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ECOLOGICAL STRATEGIES OF AQUATIC MACROPHYTES IN THE PRIPYAT RIVER BASIN. II. A FUNCTIONAL TRAIT-BASED APPROACH WITHIN AN R–K–S FRAMEWORK: FAMILY HYDROCHARITACEAE

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This study assesses the ecological strategies of aquatic macrophytes of the family Hydrocharitaceae in the Pripyat River basin using a functional trait-based approach and positions the studied species along the r–K–S continuum. The dataset was compiled from published sources and European trait databases and included key functional traits, ecological indicator values, and CSR classifications.

The results demonstrate that Hydrocharitaceae species share a relatively consistent set of traits related to adaptation to fully aquatic environments, including the predominance of submerged and free-floating growth forms, high clonality, and vegetative reproduction. At the same time, clear functional differences were observed between annual generative species of the genus *Najas* and perennial clonal species. CSR analysis revealed the predominance of intermediate and mixed strategy types (CR, CS), while assessment within the r–K–S framework showed that most species occupy intermediate positions along the r–K–S continuum.

Species such as *Elodea canadensis* and *Najas minor* are characterized by strong r-related components linked to rapid colonization ability, whereas *Hydrocharis morsus-ranae* exhibits a balanced K–r strategy and *Stratiotes aloides* demonstrates a combined K–S strategy. High specific leaf area values across the studied species indicate acquisitive resource-use patterns typical of aquatic environments.

The study confirms that ecological strategies of Hydrocharitaceae species are best interpreted as continuous combinations of functional traits which are determined by life span, reproductive mode, and environmental conditions. The integration of functional traits with CSR and r–K–S frameworks provides a useful tool for ecological assessment and interpretation of adaptive strategies in freshwater ecosystems.

The study is part of a series devoted to ecological strategies of aquatic macrophytes in the Pripyat River basin.

Key words: aquatic macrophytes, Hydrocharitaceae, functional traits, ecological strategies, CSR, r–K–S continuum, Pripyat River basin.

Problem statement. Aquatic vascular plants are key structural and functional components of freshwater ecosystems, contributing to habitat formation, nutrient cycling, trophic regulation, and biodiversity maintenance [1, 2, 3]. They play a central role in shaping the spatial organization of aquatic communities by influencing light availability, oxygen dynamics, and sediment processes [4].

Under increasing anthropogenic pressure, freshwater ecosystems undergo significant transformations, including eutrophication, hydrological alteration, and habitat fragmentation [5]. These changes particularly affect submerged and floating macrophytes, whose distribution and functional organization are highly sensitive to environmental gradients, including nutrient availability, light conditions, and disturbance regimes [6].

Understanding the ecological strategies of aquatic plants is therefore essential for interpreting their responses to environmental change [7]. Classical concepts of plant ecological strategies, including the r/K framework and CSR theory, have provided a conceptual basis for describing plant adaptation to stress, competition, and disturbance [8, 9]. However, integrative analyses combining functional traits with ecological strategy frameworks remain limited, particularly for submerged macrophytes [10, 11, 12].

Analysis of recent research. In recent decades, functional trait-based approaches have become increasingly important, allowing plant strategies to be analyzed along continuous ecological gradients rather than discrete categories [13, 14, 15]. The increasing availability of global trait databases provides new opportunities to integrate quantitative data on plant morphology, reproduction, and ecological preferences, facilitating comparative analyses across species and taxonomic groups [16].

Despite these advances, a coherent synthesis of ecological strategies in aquatic macrophytes that integrates classical concepts with trait-based approaches remains insufficiently developed. In particular, submerged macrophytes, including representatives of the family Hydrocharitaceae, exhibit specific ecological adaptations related to fully aquatic environments, clonal growth, and reduced mechanical constraints, which may influence their position along the ecological strategy continuum [17, 18, 19, 20].

Recent studies increasingly emphasize the role of functional traits in understanding plant responses to environmental gradients, community assembly, and ecosystem functioning. Nevertheless, studies integrating functional traits with ecological strategy concepts in submerged macrophytes remain relatively scarce. Functional trait-based approaches provide opportunities for integrating multiple ecological strategy components within a unified analytical framework. The present study applies this approach to Hydrocharitaceae, representing a contrasting ecological group of predominantly submerged aquatic plants.

