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ECOLOGICAL STRATEGIES OF AQUATIC MACROPHYTES IN THE PRIPYAT RIVER BASIN. III. AN INTEGRATED FUNCTIONAL FRAMEWORK: FAMILY POTAMOGETONACEAE

Ecological strategies of submerged aquatic macrophytes are difficult to interpret using conceptual frameworks developed primarily for terrestrial plants because their ability to maintain populations, recover after disturbance, and cope with adverse environmental conditions depends on specific combinations of functional traits. The proposed r–K–S framework was applied to characterize the ecological strategies of 14 Potamogetonaceae species occurring in the Pripyat River basin based on functional traits, life-history characteristics, ecological indicator values, habitat associations, and available species-specific ecological evidence.

The analysis revealed substantial functional differentiation among closely related aquatic macrophytes: predominantly competitive strategies were identified for *Potamogeton gramineus, P. lucens, P. nodosus*, and *P. praelongus*, whereas *P. alpinus, P. natans*, and *P. perfoliatus* combined competitive persistence with substantial regenerative capacity, and *P. crispus* and *P. compressus* exhibited the reverse r–K configuration, with regeneration predominating over competitive persistence. Small fine-leaved species displayed contrasting strategies: *P. obtusifolius* and *P. berchtoldii* were assigned to the r–S group, *P. rutilus* exhibited an S–r configuration, and *P. friesii* was predominantly r-oriented, whereas the most multidimensional functional profile was observed in *Stuckenia pectinata*, which combined high scores for all three components.

The results did not support a direct association between habitat specialization and stress tolerance and revealed discrepancies between some previously published classifications, particularly CSR positions, and the criterion-based r–K–S configurations, indicating that ecological strategy frameworks developed primarily for terrestrial vegetation should be applied cautiously to permanently submerged plants. Overall, the results support a

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multidimensional interpretation of aquatic macrophyte strategies in which competitive persistence, regenerative capacity, and stress tolerance are regarded as complementary functional components expressed to varying degrees.

***Keywords*:** aquatic macrophytes; Potamogetonaceae; functional traits; ecological strategies; r–K–S framework; CSR; Pripyat River basin.

Problem statement. Freshwater habitats are undergoing profound ecological changes as a result of nutrient enrichment, modification of hydrological regimes, climate-related shifts, and increasing human pressure within river catchments [1–3]. Changes in aquatic vegetation are particularly important in this context because macrophytes contribute to nutrient cycling, sediment stabilization, habitat complexity, and biological productivity, while their abundance and species composition respond sensitively to alterations in environmental conditions [4–8].

Potamogetonaceae provide a particularly informative group for examining how aquatic plants persist under contrasting freshwater conditions. Most representatives are permanently submerged, while some species develop floating leaves, and the family encompasses marked variation in plant architecture, leaf morphology, clonal development, seasonal persistence, reproductive mechanisms, and regenerative capacity [9–12]. Such variation occurs among taxonomically related species sharing a predominantly aquatic mode of life and therefore offers an opportunity to examine how different combinations of traits correspond to alternative ecological strategies [11; 13–15].

Analysis of recent research and publications. Functional trait research has increasingly shifted attention from taxonomic identity alone towards the mechanisms underlying plant responses to environmental conditions. In freshwater vegetation, this perspective has been used to examine functional diversity, community assembly, species responses to eutrophication and hydrological change, and relationships between environmental filtering and macrophyte performance [16–19]. Recent studies further demonstrate substantial variation in macrophyte functional niches among growth forms and through the growing season, as well as species-specific changes in trait expression in response to nutrient loading and other environmental gradients. Recent evidence further indicates that functional trait syndromes contribute to structuring macrophyte diversity and functional redundancy across contrasting freshwater environments [20].

For submerged plants, however, relationships between measured traits and ecological strategy are not always straightforward. Their performance depends on a suite of interacting characteristics, including shoot architecture, clonality, vegetative propagules, perennial structures, leaf properties, and mechanisms of carbon acquisition. Recent studies confirm that submerged macrophytes may exhibit considerable functional plasticity in response to water depth, turbidity, nutrient conditions, and resource availability, and that coordinated trait responses can differ substantially among species.

This complexity becomes particularly relevant when ecological strategies are inferred using frameworks developed largely from terrestrial vegetation. CSR coordinates derived from plant size and leaf-economic traits provide valuable comparative information [21], but individual traits may have a different functional significance under permanent submergence. Leaf characteristics, for example, are strongly influenced by mechanisms of inorganic carbon acquisition [22], while persistence of the whole plant may depend on rhizomes, turions, shoot fragments, or other structures that are not represented directly by leaf-economic traits. Consequently, similar positions in a leaf-based functional space do not necessarily imply similar mechanisms of persistence, regeneration, or habitat occupation.

Recent studies indicate that functional trait expression in aquatic plants is strongly context-dependent. Seasonal variation may contribute substantially to the functional niche of submerged macrophytes [23], while ecological strategy expression may also change along environmental gradients. In Lake Taihu, CSR-based analysis revealed a shift in submerged macrophytes from predominantly R towards stronger C components with increasing eutrophication, demonstrating greater strategy flexibility than in floating-leaved and emergent macrophytes [24]. Such findings indicate that ecological strategy expression in submerged macrophytes cannot be interpreted independently of environmental context and further emphasize the need to distinguish trait-derived CSR positions from the broader mechanisms underlying whole-plant persistence, regeneration, and responses to environmental constraints.

For Potamogetonaceae, this issue is especially relevant because closely related species differ markedly in size, architecture, persistence structures, reproductive allocation, regeneration mechanisms, and habitat associations. Species-specific ecological studies have

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documented substantial variation in phenotypic plasticity and life-history responses within the family [11; 14; 15], yet these different sources of evidence have rarely been considered together when interpreting ecological strategies. An assessment that separates regenerative capacity, competitive persistence, and tolerance of persistent environmental constraints may therefore provide additional insight into the functional differentiation of pondweeds.

