow galleries comprise riverine woods dominated by *Salix alba*, *Salix fragilis,* and *Populus nigra* in the floodplains of the lower Dniester, the lower Dnipro basin, the lower and middle Don and Donets system, the lower Volga basin, and the Kuma and Terek basins. In the EUNIS concept, these are riparian willow-dominated gallery forests of the eastern Ponto-Sarmatic steppe zone, developing in alluvial sites shaped by periodic flooding and fluvial sediment dynamics. In the studied floodplain, this habitat is represented by a floristically transformed variant of Eastern Ponto-Sarmatic willow galleries, in which the woody structure remains linked to riparian willow forest. At the same time, the herb layer shows substantial ruderalisation and anthropogenic alteration. Its local floristic expression is characterised by *Salix alba* together with locally diagnostic or high-fidelity species such as *Anisantha sterilis*, *Lactuca serriola*, *Fraxinus pennsylvanica*, *Ulmus minor*, *Glechoma hederacea*, *Taraxacum officinale*, *Lysimachia nummularia*, and *Papaver rhoeas*. According to the accompanying ecological plots, this cluster is further distinguished by the highest proportion of phanerophytes and the lowest soil solution mineralisation among the analysed clusters, which supports its interpretation as a more woody and less mineral-rich riparian habitat. These stands are therefore best interpreted as a transformed variant of T111223, because they retain clear affinity to Eastern Ponto-Sarmatic willow galleries through the prominence of *Salix alba* and the woody floodplain character of the vegetation. At the same time, their present-day floristic composition reflects marked disturbance, invasion, and ruderalisation. This interpretation is consistent with the geographic scope and structural concept of T111223 in EUNIS, especially for habitats of the lower Dnipro basin.

T147 Ponto-Sarmatic mixed *Populus* riverine forests comprise mixed riverine forests of the floodplains of rivers of the Pontic and Sarmatic steppes, wooded steppes, and southern nemoral forests of southern Eastern Europe, including the lower Dnipro basin. In the EUNIS concept, this habitat is dominated by or rich in *Populus alba*, *Populus nigra*, and *Populus canescens* and occupies alluvial sites shaped by periodic flooding and fluvial sediment dynamics. In the studied floodplain, this habitat is represented by a strongly transformed variant of Ponto-Sarmatic mixed *Populus* riverine forest. Its local floristic expression is characterised by a woody core with *Populus alba*, *Ulmus laevis*, *Rubus caesius*, *Crataegus fallacina,* and *Ulmus glabra*, combined with a pronounced nitrophilous and synanthropic component. High-fidelity values are particularly evident in the clusters for *Galium aparine, Alliaria petiolata*, *Celtis occidentalis*, *Acer negundo*, *Anthriscus sylvestris*, and *Chelidonium majus*. At the same time, *Populus alba* remains an important component of the woody layer. This combination indicates a floodplain poplar forest that still retains a clear affinity with the EUNIS concept of T147, but whose present-day species composition reflects substantial ruderalisation, invasion, and anthropogenic alteration. These stands are therefore best interpreted as a transformed, white-poplar-rich variant of T147, rather than as a more narrowly defined regional subtype. Such an interpretation preserves both the correct biogeographic framework for the Lower Dnipro and the evident floristic affinity to mixed *Populus* riparian forests, while acknowledging that the herb and shrub layers are now heavily modified by invasive and disturbance-tolerant species.

T1315 Sarmatic riverine oak forests comprise floodplain oak forests of the great rivers of the Sarmatic nemoral and nemoro-steppe regions, extending southwards into the Pontic region, including the lower Dnipro. In the EUNIS concept, this habitat is associated with hardwood riparian forests centred on *Quercus robur*, accompanied by other broadleaved trees of periodically flooded but relatively stable alluvial sites. In the studied floodplain, this habitat is represented by a floristically transformed floodplain oak forest. Its local floristic expression is characterised by *Quercus robur* together with *Crataegus monogyna*, *Pyrus communis,* and *Dactylis glomerata*. At the same time, the herb layer is strongly enriched by ruderal and synanthropic species such as *Stellaria media*, *Lamium purpureum*, *Anisantha tectorum*, and *Silene latifolia*. This combination indicates a hardwood floodplain forest with an oak-dominated core, but with marked anthropogenic alteration and ruderalisation. These stands are therefore best interpreted as a transformed variant of T1315, because they retain clear affinity to Sarmatic riverine oak forests through the presence of *Quercus robur* and the community's general hardwood floodplain character. At the same time, their present-day species composition reflects substantial disturbance of the original forest structure. This interpretation is consistent with the geographic scope and structural concept of T1315 in EUNIS.

R11 Pannonian and Pontic sandy steppe comprises rather open steppe grasslands of nutrient-poor sandy soils on plains and dunes of the Pannonian and Pontic regions, characterised by a continental climate, a pronounced psammophytic component, and frequent spring annuals and cryptogams. In the EUNIS concept, this habitat is characterised by open sandy-steppe vegetation, including species such as *Secale sylvestre*, *Artemisia campestris*, *Silene borysthenica*, and *Syntrichia ruralis*. In the studied floodplain, this habitat is represented by floodplain psammophytic steppe developing in elevated nutrient-poor alluvial sands, rather than by wet floodplain vegetation *sensu stricto*. Its local floristic expression is characterised by *Secale sylvestre*, *Vicia villosa*, *Artemisia campestris*, *Seseli tortuosum*, *Asparagus officinalis*, *Centaurea borysthenica*, *Chondrilla juncea*, *Carex colchica*, *Euphorbia seguieriana*, *Silene borysthenica*, and *Syntrichia ruralis*, all concentrated in Cluster 10 of the synoptic table. These stands are therefore best interpreted as a floodplain variant of R11, because their floristic core comprises continental psammophytic steppe species associated with dry, nutrient-poor sands. By contrast, their occurrence within the floodplain is explained by geomorphologically elevated sandy alluvia rather than by mesic or hydric floodplain conditions. This interpretation is consistent with the EUNIS concept of R11 as open sandy steppe vegetation with frequent annuals and cryptogams, even though in the present case, the habitat is embedded within a floodplain landscape.