Aim. The aim of this study is to assess the ecological strategies of Hydrocharitaceae species in the Pripyat River basin using a functional trait-based approach and to determine their positions along the r–K–S continuum.

Materials and Methods. The dataset used in this study was compiled from published sources and open-access databases. The species list of the Hydrocharitaceae family was based on previous floristic studies conducted by the authors [21, 22] within the study region (the Styr–Horyn sub-basin of the Pripyat River basin, Eastern Europe). All data were standardized and integrated into a unified analytical framework. The analysis focused on assessing ecological strategies using a functional trait-based approach.

Special attention was given to the integration of heterogeneous data sources and their consistent interpretation within the r–K–S framework. Ecological strategy types (CSR), functional trait data and ecological indicator values were compiled from published sources and European trait databases (e.g., [16]).

The assessment of ecological strategies was based on species functional traits grouped into three components corresponding to r-, K-, and S-strategies. Qualitative trait characteristics were converted into numerical scores reflecting their contribution to each component. Total scores for r, K, and S were calculated for each species, and their relative proportions were used to determine species positions along the r–K–S continuum. This approach enabled a generalized interpretation of ecological strategies through functional trait syndromes.

For visualization and comparative analysis, qualitative categories were converted into numerical values: Low (1), Low–Moderate (1.5), Moderate (2), Moderate–High (2.5), High (3), and Very High (3.5).

AI-based tools (ChatGPT, OpenAI) were used for language editing, manuscript structuring, and assistance with data visualization. All scientific analyses, interpretations, and conclusions were performed exclusively by the authors.

Results and Discussion. All analyzed species of the family Hydrocharitaceae are hydrophytes, predominantly represented by submerged or free-floating growth forms. Most species are perennial and exhibit pronounced clonal growth, with vegetative reproduction playing a dominant role in their life strategies [3, 6, 10, 11]. This structural uniformity highlights the importance of clonality and persistence as key adaptive mechanisms in aquatic habitats.

Elodea canadensis is characterized by rapid growth, exclusively vegetative reproduction (fragmentation) within the studied region; has the ability to form wintering shoots. The species intensively absorbs nutrients from the water column. According to the set of characteristics, it is a classic invasive species (r-K) with the ability to fill the water column and moderate tolerance to pollution (reduction in viability during hypertrophy) [18, 19, 20, 23-26].

Hydrocharis morsus-ranae has moderate growth rates, predominantly vegetative reproduction – the ability to create stolons and form dense thickets; the species has sensitivity to changes in the hydrological regime and ability to quickly capture the free surface of the water; exhibits a strategy of "avoidance" of unfavorable conditions by submerging turions [27, 28, 29].

Najas marina is a specialized species with a narrow ecological niche and high dependence on the substrate and water transparency. It is characterized by moderate growth and predominantly seed reproduction. Regarding ecological characteristics, it has a narrow ecological amplitude, tolerance to elevated mineralization but sensitivity to excessive siltation and reduced water transparency [30-32]. *N. minor* has predominantly seed reproduction, rapid growth and the ability to quickly colonize habitats, and tolerance to eutrophication [33-35].

Stratiotes aloides has predominantly vegetative clonal reproduction via rosettes, offsets and turions; formation of dense floating mats; moderate growth and ability to form dense thickets; sensitivity to environmental changes (especially light, CO_2, nutrients) [36-41].

Vallisneria spiralis is characterized by a moderate growth rate, plastic biomass allocation, intensive clonal propagation via stolons (runners), formation of dense submerged meadows, high competitive ability under suitable conditions, and strong light dependence [42– 45].

Despite this overall similarity, clear differences in life span and reproductive strategies are observed. Species of the genus *Najas* are characterized by annual life cycles and predominantly generative reproduction, whereas *E. canadensis*, *H. morsus-ranae*, *S. aloides*, and *V. spiralis* reproduce mainly vegetatively and often form extensive clonal populations. These differences represent a major axis of functional differentiation within the family and are closely linked to variation in ecological strategies.

The analyzed species exhibit a relatively consistent set of functional traits reflecting adaptation to fully aquatic environments (Table 1).

The distribution of ecological strategies within the CSR [9, 46] framework indicates the predominance of intermediate and mixed types. Competitive–ruderal (CR) and competitive–stress-tolerant (CS) strategies are typical of perennial clonal species, reflecting their ability to combine efficient resource use with persistence under relatively stable conditions. In contrast, ruderal (R) strategies are associated with annual species characterized by rapid life cycles and generative reproduction.