In the present study, these dimensions were considered within the proposed r–K–S framework, where r represents regeneration and colonization, K represents competitive persistence and space occupation, and S represents tolerance of persistent environmental constraints. The r–K–S framework has previously been applied to other families of aquatic macrophytes, providing the basis for its further development and family-level comparison [25; 26].

The aim of this study was to apply the proposed r–K–S framework to characterize the ecological strategies of Potamogetonaceae species occurring in the Pripyat River basin based on functional traits, life-history characteristics, ecological responses, and available species-specific evidence, and to compare the resulting strategy configurations with existing ecological strategy classifications and regional occurrence patterns.

The objectives were: (1) to characterize the regional occurrence and functional traits of Potamogetonaceae species; (2) to assess the relative expression of regeneration and colonization (r), competitive persistence and space occupation (K), and tolerance of persistent environmental constraints (S); (3) to identify the resulting r–K–S strategy configurations; and (4) to compare these configurations with published ecological strategy classifications, CSR coordinates, and regional occurrence patterns.

This study represents the third family-level application of the proposed r–K–S framework and contributes to a broader functional interpretation of ecological strategies in aquatic macrophytes.

Materials and Methods. Conceptual framework. Ecological strategies were interpreted within an integrated r–K–S conceptual framework drawing conceptually on classical r/K selection theory [27], CSR strategy theory [28], and contemporary trait-based ecology. Rather than assigning species to discrete strategy types a priori, the framework considers three complementary dimensions of ecological adaptation: regeneration and colonization (r), competitive persistence and space occupation (K), and tolerance of persistent environmental constraints (S).

Species may therefore express different combinations of these components along a continuous functional spectrum.

The assessment integrated multiple lines of evidence, including functional traits, life-history characteristics, ecological indicator values, habitat associations, species-specific experimental and observational evidence, published ecological strategy classifications, and field observations. In particular, published ecological information on habitat preferences, ecological amplitude, life-history characteristics, reproductive and regenerative mechanisms, and adaptive responses was considered together with field observations to support strategy interpretation (Fig. 1).

Study area. The study was conducted in the Pripyat River basin, a large transboundary river system within the Polisia region of Eastern Europe. The basin is characterized by extensive wetlands, floodplain ecosystems, and a high diversity of freshwater habitats. Hydrological conditions range from relatively fast-flowing and slow-flowing rivers to oxbow lakes, standing waters, and temporarily flooded habitats. The regional climate is temperate continental, with relatively high humidity and pronounced seasonal hydrological fluctuations. Aquatic vegetation includes submerged, floating-leaved, free-floating, and emergent macrophyte communities.

Floristic investigations were conducted between 2010 and 2025 in four physiographic regions of the Styr – Horyn part of the Pripyat River basin: Volyn Polisia, Zhytomyr Polisia, Small Polisia, and Volyn Upland.

Species Selection and Data Sources. The functional strategy assessment included Potamogetonaceae species recorded during regional floristic surveys conducted by the authors, supplemented by two species (*Potamogeton alpinus* and *P. rutilus*) historically reported from the study region but not confirmed during the 2010–2025 surveys. The hybrid *P.* × *salicifolius*, although recorded in the regional flora, was excluded from the strategy assessment because its functional characteristics may reflect a combination of parental traits. Species occurrence information was supplemented with published sources. Taxonomic nomenclature follows World Flora Online [29].

Functional traits and ecological indicators. Functional trait and ecological information were compiled from scientific literature, floristic and ecological databases, and published trait classifications. Priority was given to characteristics related to resource acquisition, structural

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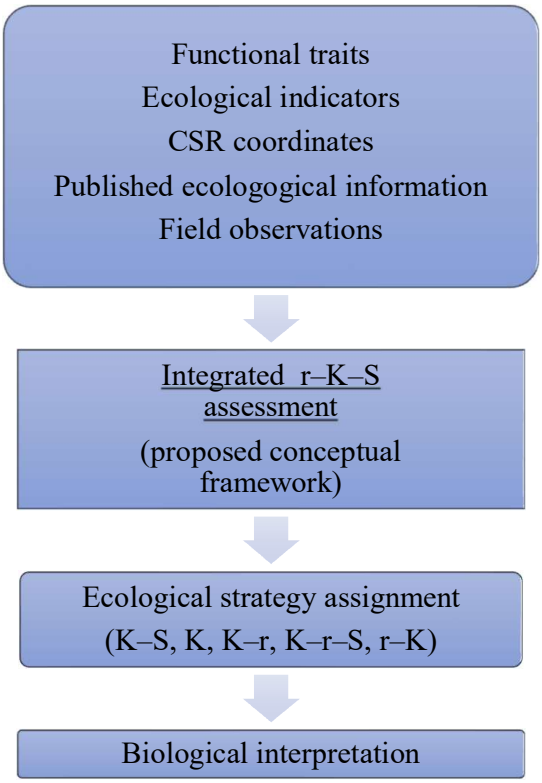


Fig. 1. Conceptual framework for the integrated assessment of ecological strategies in Potamogetonaceae

persistence, clonality, regeneration, dispersal, and responses to environmental constraints and disturbance [30]. The analysed characteristics included growth form, life span, clonality, reproductive strategy, dispersal mode, plant size, leaf morphology, persistent vegetative structures, habitat preferences, trophic associations, and responses to light and other environmental factors.

Ecological information was supplemented using the Database of European Vegetation, Habitats and Flora (FloraVeg) [31], including Ellenberg-type nutrient (N) and light (L) indicator values. Available CSR coordinates calculated according to the StrateFy approach [21] were used as an independent source of functional information and were not considered directly equivalent to the r–K–S components.

Assessment of ecological strategies. For each species, the relative expression of the r, K, and S components was evaluated using a criterion-based semi-quantitative assessment. Each component was represented by six diagnostic criteria reflecting functional traits, life-history characteristics, and species-specific ecological responses. Individual criteria were scored as 0 when the corresponding characteristic was not supported or was demonstrably absent, 0.5 when it was supported by

available evidence, and n/a when the available information was insufficient for reliable assessment.