The topographic variables revealed a clear geomorphological differentiation of habitat types (Fig. 1). The strongest contrasts were associated with elevation (DEM), topographic position indices, particularly TPI 11 × 11, and the topographic wetness index (TWI). By contrast, the slope showed comparatively weaker differentiation among habitats. The habitats R11, T111223, T147, and T1315 were generally associated with higher elevations and positive TPI values, indicating their occurrence on elevated and locally convex landforms of the sandy terrace. Within this group, R11 was additionally characterised by relatively low slope, roughness, and TRI values, suggesting comparatively flat, elevated, sandy surfaces, whereas T111223, T147, and T1315 occupied similarly elevated but more structurally heterogeneous positions. Meanwhile, Q61, Q62, F9.12, R5523, Q516, C3.6, and C2.3 were associated with lower elevations, predominantly negative TPI values, and higher TWI, indicating depressions, lower alluvial positions, and moisture-accumulating landforms. Among them, F9.12, R5523, and Q516 were further distinguished by relatively high roughness and TRI values, consistent with more heterogeneous river-margin or humid-depression topography, whereas Q61 and Q62 were linked to the lowest geomorphological positions. R1BA11 occupied an intermediate position, being relatively low in elevation but less clearly associated with wet depressions than the alluvial and water-margin habitats. Overall, the observed pattern indicates that habitat-type diversity is strongly structured by the contrast between elevated, convex, well-drained sandy landforms and lower, concave, moisture-accumulating alluvial depressions.

The box plots revealed clear differences in phytoindication scores among habitat types, indicating pronounced ecological differentiation of the studied communities (Fig. 2). Psammophytic grasslands were generally characterised by higher light availability, temperature regime, continentality, soil reaction, and naturalness, reflecting their occurrence in elevated, dry, and relatively undisturbed sandy sites. By contrast, shore habitats showed higher soil moisture and nutrient availability, consistent with their association with lower, wetter, and more alluvial positions in the landscape. Grassland habitats occupied an intermediate position for most phytoindication variables. At the same time, forest and shrub habitats tended to be associated with lower light availability and, in some cases, greater moisture and nutrient supply. Hemeroby also varied significantly among habitat types, indi-

cating differences in the degree of anthropogenic transformation. The observed pattern demonstrates that habitat-type diversity is accompanied by consistent differentiation in ecological conditions as reflected by phytoindication scores. Psammophytic grasslands are shifted towards higher values of light availability, temperature, continentality, soil reaction, and naturalness, consistent with their occurrence in dry, elevated, sandy sites. Wetlands, in turn, are associated with higher soil moisture and nutrient availability, reflecting their confinement to wetter and more productive parts of the landscape. Forest habitats are characterised by reduced light availability and comparatively moist conditions, whereas shrub habitats generally occupy intermediate positions between forest and open habitats. Shore habitats also exhibit transitional values, but remain closer to the wetter end of the ecological spectrum.

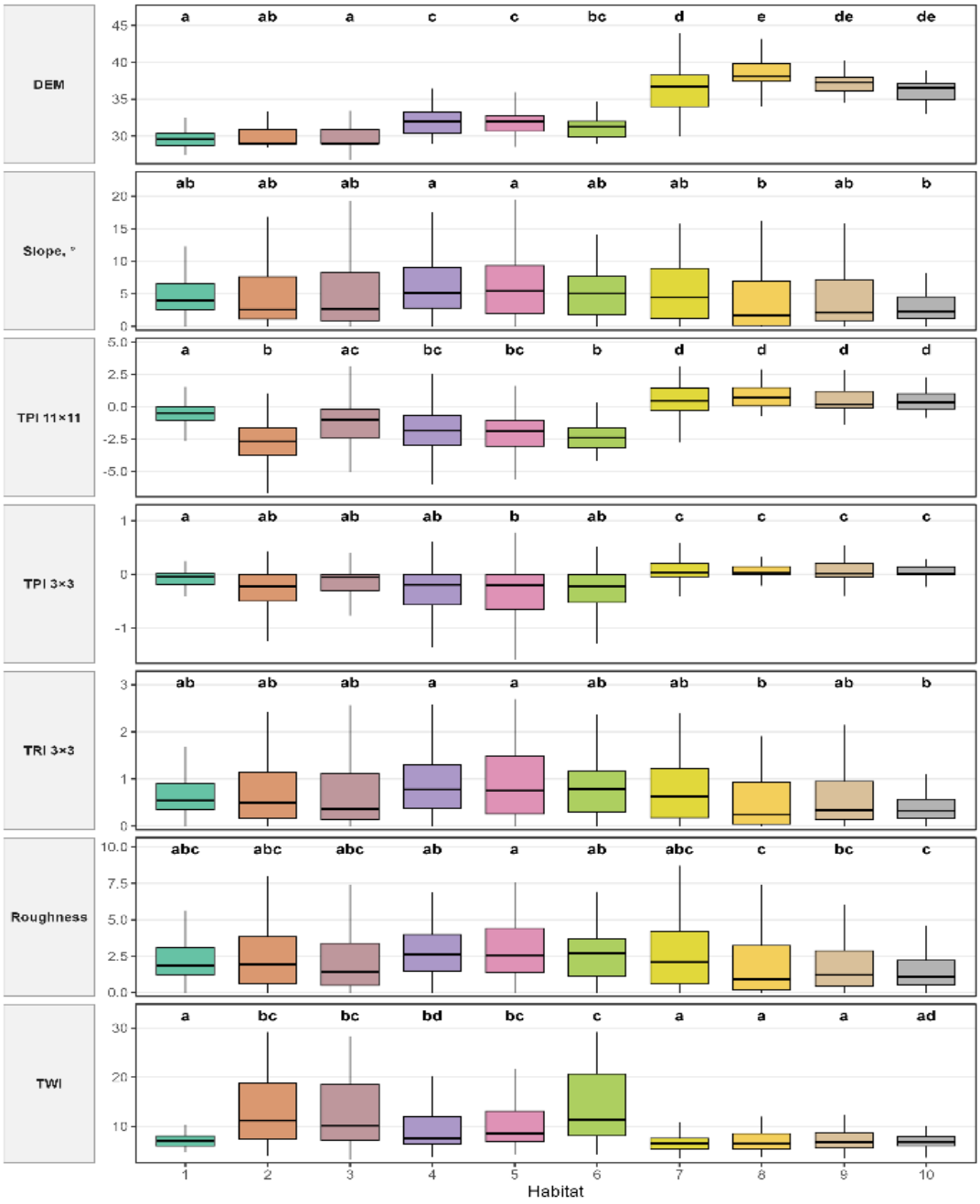

Fig. 1. Box plots showing the variation in topographic variables among habitat types: The horizontal line inside each box represents the median; the box indicates the interquartile range (25th to 75th percentile); the whiskers extend to the smallest and largest values that do not exceed 1.5 × IQR from the box boundaries; letters above the boxes indicate statistically homogeneous groups according to Dunn's post hoc test with Holm-adjusted P-values; identical letters denote no statistically significant difference between habitat types, whereas different letters indicate a statistically significant difference: 1 – R1BA11 Corispermum pioneer swards; 2 – Q61 Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation; 3 – Q62 Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation; 4 – F9.12 Lowland and collinar riverine *Salix* scrub comprises linear shrubby willow formations along river banks in plains, hills, and low mountains, developing in alluvial substrates subject to periodic flooding and fluvial disturbance; 5 – R5523 Continental tall-herb communities of humid meadows comprise river-bank and freshwater humid-depression tall-herb vegetation of the continental steppe zone; 6 – Q516 *Phalaris arundinacea* beds comprise vegetation of the margins of lakes, rivers, brooks, and swamps dominated by *Phalaris arundinacea*, either in relatively pure stands or mixed with other tall wetland species; 7 – T111223 Eastern Ponto-Sarmatic steppe willow galleries; 8 – T147 Ponto-Sarmatic mixed *Populus* riverine forests; 9 – T1315 Sarmatic riverine oak forests; 10 – R11 Pannonian and Pontic sandy steppe; 11 – C3.6 – Unvegetated or sparsely vegetated shores with soft or mobile sediments; 12 – C2.3 Permanent non-tidal, smooth-flowing watercourses