Functional traits further support the observed patterns of ecological differentiation. Specific leaf area values are relatively high across all species, indicating an acquisitive strategy associated with efficient resource uptake in aquatic environments. At the same time, variation in leaf morphology reflects adaptation to hydrodynamic conditions and light availability, with dissected leaves characteristic of *Najas* species and broader leaves typical of other taxa. These trait combinations contribute to species positioning along the r–K–S continuum and reinforce the role of functional traits as integrative descriptors of ecological strategies.

The ecological context of the studied species is characterized by relatively stable hydrological conditions, as most species are associated with stand-

Table 1. **Functional traits and ecological indicator values of Hydrocharitaceae species in relation to ecological strategies**

Species	Growth form	Life span	Clonality	Reproductive strategy	SLA	CSR	Nutrient (N)	Light (L)
Elodea canadensis	submerged	per.	yes	vegeta-tive-dominant	37.26	CR	7	6.7
Hydrocharis morsus-ranae	free-floating	per.	yes	vegeta-tive-dominant	40.37	S	6.7	7.3
Najas minor	submerged	ann.	no	genera-tive-dominant	43.34	R	4.2	5.9
Najas marina	submerged	ann.	no	genera-tive-dominant	36.52	R	5.9	5.2
Stratiotes aloides	rooted floating-leaved	per.	yes	vegeta-tive-dominant	23.51	CS	6.2	7.1
Vallisneria spiralis	submerged	per.	yes	vegeta-tive-dominant	44.1	CS	5.8	6.5

Note. Growth forms: submerged – rooted or free within the water column; free-floating – surface-floating; free-floating (rooted) – rooted with floating leaves. Life span: per. – perennial; ann. – annual. Reproductive strategy: vegetative-dominant – clonal; generative-dominant – seed-based. SLA: specific leaf area (mm^2 mg^{-1}). CSR: competitive (C), stress-tolerant (S), ruderal (R). Nutrient (N) and light (L) values follow Ellenberg-type ecological indicator scales. Data sources: CSR classification functional traits and ecological indicator values compiled from hydrobotanical sources and contemporary European trait databases [16].

ing or slow-flowing water bodies. Nutrient preferences range from mesotrophic to eutrophic conditions, indicating adaptation to moderately and highly productive habitats. Light conditions vary from intermediate to high, reflecting the importance of light availability in structuring submerged plant communities. These environmental gradients interact with species-specific trait combinations to shape the observed distribution of ecological strategies.

The predominance of vegetative reproduction among most Hydrocharitaceae species highlights the importance of clonal growth as a key adaptive mechanism in aquatic environments. Clonality promotes persistence, resource acquisition, and spatial expansion, enabling efficient occupation of available niches. The coexistence of vegetative and generative reproduction further reflects adaptive responses to environmental variability.

The integration of functional traits into the r–K–S framework reveals distinct patterns in the positioning of species along the continuum (Table 2). The proposed r–K–S assignments should not be interpreted as fixed species categories, but rather as generalized positions within a functional ecological continuum. Due to ecological plasticity and environmental variability, species may shift along the continuum depending on habitat conditions, disturbance intensity, nutrient availability, and competitive interactions. The proposed visualization potentially provides a basis for future interpretation of ecological niche structure through functional strategy space.

Table 2. **Generalized assessment of ecological strategies of Hydrocharitaceae species along the r–K–S continuum based on functional trait analysis**

Species	r	K	S	Strategy interpretation	Group
Elodea canadensis	Very High r=3.5	High K=3	Moderate S=2	invasive species with strong colonization ability and strong competitive performance	r-K
Hydrocharis morsus-ranae	Moderate–High r=2.5	Moderate–High K=2.5	Moderate S=2	species with balanced colonization and competitive traits, characterized by pronounced seasonal dynamics	K-r
Najas minor	High r=3	Moderate K=2	Moderate S=2	opportunistic species characterized by high colonization ability and moderate competitive performance	r
Najas marina	Low–Moderate r=1.5	Low–Moderate K=1,5	High S=3	predominantly stress-tolerant specialist species adapted to elevated mineralization with weak ruderal features and limited competitive ability	S-r
Stratiotes aloides	Moderate r=2	High K=3	High S=3	species combining strong competitive ability with high stress tolerance and marked seasonal dynamics	K-S
Vallisneria spiralis	Moderate–High r=2.5	High K=3	Moderate S=2	competitive species forming stable communities with moderate colonization capacity	K-r

Note. Strategy components (r, K, S) are based on aggregated scores derived from functional traits (see Methods). Qualitative categories (Low–Very High) correspond to numerical values used in the analysis. Group indicates dominant combinations of ecological strategy components.