An additional, seventh independent literature-based reference criterion was incorporated for each strategy component when suitable external information was available. This criterion was based on published ecological strategy classifications and/or available CSR coordinates and was scored using the same 0/0.5/n/a system. External classifications were treated as an additional line of evidence rather than as direct equivalents of the r–K–S framework. The absence of a particular strategy component from an external classification was therefore not automatically interpreted as evidence of its absence.

Criterion scores were summed separately for the r, K, and S components, with n/a entries contributing no numerical value to the sum. With seven criteria and a maximum contribution of 0.5 per criterion, the theoretical maximum score for each component was 3.5. For descriptive interpretation, component scores were classified as Very Low (0.5), Low (1.0), Low–Moderate (1.5), Moderate (2.0), Moderate–High (2.5), High (3.0), and Very High (3.5). A score of 0 indicated that none of the evaluated criteria supported the respective component. Scores were not adjusted for missing information; consequently, values for data-deficient species were interpreted with additional caution.

Final strategy groups were assigned from the relative configuration of the three component scores, considering the dominant component and ecologically meaningful secondary components rather than applying fixed numerical thresholds. Thus, similar absolute scores could result in different strategy assignments when they reflected contrasting functional syndromes supported by species-specific ecological evidence. Cases in which species-specific evidence was limited and no independent external reference criterion was available were treated as tentative.

Comparative interpretation focused on relationships among strategy components, functional trait combinations, habitat preferences, trophic conditions, disturbance regimes, and regional species distribution.

Use of AI-assisted tools (ChatGPT, OpenAI) were used exclusively to improve the linguistic quality of the manuscript, assist in text editing and organization, and support the preparation of graphical materials. The authors were responsible for all scientific concepts, methodological decisions, data collection, analyses, interpretation of results, verification of scientific content, and final conclusions.

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Results and Discussion. Floristic investigations conducted between 2010 and 2025 recorded 13 species of Potamogetonaceae in the Styr–Horyn part of the Pripyat River basin, including the hybrid Potamogeton × salicifolius Wolfg. All species occurred in Volyn Polisia, whereas species richness decreased to 10 species in Zhytomyr Polisia and 10 species in Volyn Upland and 9 species in Male Polisia. The lower species richness observed in the southern part of the basin coincided with areas characterized by greater anthropogenic transformation and may reflect differences in land-use intensity and habitat conditions. For the functional strategy assessment, two additional species (*Potamogeton alpinus* and *P. rutilus*), historically reported from the study region in the Green Data Book of Ukraine [32], were also included despite the lack of information on their current localities within the study region (Table 1). The hybrid *P.* × *salicifolius* was included in the regional floristic inventory but excluded from the functional strategy assessment; thus, 14 species were subjected to r–K–S analysis.

Table 1

Regional occurrence of Potamogetonaceae species included in the functional strategy assessment

Species	Regional distribution	Frequency	Source
Potamogeton alpinus Balb.	3*	1*	[32]
P. berchtoldii Fieber	1-4	2	Present study
P. compressus L.	1, 4	1	Present study
P. crispus L.	1-4	3	Present study
P. friesii Rupr.	1-4	1	Present study
P. gramineus L.	1-3	1	Present study
P. lucens L.	1-4	2	Present study
P. natans L.	1-4	3	Present study
P. nodosus Poir.	1-4	2	Present study
P. obtusifolius Mert. et W.D.J. Koch	1, 4	1	Present study
P. perfoliatus L.	1-4	3	Present study
P. praelongus Wulfen	1	1	Present study
P. rutilus Wolfg.	1*	1*	[32]
P. × *salicifolius* Wolfg.	1-4	2	Present study
Stuckenia pectinata (L.) Böerner	1-4	4	Present study

Note. Regional distribution: 1 – Volyn Polisia, 2 – Zhytomyr Polisia, 3 – Small Polisia, 4 – Volyn Upland. Frequency of occurrence based on route surveys conducted in 2010–2025: 1 – rare (single localities; <20% of plots); 2 –

uncommon (20–40% of plots); 3 – common (40–60% of plots); 4 – frequent (60–80% of plots). *data are given according to the Green Data Book of Ukraine [32], recent occurrences have not been confirmed. Source: compiled by the authors based on original research data.

Despite belonging to the same family, Potamogetonaceae species showed considerable variation in functional traits and ecological strategy combinations within the integrated r–K–S framework. The analysed species formed a continuous functional gradient extending from highly competitive tall macrophytes to species combining competitive, ruderal, and stress-tolerant traits, reflecting adaptation to contrasting hydrological conditions and environmental gradients. These results support the view that ecological strategies in aquatic macrophytes are better interpreted as multidimensional patterns of functional traits rather than as discrete strategy types [13; 16; 17].

Although CSR coordinates calculated using the StrateFy approach [21] placed many Potamogetonaceae species close to the ruderal axis (Table 2), this pattern requires careful ecological interpretation. StrateFy provides a globally standardized CSR classification based primarily on leaf area, leaf dry matter content and specific leaf area, representing major dimensions of plant size and leaf economics [21]. However, the functional significance of these traits may differ in permanently submerged macrophytes, where plant performance is strongly influenced by hydrological dynamics, underwater light availability, water chemistry and inorganic carbon acquisition. In particular, leaf economic traits such as SLA may reflect adaptations associated with carbon acquisition under submerged conditions, in addition to the ecological processes represented by their conventional CSR interpretation [21, 22]. Therefore, CSR coordinates were treated here as an independent complementary line of evidence rather than as direct equivalents of the proposed r–K–S strategy components. The r–K–S assessment additionally incorporated species-specific information on growth and persistence, vegetative and generative reproduction, propagule formation and dispersal, disturbance responses, environmental tolerance and habitat ecology.