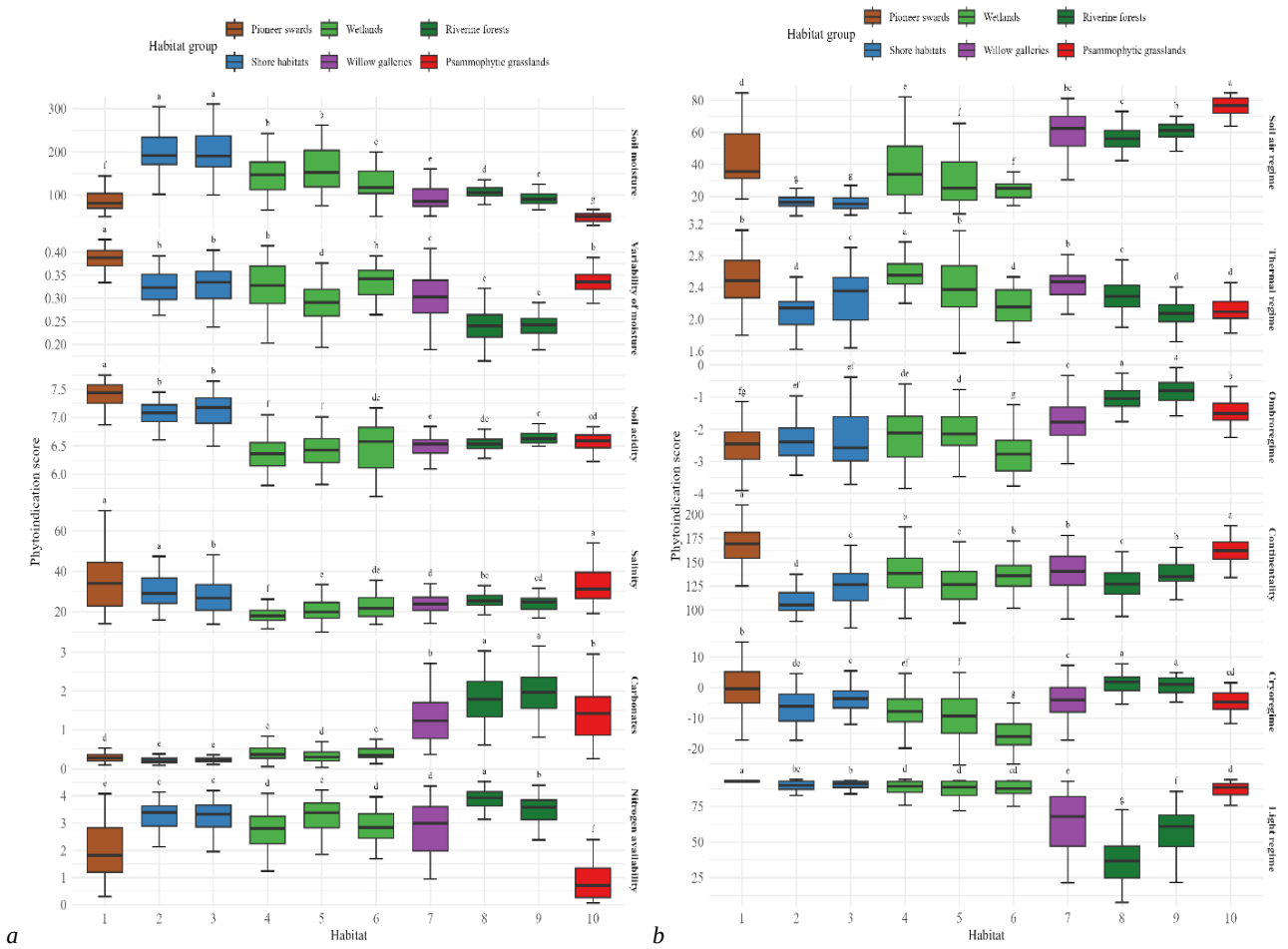

Fig. 2. Box plots showing the variation in Didukh phytoindication scores among habitat types: *a* – edaphic and soil-moisture-related indicators: Hd, fH, Rc, Sl, Ca, Nt; *b* – aeration, climatic, and light-related indicators: Ae, Tm, Om, Kn, Cr, Lc; the horizontal line inside each box represents the median; the box indicates the interquartile range (25th to 75th percentile); the whiskers extend to the smallest and largest values that do not exceed 1.5 × IQR from the box boundaries; letters above the boxes indicate statistically homogeneous groups according to Dunn's post hoc test with Holm-adjusted P-values; identical letters denote no statistically significant difference between habitat types, whereas different letters indicate a statistically significant difference: 1 – R1BA11 *Corispermum* pioneer swards; 2 – Q61 Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation; 3 – Q62 Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation; 4 – F9.12 Lowland and collinar riverine *Salix* scrub comprises linear shrubby willow formations along river banks in plains, hills, and low mountains, developing in alluvial substrates subject to periodic flooding and fluvial disturbance; 5 – R5523 Continental tall-herb communities of humid meadows comprise river-bank and freshwater humid-depression tall-herb vegetation of the continental steppe zone; 6 – Q516 *Phalaris arundinacea* beds comprise vegetation of the margins of lakes, rivers, brooks, and swamps dominated by *Phalaris arundinacea*, either in relatively pure stands or mixed with other tall wetland species; 7 – T111223 Eastern Ponto-Sarmatic steppe willow galleries; 8 – T147 Ponto-Sarmatic mixed Populus riverine forests; 9 – T1315 Sarmatic riverine oak forests; 10 – R11 Pannonian and Pontic sandy steppe; 11 – C3.6 – Unvegetated or sparsely vegetated shores with soft or mobile sediments; 12 – C2.3 Permanent non-tidal, smooth-flowing watercourses

The CSR ternary diagrams indicate clear differences among habitat types in the relative importance of competitor (C), stress-tolerator (S), and ruderal (R) components (Fig. 3). Q61, Q62, T111223, and T147 are shifted towards a stronger competitive component, whereas F9.12 and Q516 are more clearly displaced towards the stress-tolerant part of the CSR space. T1315 and R11 occupy a more compact position in the lower central part of the diagrams, indicating comparatively low competitive values and a predominance of mixed stress-tolerant and ruderal characteristics. R1BA11 and especially R5523 display broader point clouds, reflecting greater internal heterogeneity and a wider range of CSR strategies. Overall, the diagrams indicate that habitat-type differentiation is accompanied by consistent shifts in plant-strategy composition, from more competitive assemblages to communities characterised by stronger stress-tolerant or ruderal components.