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Table 2

Functional traits, CSR coordinates and ecological indicator values of Potamogetonaceae species

Species	Growth form	Reproductive strategy	SLA ($mm^2\ mg^{-1}$)	Strategy type, Dubyna et al. [33]	CSR coordinates (%)			Nutrient (N value)	Light (L value)
					C	S	R		
1	2	3	4	5	6	7	8	9	10
Potamogeton alpinus	submerged	vegetative dominant (clonal)	92.77	R	19	0	81	4.8	7
P. berchtoldii	submerged	mixed (vegetative dominant)	49.5	n.d.	n.d.	n.d.	n.d.	5.3	6.7
P. compressus	submerged	vegetative dominant (clonal)	88.47	K	9	0	91	4.3	6.8
P. crispus	submerged	vegetative dominant (clonal)	60.57	R	10	0	90	n.d.	5.9
P. friesii	submerged	vegetative dominant (clonal)	n.d.	R	n.d.	n.d.	n.d.	5.4	6.7
P. gramineus	submerged	vegetative dominant (clonal)	48.16	C	19	13	68	3.9	7.5
P. lucens	submerged	mixed (vegetative dominant)	66.51	K	31	7	62	7.1	6.1
P. natans	submerged with floating leaves	mixed (vegetative dominant)	27.52	K	42	18	40	n.d.	6.4
P. nodosus	submerged with floating leaves	mixed (vegetative dominant)	34.9	S	47	0	53	5.1	6.4
P. obtusifolius	submerged	mixed (vegetative dominant)	67.86	R	6	30	64	5.8	6.5
P. perfoliatus	submerged	mixed (vegetative dominant)	86.18	K-S-R	16	8	76	4.9	6
P. praelongus	submerged	mixed (vegetative dominant)	n.d.	S	n.d.	n.d.	n.d.	4.4	7.5

Continuation of the table 2

P. rutilus	submerged	mixed (vegetative dominant)	n.d.	S	n.d.	n.d.	n.d.	5	7.1
S. pectinata	submerged	mixed (vegetative dominant)	44.91	K	0	20	80	6.6	6.2

Note. Functional traits and ecological indicator values were compiled from published hydrobotanical literature and contemporary European trait databases. CSR coordinates (C%, S%, R%) were calculated using the StrateFy method [21], where sufficient data were available. Nutrient (N) and Light (L) values follow Ellenberg-type ecological indicator scales [31]. n.d. = no data available.

The generalized r–K–S assessment (Table 3) identified several major ecological strategy groups within Potamogetonaceae.

Table 3

Generalized assessment of ecological strategies of Potamogetonaceae species along the r–K–S continuum based on functional trait analysis

Species	r	K	S	Strategy interpretation	Group
P. alpinus	2.0	2.5	1.0	persistent rhizomatous macrophyte with clonal persistence, disturbance-related regeneration and hydrodynamic stress avoidance	K–r
P. berchtoldii	2.5	0.5	1.5	small clonal macrophyte with high regeneration capacity and moderate stress tolerance	r–S*
P. compressus	2.0	1.5	0.5	early-successional clonal macrophyte with rapid space colonization	r–K
P. crispus	3.5	2.5	1.5	rapidly regenerating clonal macrophyte combining strong colonization capacity with substantial vegetative persistence	r–K
P. friesii	2.0	0.5	1.0	fine-leaved turion-forming macrophyte with an early-successional tendency and seasonal regeneration	r
P. gramineus	1.0	3.0	1.0	persistent plastic competitor adapted to seasonal hydrological variability	K
P. lucens	1.0	3.5	1.0	large persistent rhizomatous competitor of clear mesotrophic waters	K
P. natans	2.5	3.5	1.0	persistent floating-leaved competitor with high clonal expansion capacity	K–r
P. nodosus	1.0	3.5	0.5	large persistent riverine competitor with high morphological plasticity	K

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Continuation of the table 3

P. obtusifolius	2.5	0.0	2.0	small turion-forming specialist with high regenerative capacity and tolerance of nutriaent-poor, chemically constrained waters	r–S
P. perfoliatus	2.5	3.0	1.0	large clonal competitor with rapid spatial expansion	K–r
P. praelongus	0.5	3.0	1.0	large persistent rhizomatous competitor of clear, deep-water habitats	K
P. rutilus	1.0	0.5	1.5	small oligo-mesotrophic macrophyte with specialized seasonal persistence	S–r
S. pectinata	3.5	3.0	2.5	highly plastic clonal macrophyte combining rapid regeneration, competitive growth and stress tolerance	r–K–S

Note. * Strategy assignment is tentative due to limited species-specific evidence and the absence of an independent validation criterion.

The r–S group included Potamogeton obtusifolius and *P. berchtoldii*. Both are small macrophytes combining relatively high regenerative capacity with a measurable stress-tolerance component, although the evidence supporting their regenerative traits differs between [34; 35]. *P. obtusifolius* showed a particularly weak competitive component (r = 2.5, K = 0.0, S = 2.0), whereas *P. berchtoldii* showed a similar but less strongly differentiated configuration (r = 2.5, K = 0.5, S = 1.5) (Fig. 2). Their functional profiles therefore reflect a combination of regeneration and persistence under environmental constraints rather than competitive space occupation.

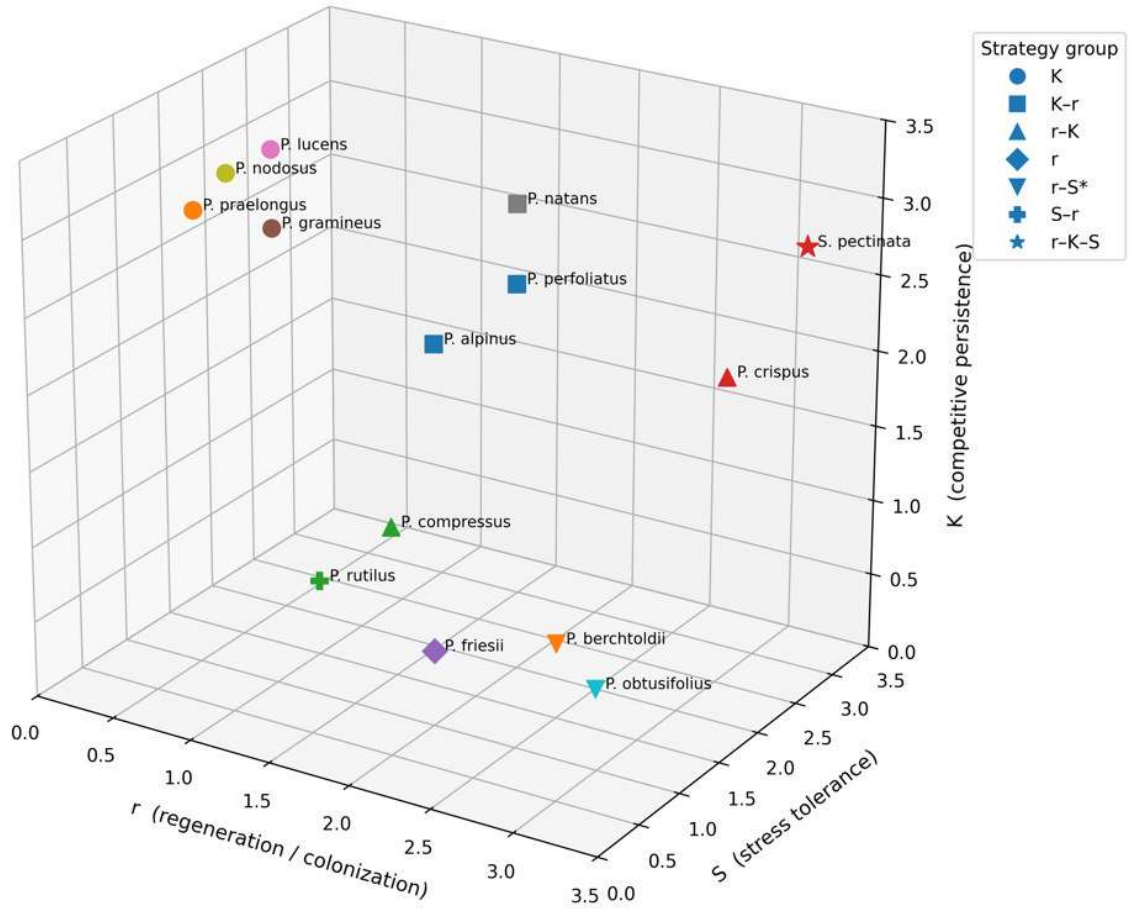


Fig. 2. Functional positioning of Potamogetonaceae species within the r–K–S strategy space. Species positions are based on the semi-quantitative scores of the ruderal (r), competitive (K), and stress-tolerant (S) strategy components. Different symbols indicate the strategy groups identified from the relative configuration of the three components. Axes range from 0 to 3.5, corresponding to the cumulative criterion-based scores used in the assessment

The K strategy group comprised *P. gramineus*, *P. lucens*, *P. nodosus*, and *P. praelongus*. These species were characterized by comparatively strong competitive components (K = 3.0–3.5), associated with different combinations of perennial persistence, structural development, clonal growth, and effective occupation of the water column [11; 14; 15]. The strongest K expression occurred in *P. lucens* and *P. nodosus* (K = 3.5), whereas *P. gramineus* and *P. praelongus* reached K = 3.0. Their r and S components remained comparatively weak, indicating that long-term persistence and resource acquisition, rather than rapid regeneration or broad stress tolerance, constituted the predominant functional dimension of their strategies (Fig. 3).

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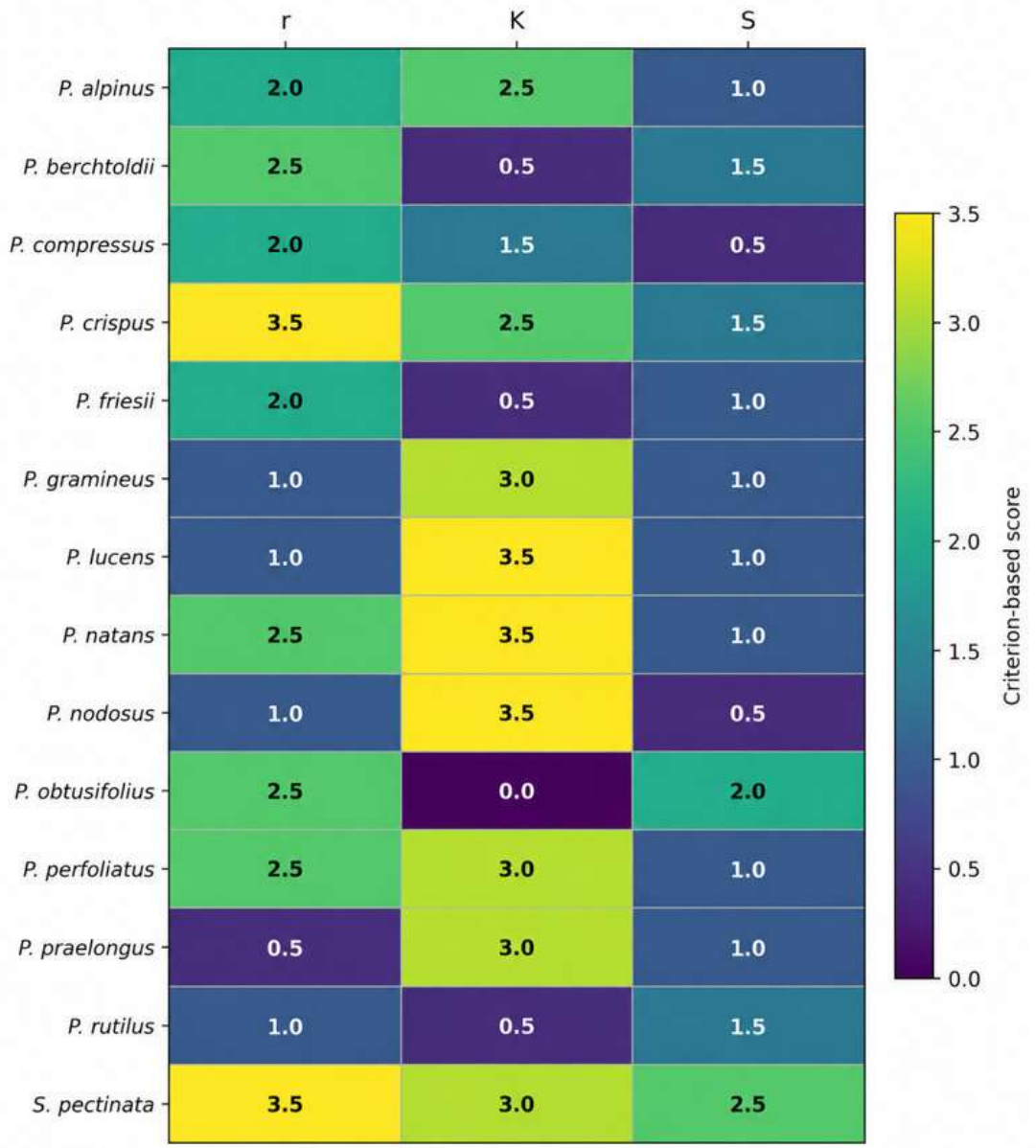