Detrended correspondence analysis was applied as an exploratory ordination to determine the most appropriate constrained ordination method for the subsequent analysis. The first DCA axis had a length of 8.60 standard deviation units, which substantially exceeded the commonly used threshold of 2–3 SD units. This indicates a high rate of species turnover along the main compositional gradient and suggests predominantly unimodal species responses. Therefore, the use of Canonical Correspondence Analysis (CCA) in the subsequent ordination was considered justified. A constrained ordination of the environmental variables showed that habitat type had a highly significant effect on the variation in these variables. Canonical Correspondence Analysis (CCA) with habitat type as the explanatory factor revealed a significant model effect (χ^2 = 0.0082, F = 68.26, P < 0.001). This indicates that water type is associated with statistically significant differences in the overall environmental conditions represented by the selected ecological predictors. A permutation test by term yielded the same result because the model included only one explanatory factor. In this respect, water type can be regarded as an important determinant of the environmental differentiation of the studied communities.

A Partial CCA was then applied to evaluate the effect of the environmental predictors on species composition while controlling for habitat type. The global permutation test demonstrated that the set of predictors had a highly significant effect on species composition (χ^2 = 3.56, F = 8.88, P < 0.001). The constrained fraction corresponded to 3.45% of the total inertia in species composition. All predictors were individually significant in sequential tests, with χ^2 values ranging from 0.16 for Ae to 0.40 for Hd, and F-ratios ranging from 5.49 to 13.81 (Table 1).

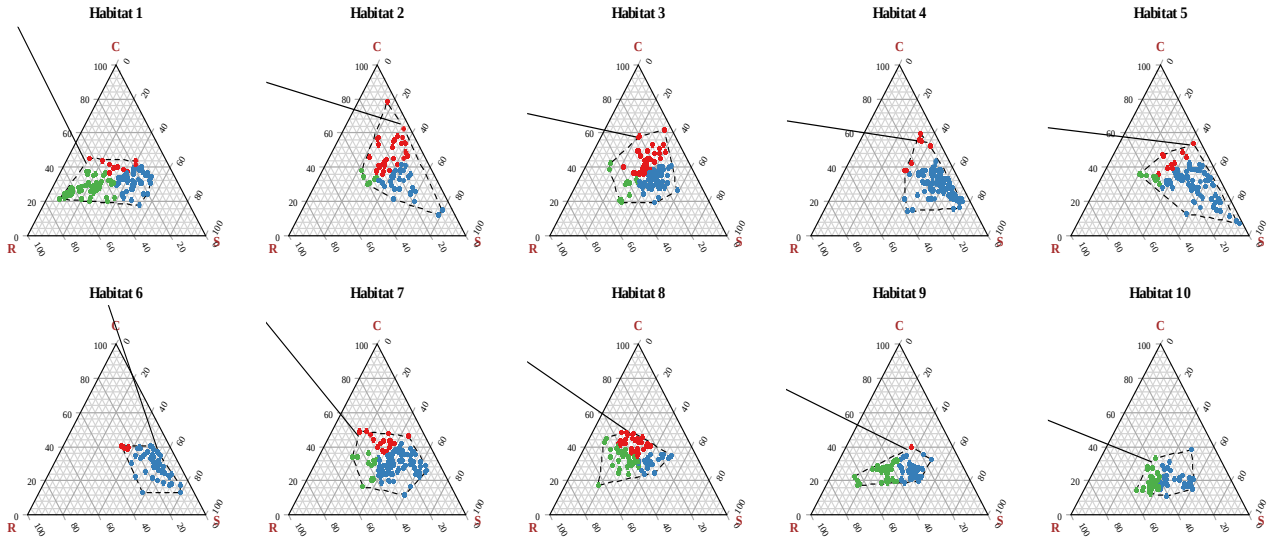

Fig. 3. CSR ternary diagrams of vegetation *relevés* for the ten habitat types: points represent individual *relevés* and are coloured by the dominant CSR strategy component: competitor (red), stress-tolerator (blue), and ruderal (green); dashed lines indicate convex hulls enclosing the point clouds

Table 1
Results of Canonical Correspondence Analysis (CCA) and principal component analysis (PCA) for environmental variables

Variable	CCA			PCA			
	Df	Chi-square	*F*-ratio	PC1, λ = 3.7, 26.4% variation explained	PC2, λ = 3.4, 24.0% variation explained	PC3, λ = 1.8, 12.9% variation explained	PC4, λ = 1.3, 9.6% variation explained
Hd	1	0.39	13.81	0.25	0.42	–0.05	0.11
fH	1	0.31	10.91	0.31	–0.38	–0.04	0.05
Rc	1	0.39	13.80	0.23	–0.15	0.37	0.41
Sl	1	0.21	7.36	0.12	–0.19	0.51	0.09
Ca	1	0.21	7.42	–0.44	–0.05	0.17	–0.09
Nt	1	0.31	10.90	–0.10	0.44	0.03	0.19
Ae	1	0.16	5.49	–0.36	–0.30	0.10	–0.11
Tm	1	0.25	8.82	–0.01	0.02	–0.36	0.57
Om	1	0.16	5.54	–0.38	0.15	0.04	–0.07
Kn	1	0.19	6.55	–0.02	–0.39	0.03	–0.01
Cr	1	0.18	6.23	–0.22	0.02	0.32	0.59
Lc	1	0.27	9.41	0.40	–0.16	–0.08	–0.07
Naturalness	1	0.27	9.51	0.29	0.30	0.28	–0.21
Hemeroby	1	0.25	8.60	–0.06	–0.20	–0.49	0.19
Residual	862	24.66	–	–	–	–0.05	0.11

The largest contributions were associated with Hd, Rc, fH, and Nt, whereas Ae, Om, and Cr showed comparatively smaller, though still highly significant, effects. Principal component analysis of the environmental predictors revealed that the first four axes accounted for a substantial proportion of the total variation. According to the loadings presented in Table 1, PC1 (λ = 3.7, 26.4% of variation explained) was positively related to Lc, fH, Naturalness, and Hd, and negatively related to Ca, Ae, Om, and Cr. This axis can therefore be interpreted as a gradient contrasting communities with higher values of these structural and naturalness-related characteristics against communities associated with higher calcium status, aeration, ombroregime, and cryoregime. PC2 (λ = 3.4, 24.0%) was positively associated mainly with Nt, Hd, and naturalness, and negatively with fH, Kn, Ae, and hemeroby, thus reflecting a second major gradient opposing more natural conditions to more hemerobic ones. PC3 (λ = 1.8, 12.9%) was most strongly related to Sl, Rc, Cr, naturalness, and hemeroby, whereas PC4 (λ = 1.3, 9.6%) was mainly defined by Tm and Cr, with additional positive contributions from Rc.