Fig. 3. Heatmap of r–K–S strategy component scores in Potamogetonaceae species

The K–r group included *P. alpinus*, *P. natans*, and *P. perfoliatus*. These species combined competitive persistence with a substantial regenerative component, although the relative contribution of the two dimensions differed among species [14; 36–38]. P. natans showed the strongest competitive component (r = 2.5, K = 3.5, S = 1.0), while *P. perfoliatus* combined similarly high r and K scores (2.5 and 3.0, respectively). In *P. alpinus*, the two components were more closely balanced (r = 2.0, K = 2.5, S = 1.0), reflecting the combination of rhizomatous persistence with disturbance-related regeneration and morphological responses to hydrodynamic constraints [37]. Thus, the K–

r syndrome was associated with the capacity to maintain established populations while retaining substantial potential for vegetative regeneration and spatial expansion.

The reverse configuration, with regeneration predominating over competitive persistence, characterized the r–K group, represented by *P. crispus* and *P. compressus*. Both species possess substantial regenerative capacity, although the underlying ecological mechanisms differ. P. crispus showed a particularly strong regenerative component (r = 3.5) combined with substantial competitive persistence (K = 2.5), consistent with its pronounced morphological plasticity and capacity for vegetative regeneration [39]. *P. compressus* showed a weaker but similarly directed configuration (r = 2.0, K = 1.5); its capacity for vegetative persistence and regeneration through turions, together with its occurrence in open and disturbed aquatic habitats, is consistent with a predominantly regenerative strategy [36; 40; 41]. Both species therefore occupied transitional positions between rapid regeneration/colonization and longer-term vegetative persistence.

Three further strategy configurations were represented by individual species. *P. friesii* showed a predominantly r strategy (r = 2.0, K = 0.5, S = 1.0), consistent with its fine-leaved morphology, turion formation, seasonal regeneration, and association with early-successional aquatic habitats [34; 42]. *P. rutilus* occupied an S–r position (r = 1.0, K = 0.5, S = 1.5), combining low structural investment with specialization for oligo-mesotrophic conditions and seasonal persistence through turion formation [43; 44].

Stuckenia pectinata exhibited the most multidimensional strategy, with high scores for all three components (r = 3.5, K = 3.0, S = 2.5), and was therefore classified as r–K–S. Its functional profile combined rapid regeneration, strong clonal and competitive capacity, and tolerance of a comparatively broad range of environmental conditions [45–48].

The resulting distribution of species demonstrated that the r, K, and S components occurred in different combinations rather than forming sharply separated strategy classes. This pattern is consistent with contemporary trait-based concepts that describe plant ecological strategies as multidimensional continua of functional variation rather than strictly discrete [49]. Competitive persistence predominated among several large or structurally persistent species, whereas regeneration was particularly important in turion-forming and early-successional taxa. The S component was generally less pronounced and occurred

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mainly as a secondary component in combination with r rather than as an independently dominant strategy. No species was assigned to a purely S strategy.

Comparison with regional occurrence patterns revealed some correspondence between functional strategy configurations and species distribution. Species combining strong competitive and regenerative components, such as *P. natans*, *P. perfoliatus*, *P. crispus*, and particularly *S. pectinata*, were among the more widely distributed taxa in the study area. In contrast, several species with restricted or historically documented regional occurrence, including *P. obtusifolius*, *P. berchtoldii*, and *P. rutilus*, were characterized by relatively weak K components and greater contributions of either r or S. Although these relationships were not tested statistically, the observed pattern suggests that regional occurrence may reflect different combinations of persistence, regeneration, and tolerance of environmental constraints rather than variation along a single strategy axis.

Overall, the criterion-based assessment revealed substantial functional differentiation among Potamogetonaceae species. The resulting strategy configurations corresponded broadly to differences in species morphology, life-history characteristics, habitat associations, and regional occurrence, while also identifying intermediate and multidimensional strategies that could not be adequately represented by a single categorical strategy type.

Ecological interpretation of the r–K–S strategy patterns. Rather than forming discrete ecological types, the studied species occupied different positions along the r–K–S continuum, reflecting contrasting combinations of regenerative capacity, competitive persistence, and tolerance of environmental constraints. Competitive and regenerative components predominated across the family, whereas a strong independent S component was uncommon. This pattern is consistent with the ecology of submerged macrophytes, in which persistence and rapid vegetative regeneration may represent alternative or complementary responses to hydrological variability and disturbance [7; 16].

A pronounced K component characterized several large or structurally persistent species, including *P. lucens, P. nodosus, P. gramineus*, and *P. praelongus*. Their functional profiles were associated primarily with perennial persistence, clonal occupation of space, structural development, and effective resource acquisition [50–52]. Similar competitive characteristics were expressed by *P. natans* and *P.*

perfoliatus, although in these species they were accompanied by stronger regenerative components, resulting in K–r rather than predominantly K strategies. This distinction illustrates an important feature of aquatic plant strategies: competitive persistence does not necessarily imply low regenerative capacity. In dynamic aquatic environments, extensive clonal growth may simultaneously contribute to long-term space occupation and rapid vegetative expansion [11; 14].

The importance of regeneration was particularly evident in *P. crispus*, *P. compressus*, *P. friesii*, *P. berchtoldii*, and *P. obtusifolius*. Turion formation, vegetative propagation, seasonal regeneration, and, in some species, the capacity to exploit open or early-successional habitats contributed to relatively high r scores. *P. crispus* represented the strongest expression of this syndrome while retaining a substantial K component. This combination is consistent with its high vegetative regeneration capacity, including rapid sprouting and re-sprouting from turions and the ability of detached shoot fragments to survive, grow, and produce new turions [39; 53; 54]. In contrast, the fine-leaved *P. friesii* showed a predominantly r-oriented strategy with only a weak K component. Its turion-based seasonal regeneration and association with early-successional aquatic habitats support an interpretation emphasizing regeneration rather than long-term structural dominance [34; 42].

An important outcome of the present analysis was the position of several relatively small and regionally restricted species. In the preliminary expert assessment, habitat specialization had tended to be interpreted as evidence of a strong S component, resulting in several species being assigned to K–S strategies. The criterion-based assessment did not support this generalization. *P. obtusifolius* and *P. berchtoldii* were instead positioned within the r–S group, while *P. rutilus* showed an S–r strategy. These species combined some capacity to function under nutrient limitation or other environmental constraints with relatively low structural investment and weak competitive components.

This distinction is ecologically important because habitat specialization should not automatically be equated with stress tolerance. A restricted habitat range may result from specific environmental requirements, limited dispersal, weak competitive ability, or historical constraints, rather than from a generalized physiological capacity to tolerate environmental stress. Consequently, rarity or restricted

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distribution alone should not be interpreted as evidence of an S strategy. The revised assessment therefore suggests that some specialized pondweeds may persist through combinations of seasonal regeneration and tolerance of particular environmental constraints rather than through the generalized stress-tolerance syndrome initially assumed.

P. praelongus provides a particularly illustrative example. It was characterized as an S strategist by Dubyna et al. [33], and its association with relatively specific clear-water habitats could superficially support such an interpretation. However, species-specific evidence indicates strong structural persistence through its large size, perennial rhizome, and long-term clonal occupation of suitable habitats, whereas available evidence for tolerance of prolonged light limitation, adverse sediment conditions, pollution, or broad chemical stress is limited or does not indicate a strong generalized stress-tolerance syndrome [55]. The resulting K-dominated profile therefore emphasizes persistence and structural investment rather than generalized stress tolerance. This example demonstrates the value of distinguishing environmental specialization from tolerance of chronic environmental constraints.

The comparison with previously published strategy classifications also revealed several apparent discrepancies. The classification of Dubyna et al. [33] and CSR coordinates derived using StrateFy do not always correspond to the r–K–S positions obtained here. Particularly striking examples occur among species assigned high R coordinates by StrateFy, including several perennial and strongly clonal pondweeds. Such differences are not necessarily contradictory because CSR and the proposed r–K–S framework describe ecological strategies using different sets of functional information. StrateFy derives CSR positions from leaf area, specific leaf area and leaf dry matter content [21], whereas the present assessment additionally incorporates clonality, persistent structures, regeneration mechanisms, habitat occupation, responses to disturbance, and species-specific ecological evidence.

This distinction may be especially important for permanently submerged macrophytes. High SLA can contribute to an acquisitive trait profile and consequently to a strong R signal in CSR trait space (Pierce et al., 2017), while the same species may simultaneously maintain persistent clonal systems or regenerate rapidly through specialized vegetative propagules. Thus, similar leaf-economic traits may coexist with markedly different persistence and regeneration mechanisms in aquatic plants. Consequently, CSR coordinates should not automatically

be interpreted as direct equivalents of the r, K, and S components defined in the present framework.

Stuckenia pectinata exhibited the most multidimensional functional profile, with high scores for all three components. Its combination of rapid vegetative regeneration, strong clonal persistence, and broad tolerance of environmental conditions is consistent with the exceptionally wide ecological amplitude reported for the species [45–48]. Rather than representing a compromise among strategies, the r–K–S position of *S. pectinata* may therefore reflect the coexistence of complementary functional mechanisms that permit persistence across heterogeneous and frequently disturbed aquatic environments.

Although these relationships were not tested statistically, regional distribution patterns provided additional ecological context for the strategy assessment. Several widespread species combined substantial K and r components, suggesting that the capacity both to maintain established populations and to regenerate or expand vegetatively may favour persistence across heterogeneous river-basin landscapes. Conversely, some of the more restricted species were characterized by weak K components and stronger relative contributions of r and/or S. Thus, restricted distribution within Potamogetonaceae cannot be explained simply by increasing stress tolerance. It may instead arise from different combinations of habitat specialization, limited competitive ability, regeneration mode, dispersal constraints, and sensitivity to environmental change.

These findings also emphasize the importance of interpreting ecological strategies as multidimensional continua rather than mutually exclusive categories. Closely related species may achieve persistence through markedly different combinations of traits, and individual traits may contribute to more than one ecological function. Clonal growth, for example, may promote long-term persistence and space occupation but may also enable rapid regeneration following disturbance. Similarly, specialized resting structures can contribute both to seasonal persistence and to rapid population recovery. The ecological significance of a trait therefore depends on the functional and environmental context in which it is expressed [16; 17].