The ordination pattern clearly shows that the principal components of environmental variability closely correspond to the main axes of community variation, indicating that the differentiation of habitats is governed by the same leading ecological gradients (Fig. 4). PC1 is primarily marked by the joint variation of Lc, fH, Hd, and naturalness, opposed to Ca, Ae, Om, and Cr, whereas PC2 is mainly associated with Hd and Nt in contrast to fH and Kn, with a secondary contribution of naturalness. Therefore, the diversity of habitat types can be interpreted as a consequence of differentiation along these two major synthetic ecological gradients.

The spatio-temporal pattern of habitats in the southern floodplain part of Khortytsia Island changed profoundly between 2022 and 2025 in response to the destruction of the Kahovka Reservoir in 2023 (Fig. 5). In 2022, the area was still characterised by the persistence of floodplain water bodies, river-margin habitats, and relatively stable aquatic and wetland vegetation. The first stage of post-catastrophic transformation, evident as early as 2023, was characterised by the rapid disappearance of internal floodplain water bodies on the island and the contraction of permanently inundated habitats. As the water level continued to decline, large areas of the former Dnipro riverbed and associated shallow-water zones became exposed, which led to the rapid expansion of unvegetated or sparsely vegetated substrates and pioneer habitats of freshly exposed sediments. During the subsequent phase, especially in 2024–2025, these newly exposed surfaces underwent rapid successional differentiation. A heterogeneous mosaic of pioneer swards, ephemeral river-margin communities, wet tall-herb stands, reed canary-grass beds, and willow scrub progressively replaced the initially dominant open alluvial and shoreline habitats. At the same time, substantial changes also occurred in the previously terrestrial part of the island, where alterations in the hydrological regime affected the spatial configuration and relative extent of wetland, shrub, forest, and psammophytic habitats. As a result, the vegetation cover shifted from a comparatively stable floodplain pattern towards a highly dynamic post-reservoir mosaic shaped by drainage, sediment exposure, and accelerated succession.

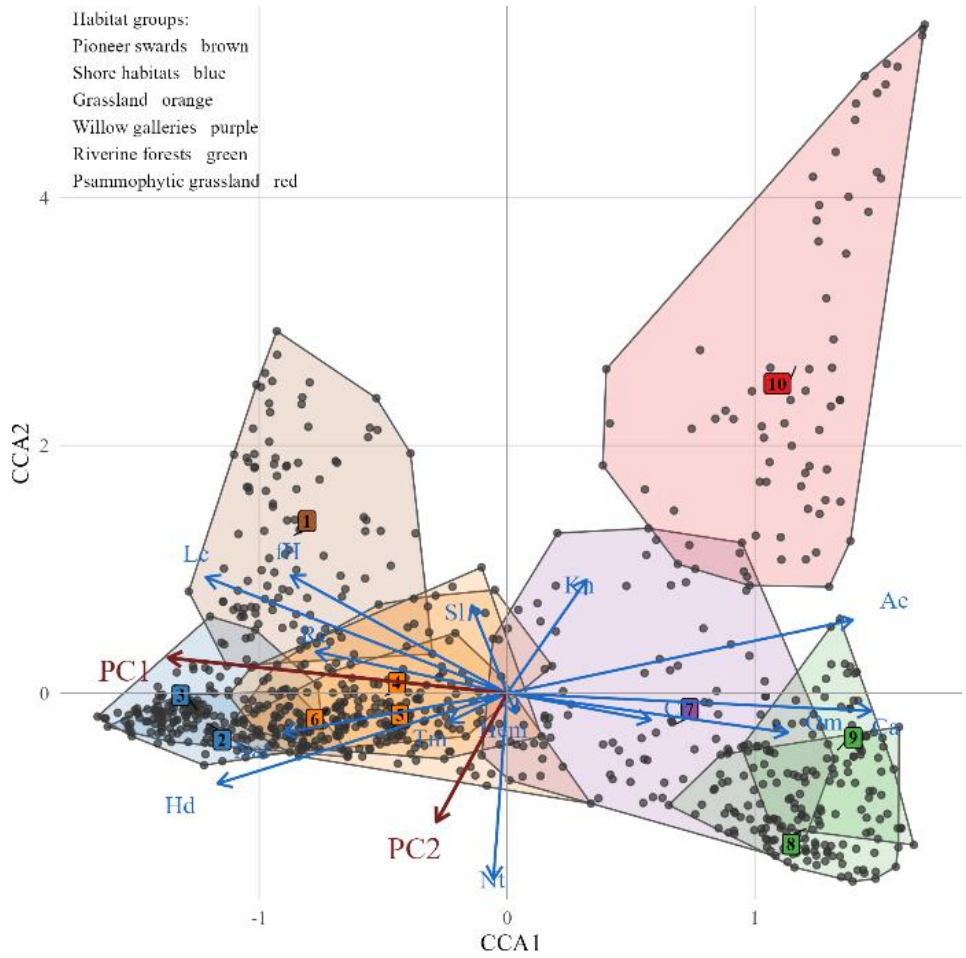

Fig. 4. Canonical Correspondence Analysis (CCA) ordination diagram of habitats and their relationships with environmental variables: *1* – R1BA11 *Corispermum* pioneer swards; *2* – Q61 Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation; *3* – Q62 Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation; *4* – F9.12 Lowland and collinar riverine *Salix* scrub comprises linear shrubby willow formations along river banks in plains, hills, and low mountains, developing in alluvial substrates subject to periodic flooding and fluvial disturbance; *5* – R5523 Continental tall-herb communities of humid meadows comprise river-bank and freshwater humid-depression tall-herb vegetation of the continental steppe zone; *6* – Q516 *Phalaris arundinacea* beds comprise vegetation of the margins of lakes, rivers, brooks, and swamps dominated by *Phalaris arundinacea*, either in relatively pure stands or mixed with other tall wetland species; *7* – T111223 Eastern Ponto-Sarmatic steppe willow galleries; *8* – T147 Ponto-Sarmatic mixed Populus riverine forests; *9* – T1315 Sarmatic riverine oak forests; *10* – R11 Pannonian and Pontic sandy steppe; *11* – C3.6 – Unvegetated or sparsely vegetated shores with soft or mobile sediments; *12* – C2.3 Permanent non-tidal, smooth-flowing watercourses

Discussion

Harmonisation of habitat nomenclature with EUNIS is necessary to link locally distinguished vegetation units to a standardised, widely recognised habitat classification framework (Rendón et al., 2025). Such harmonisation ensures that habitat interpretation is not limited to local naming practices but is based on formal definitions, official keys, fact sheets, and crosswalks, thereby improving the reproducibility and transparency of classification. It also makes the results comparable with other regional and European studies, habitat maps, and conservation assessments. This is especially important for transformed floodplain ecosystems, where many local communities are best interpreted as regional or disturbance-modified variants of broader EUNIS habitat concepts rather than as isolated local units. In addition, harmonisation allows nomenclatural consistency across revisions of the EUNIS hierarchy. In the context of the Kahovka disaster, harmonisation of locally identified habitat types with EUNIS is important because it translates site-specific post-catastrophic changes into a standardised classification framework that is understandable and comparable at the European and international levels. This is especially relevant for communicating the scale of environmental damage caused by Russian aggression, since the observed changes can then be described not merely as local vegetation shifts, but as the loss, transformation, or replacement of formally recognised habitat types. In the studied floodplain, the destruction of the Kahovka Reservoir triggered a profound reorganisation of hydrology, shoreline morphology, soil-moisture conditions, and habitat structure, resulting in the contraction of permanently inundated habitats and the rapid expansion of pioneer, shore, tall-herb, scrub, and transformed forest habitats. By aligning these changes with EUNIS concepts, the results become suitable for international conservation assessments, cross-regional comparisons, and evidence-based communication of war-related environmental damage. Habitat identification in the present study was based on a hierarchical combination of floristic, geomorphological, and physiognomic criteria rather than on any single diagnostic feature. The primary basis was floristic classification: Vegetation *relevés* were first grouped by TWINSPAN into operational floristic units, after which diagnostic species were identified using fidelity values and the statistical significance of indicator analysis. These synoptic tables provided the local species-based framework for habitat assignment. However, final identification was not limited to local floristic distinctness alone, but was validated through comparison with EUNIS key navigation, fact-sheets, formal definitions, and official crosswalks. Geomorphological position and morphometric terrain variables served as additional criteria when floristic evidence alone was insufficient for unambiguous discrimination among candidate habitat types, especially along the major floodplain gradient from elevated, well-drained sandy surfaces to lower, wetter alluvial depressions. Vegetation physiognomy also

played an important interpretive role, particularly in distinguishing scrub from forest, drawdown-shore communities from reed beds, and tall-herb stands from other wetland formations. Such a multi-criteria approach was especially necessary under the post-catastrophic conditions of the Khortytsia floodplain, where habitat transformation, ruderalisation, and rapid succession often produced local or disturbed variants of broader EUNIS habitat concepts rather than textbook expressions of them.