Overall, the present analysis suggests that an integrated r–K–S interpretation can reveal functional differences among aquatic macrophytes that are obscured when species are assigned directly to conventional strategy categories. At the same time, the approach should

ISSN 3154-8059

be considered a working ecological framework rather than a definitive classification system. Species-specific information remains uneven, particularly for rare taxa, and several criteria could not be evaluated reliably for all species. Further application to additional macrophyte families, together with experimental testing and expansion of species-specific functional trait data, will be necessary to evaluate the generality of the proposed framework.

Conclusion. Potamogetonaceae species of the Pripyat River basin exhibited substantial functional differentiation despite their close taxonomic relatedness and predominantly aquatic growth form. Variation in plant architecture, clonality, regenerative mechanisms, persistence structures, habitat associations, and responses to environmental constraints resulted in different combinations of ruderal (r), competitive (K), and stress-tolerant (S) components.

The criterion-based assessment revealed a range of intermediate and multidimensional strategy configurations rather than sharply separated ecological categories. Predominantly competitive strategies were identified in *P. gramineus, P. lucens, P. nodosus*, and *P. praelongus*. Competitive persistence predominated over regeneration in the K–r strategies of *P. alpinus, P. natans*, and *P. perfoliatus*, whereas the reverse r–K configuration characterized *P. crispus* and *P. compressus*. Regeneration and stress tolerance contributed more strongly to the strategies of the smaller, fine-leaved species *P. obtusifolius, P. berchtoldii*, and *P. rutilus*, while *P. friesii* showed a predominantly ruderal tendency. *Stuckenia pectinata* exhibited the most multidimensional functional profile, combining strong r, K, and S components.

The results did not support a simple relationship between habitat specialization and stress tolerance. Several regionally restricted species showed relatively weak competitive components combined with regenerative and/or stress-tolerant traits, indicating that restricted occurrence or ecological specialization should not itself be interpreted as evidence of a predominantly stress-tolerant strategy. Instead, ecological specialization in aquatic macrophytes may reflect different combinations of habitat requirements, regeneration mechanisms, competitive ability, and tolerance of environmental constraints.

Comparison with published strategy classifications and CSR coordinates revealed both agreements and substantial discrepancies. In particular, high ruderal components derived from CSR coordinates did not always correspond directly to r-dominated strategies in the criterion-based assessment. These differences indicate that ecological strategy

dimensions derived primarily from terrestrial plant traits should be interpreted cautiously when applied to permanently submerged macrophytes.

The integration of functional traits, life-history characteristics, ecological indicator values, species-specific ecological evidence, and independent literature-based strategy information provided a multidimensional representation of ecological differentiation within Potamogetonaceae. The resulting r–K–S configurations should therefore be regarded as evidence-based ecological interpretations rather than fixed strategy categories.

Further application of the approach to other aquatic macrophyte groups, supported by additional species-specific ecological and experimental evidence, will be necessary to evaluate its broader applicability and refine the criteria used to distinguish regeneration, competitive persistence, and stress tolerance in aquatic plants.

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ЕКОЛОГІЧНІ СТРАТЕГІЇ ВОДНИХ МАКРОФІТІВ У БАСЕЙНІ РІЧКИ ПРИП'ЯТЬ. ІІІ. ІНТЕГРОВАНА ФУНКЦІОНАЛЬНА КОНЦЕПЦІЯ: РОДИНА POTAMOGETONACEAE

Екологічні стратегії занурених водних макрофітів складно інтерпретувати за допомогою концептуальних підходів, розроблених переважно для наземних рослин, оскільки їхня здатність підтримувати

популяції, відновлюватися після порушень і витримувати несприятливі умови водного середовища залежить від специфічних комбінацій функціональних ознак. У дослідженні застосовано запропоновану концепцію r–K–S для характеристики екологічних стратегій 14 видів родини Potamogetonaceae басейну річки Прип'ять на основі функціональних ознак, особливостей життєвого циклу, екологічних індикаторних значень, приуроченості до оселищ і доступних видоспецифічних екологічних даних.

Аналіз виявив значну функціональну диференціацію близькоспоріднених водних макрофітів: переважно конкурентні стратегії встановлено для *Potamogeton gramineus, P. lucens, P. nodosus* і *P. praelongus*, тоді як *P. alpinus, P. natans* і *P. perfoliatus* поєднували конкурентну стійкість із істотною регенеративною здатністю, а для *P. crispus* і *P. compressus* встановлено протилежну конфігурацію r–K із переважанням регенеративної компоненти. Дрібні тонколисті види характеризувалися контрастними стратегіями: *P. obtusifolius* і *P. berchtoldii* віднесено до групи r–S, *P. rutilus* – до S–r, *P. friesii* характеризувався переважно r-орієнтованою стратегією, тоді як найбільш багатовимірний профіль виявлено у *Stuckenia pectinata*, що поєднував високі значення всіх трьох компонент.

Результати не підтвердили прямого зв'язку між спеціалізацією до певних оселищ і стрес-толерантністю та виявили розбіжності між окремими опублікованими класифікаціями, зокрема CSR-позиціями, і критеріальними r–K–S конфігураціями, що свідчить про необхідність обережного застосування до постійно занурених рослин систем екологічних стратегій, розроблених переважно для наземної рослинності. Загалом отримані результати обґрунтовують доцільність багатовимірної інтерпретації екологічних стратегій водних макрофітів, за якої конкурентна стійкість, регенеративна здатність і стрес-толерантність розглядаються як взаємодоповнюючі та різною мірою виражені функціональні компоненти.

***Ключові слова*:** водні макрофіти; Potamogetonaceae; функціональні ознаки; екологічні стратегії; концепція r–K–S; CSR; басейн Прип'яті.

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