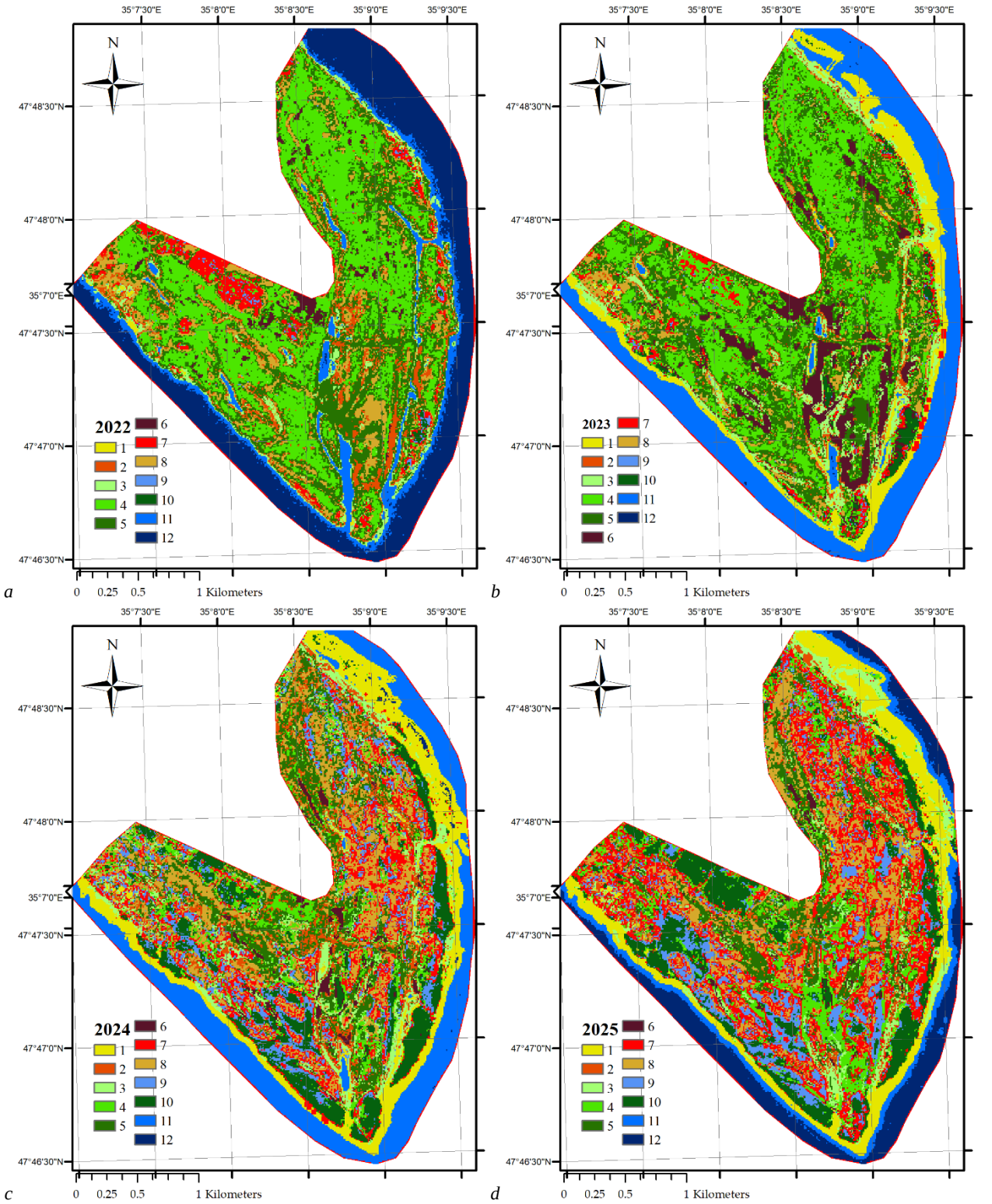

Fig. 5. Spatial variation in the distribution of habitat types classified according to EUNIS: *1* – R1BA11 Corispermum pioneer swards; *2* – Q61 Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation; *3* – Q62 Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation; *4* – F9.12 Lowland and collinar riverine *Salix* scrub comprises linear shrubby willow formations along river banks in plains, hills and low mountains, developing in alluvial substrates subject to periodic flooding and fluvial disturbance; *5* – R5523 Continental tall-herb communities of humid meadows comprise river-bank and freshwater humid-depression tall-herb vegetation of the continental steppe zone; *6* – Q516 *Phalaris arundinacea* beds comprise vegetation of the margins of lakes, rivers, brooks, and swamps dominated by *Phalaris arundinacea*, either in relatively pure stands or mixed with other tall wetland species; *7* – T111223 Eastern Ponto-Sarmatic steppe willow galleries; *8* – T147 Ponto-Sarmatic mixed *Populus* riverine forests; *9* – T1315 Sarmatic riverine oak forests; *10* – R11 Pannonian and Pontic sandy steppe; *11* – C3.6 Unvegetated or sparsely vegetated shores with soft or mobile sediments; *12* – C2.3 Permanent non-tidal, smooth-flowing watercourses

Geomorphological factors made a substantial contribution to habitat differentiation by providing the spatial framework within which floristic variation was expressed (Castañeda et al., 2020). Elevation (DEM) was the most important variable, effectively separating the habitats into three major groups: R1BA11, Q61, and Q62; F9.12, R5523, and Q516; and T111223, T147, T1315, and R11. This sequence reflects a transition from lower alluvial and shore-related positions through intermediate wet floodplain sites to higher, better-drained elements of the sandy terrace. Other terrain derivatives further refined this pattern by characterising the local specificity of particular habitat types. TPI showed that R1BA11, although belonging to the lower geomorphological block, occupies relatively elevated or weakly convex microsites within the low floodplain, which is otherwise more typical of higher habitats. Slope reached its highest values in F9.12, while TRI was highest in F9.12 and R5523, indicating the greatest structural heterogeneity in river-margin and humid-depression habitats. In turn, TWI most clearly distinguished Q61, Q62, and Q516, emphasising their association with lower, moisture-accumulating parts of the floodplain. DEM defined the main altitudinal gradient of habitat differentiation. By contrast, TPI, TRI, slope, and TWI provided additional detail that helped to distinguish between shore, depression, pioneer sandy, and elevated terrace-related habitats. The geomorphological control of habitat differentiation reveals the roles of parent materials and the redistribution of moisture and solar energy across the floodplain landscape. The contrast between elevated, convex, well-drained sandy landforms and lower, concave, moisture-accumulating alluvial depressions defines the spatial segregation of habitat types and shapes their ecological regimes. This interpretation is consistent with the phytoindication patterns, which show that psammophytic habitats are associated with drier, warmer, and more light-exposed conditions. At the same time, shore and wet floodplain habitats are linked to higher soil moisture and more productive alluvial positions. In this context, the catastrophic lowering of water levels after the destruction of the Kahovka Reservoir should be regarded as a hydrological disturbance and as a driver of profound shifts in the moisture regime, drainage conditions, substrate exposure, and surface energy balance. Such changes are expected to affect both the present condition and the future diversity of habitats, because they promote drainage, accelerated succession, ruderalisation, and the formation of novel post-catastrophic habitat mosaics.

Phytoindication of ecological factors plays a central role in understanding habitat differentiation, as it enables moving from a purely floristic description to an interpretation of the underlying environmental gradients structuring vegetation cover (Nykytiuk et al., 2025). In the present study, habitat types differed in species composition and in their position along complex ecological axes related to moisture, substrate aeration, nutrient availability, soil reaction, temperature regime, light availability, and continentality. In this respect, phytoindication values allowed the identified habitats to be interpreted not simply as formal classification units, but as expressions of different ecological states of the floodplain landscape. The results clearly show that phytoindication captures the main directions of ecological differentiation among habitat types. Psammophytic habitats were associated with higher values of light availability, temperature regime, continentality, soil reaction, and naturalness, which is consistent with their occurrence on elevated, drier, and better-drained sandy surfaces. By contrast, shore and wet floodplain habitats showed higher values of soil moisture and nutrient availability, reflecting their association with lower, wetter, and more productive alluvial positions. Forest and shrub habitats, in turn, were characterised by lower light availability and, in some cases, higher moisture and nutrient supply. Ordination analysis further demonstrated that these phytoindication-based environmental predictors contributed significantly to compositional differentiation, with the strongest effects associated with Hd, Rc, fH, and Nt. In the post-catastrophic context of the Khortytsia floodplain, this approach is especially important because it reveals how the destruction of the Kahovka Reservoir has altered moisture, aeration, fertility, and light regimes, thereby shaping the present condition and future differentiation of habitat diversity. PCA axes are derived statistically from the covariance (or correlation) structure of the environmental variables included in the analysis. They are not directly measured factors but synthetic gradients that represent the main directions of joint variation among the predictors. Therefore, each PCA axis should be interpreted in terms of the variables with the strongest loadings, rather than as a single independent ecological factor. The PCA axes should be interpreted not as isolated variables, but as synthetic ecological gradients along which habitat types diverge. The first two axes are the most important because, together, they explain more than half of the variation in environmental predictors. At the same time, the strongest overall contributions come from Hd, Rc, fH, and Nt. PC1 can be interpreted as the principal gradient of soil and air moisture, accompanied by inverse changes in carbonate content. Along this axis, the clearest contrast is between wetter and less carbonate-rich habitats, such as Q61, Q62, R5523, Q516, and partly F9.12, and drier, more aerated, and more carbonate-rich habitats, especially R11 and, to some extent, R1BA11. The forest habitats T111223, T147, and T1315 most likely occupy intermediate positions, being less dry than R11 but less open and hydromorphic than the drawdown-shore and wetland communities. PC2 reflects the joint roles of moisture and nitrogen availability, thereby distinguishing highly productive wet habitats, particularly R5523, Q516, and Q61, from drier, less fertile sandy habitats such as R11 and R1BA11. At the same time, Q62 occupies an intermediate mesotrophic position. PC3 represents a finer substrate-chemistry gradient, mainly associated with soil reaction and salinity, separating habitats of exposed or alluvial substrates from woody floodplain habitats with lower mineralisation; in this respect, T111223 is especially informative because it shows the lowest soil-solution mineralisation. PC4 may be interpreted as an even narrower axis of substrate reaction, although formally it also includes temperature- and cryoregime-related variation. In practical terms, it refines the ecological separation among habitats that are already relatively close in hydrological position but differ in the chemical properties of their substrates. Overall, the PCA shows that the first two axes mainly describe hydrological and trophic differentiation of habitats, whereas the third and fourth axes add the chemical specificity of the substrate.

Naturalness and hemeroby should be interpreted not as primary abiotic drivers, but as integrative descriptors of habitat condition (Nykytiuk et al., 2025). They reflect the extent to which vegetation retains its natural organisation or, conversely, shows signs of anthropogenic transformation. The fact that naturalness has appreciable loadings on all major PCA axes (PC1 = 0.29, PC2 = 0.30, PC3 = 0.28, PC4 = –0.21) indicates that naturalness is not linked to a single environmental gradient, but is shaped jointly by hydrological conditions, nutrient regime, substrate chemistry, and habitat structure. Hemeroby shows a different pattern, with its strongest loading on PC3 (–0.49), weaker contributions to PC2 (–0.20) and PC4 (0.19), and only a negligible contribution to PC1 (–0.06). This suggests that anthropogenic transformation in the studied floodplain is most strongly expressed along the finer gradient of substrate chemistry, and is also related to the combined moisture–fertility gradient represented by PC2. Thus, both naturalness and hemeroby permeate the entire PCA structure because habitat transformation in the Khortytsia floodplain is not confined to a single ecological dimension, but is embedded in the overall reorganisation of hydrology, substrate properties, nutrient conditions, and floristic structure. This interpretation is further supported by the presence of several habitat types represented by transformed or ruderalised variants, indicating that post-catastrophic and anthropogenic impacts are deeply integrated into the present ecological differentiation of habitats.

In the CSR context, the habitat types differ in floristic composition and in their prevailing adaptive strategies related to competition, stress tolerance, and disturbance. Q61, Q62, T111223, and T147 are shifted toward a stronger competitive component, indicating habitats associated with relatively productive conditions, where resource acquisition and competitive exclusion play important roles. In Q61 and Q62, this pattern is likely related to nutrient-rich alluvial substrates and the rapid colonisation of newly exposed surfaces after water-level decline. By contrast, in T111223 and T147, it reflects the structural importance of woody vegetation and the generally higher resource availability of floodplain forest habitats. Meanwhile, F9.12 and Q516

are more clearly displaced towards the stress-tolerant part of the CSR space, suggesting that their vegetation is shaped more strongly by ecological instability, hydrological variability, and tolerance to environmental stress than by competitive dominance. T1315 and R11 occupy a more compact position in the lower central part of the triangle, with comparatively low competitive values and a predominance of mixed stress-tolerant and ruderal characteristics. In R11, this is consistent with dry, nutrient-poor sandy conditions. At the same time, in T1315, it likely reflects the transformed state of the floodplain oak forest and the strong admixture of ruderal and synanthropic species. R1BA11 and especially R5523 show broad point clouds, indicating greater internal heterogeneity and a wider range of CSR strategies. This suggests that pioneer sandy vegetation and humid tall-herb communities are ecologically less uniform and may shift among competitive, stress-tolerant, and ruderal tendencies depending on local moisture, disturbance, and successional stage. The CSR pattern shows that habitat differentiation in the Khortytsia floodplain is expressed in environmental position and in contrasting modes of ecological persistence and post-catastrophic adjustment.

The dynamic aspect of habitat structure is particularly important because the Kahovka disaster caused a profound and multidirectional transformation of the spatial organisation of habitats in the floodplain part of Khortytsia Island. These changes affected not only the water bodies surrounding the island and the internal floodplain water bodies, but also the terrestrial parts of the floodplain, whose ecological condition was closely linked to the abrupt disruption of the hydrological regime. The study shows that, even at the initial post-disaster stage, some floodplain water bodies disappeared, permanently inundated habitats contracted, and large areas of the former riverbed and shallow-water zones became exposed. These newly exposed surfaces then became centres of rapid successional reorganisation, leading to the formation of a mosaic of pioneer, shore, tall-herb, scrub, and forest habitats. At the same time, changes also extended to previously more stable terrestrial parts of the floodplain, where an altered moisture regime, drainage conditions, and root-zone environment created preconditions for further vegetation transformation. Therefore, the disaster should be understood not as a single shift in habitat configuration, but as the beginning of a long-term process of spatial and ecological reorganisation that has continued since the destruction of the Kahovka Reservoir and is likely to proceed further through drainage, succession, ruderalisation, and the emergence of new post-catastrophic habitat mosaics.

The European Union biodiversity targets emphasise that the protection and restoration of ecosystems must become a central element of contemporary environmental policy. From this perspective, the Dnipro floodplain within the former Kahovka Reservoir should be considered a highly promising area for protected status. The spontaneous formation of new habitats, the rapid development of floodplain vegetation, and the conservation significance of the newly established communities demonstrate that this territory has already become an important site of ecological recovery. Establishing a protected area here would therefore not only contribute to biodiversity conservation but also provide an internationally legible response to the large-scale environmental destruction caused by the war. At the same time, such protection is fully compatible with the idea of Ukraine's post-war reindustrialisation, provided that this process is grounded in knowledge-intensive technologies, ecological modernisation, and non-exhaustive forms of resource use rather than in renewed pressure on natural ecosystems.

Conclusion

The floodplain of Khortytsia Island is now a highly dynamic area shaped by post-catastrophic processes, where the interplay of plant composition, geomorphology, ecological regimes, and vegetation strategies creates diverse habitats. Using geobotanical surveys, geomorphological data, and vegetation analysis, we identified ten terrestrial and two water-related habitat types, aligning them with the EUNIS classification for broader European comparison. Habitat differentiation mainly depends on moisture levels, substrate pH, and nutrients, while geomorphological features define the spatial context of these ecological differences. CSR patterns reveal that habitat types vary in species composition, environmental conditions, and dominant adaptive strategies related to competition, stress tolerance, and disturbance. The break of the dam of the Kahovka Reservoir triggered a major reorganisation of habitats around the island, affecting surrounding water bodies, internal floodplain waters, and terrestrial areas. The reduced extent of permanently flooded habitats, exposure of new alluvial surfaces, and rapid succession have created a new mosaic of pioneer, shoreline, wetland, scrub, and forest habitats. These ongoing changes suggest continued ecological transformation through drainage, succession, ruderalisation, and reorganisation. This study documents the current habitat diversity in Khortytsia's floodplain and provides crucial insights into the long-term ecological impacts of the Kahovka disaster.

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