Species such as *E. canadensis* and *N. minor* are characterized by a strong contribution of r-related traits associated with high colonization ability and rapid population expansion. A stress-tolerant ruderal (S–r) strategy is observed in *N. marina*, reflecting adaptation to elevated mineralization and environmentally constrained habitats. In contrast, *H. morsus-ranae* exhibits a balanced K–r strategy associated with stable population maintenance and efficient surface colonization. *V. spiralis* exhibits a combined K–r strategy, while *S. aloides* demonstrates a balanced K–S strategy, combining competitive ability with tolerance to environmental stress.

Visualization of the three-dimensional space of ecological strategies and the location of the studied species is in Figure 1. The relative size of the semi-transparent regions reflects the generalized ecological plasticity and potential variability of species positions within the r–K–S space. The proposed space may also be interpreted as a generalized representation of ecological niche structure mediated through functional trait syndromes and ecological strategy combinations.

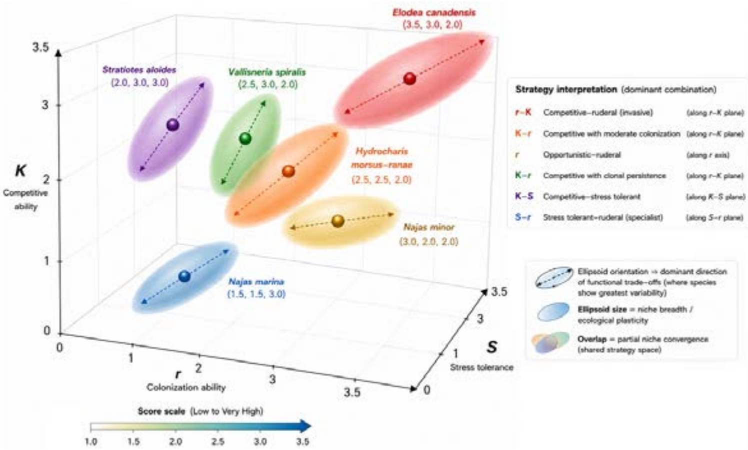

Fig. 1. **Distribution of Hydrocharitaceae species within the r–K–S ecological strategy space**

An important aspect of the results is the presence of invasive species within the studied group. In particular, *E. canadensis* is a well-known invasive macrophyte widely distributed in European freshwater ecosystems. Its classification as a competitive–ruderal strategist is consistent with its high colonization ability, rapid vegetative propagation, and broad ecological amplitude. The dominance of clonal growth, together with relatively high specific leaf area, enables this species to form dense stands and outcompete native vegetation [20, 25, 27]. This example illustrates how the integration of functional traits and ecological strategy frameworks can provide insight into the mechanisms underlying plant invasiveness in aquatic ecosystems.

Comparison with representatives of Alismataceae reveals notable differences in the expression of ecological strategies. While Alismataceae include a broader range of life forms and ecological niches, Hydrocharitaceae species are more strongly associated with submerged aquatic habitats, resulting in a narrower but more coherent distribution of strategies. This contrast highlights the role of habitat specialization in shaping functional diversity and supports the applicability of trait-based approaches across different taxonomic groups of aquatic macrophytes.

Overall, the studied species occupy intermediate positions along the r–K–S continuum, reflecting continuous combinations of competitive, ruderal, and stress-tolerant traits rather than discrete strategy types. The observed variation is primarily driven by differences in life span, reproductive mode, and environmental conditions. The results confirm that the integration of functional traits with ecological strategy frameworks provides a robust tool for understanding plant adaptation in freshwater ecosystems.

The proposed framework provides a flexible basis for ecological assessment, monitoring, and management of aquatic vegetation. Future development of the approach may include quantitative modeling and expanded visualization of species distribution within the r–K–S space.

Conclusions. The present study demonstrates that Hydrocharitaceae species share a relatively consistent set of functional traits associated with adaptation to fully aquatic environments, while simultaneously exhibiting meaningful variation in ecological strategies. This variation is primarily related to differences in life span and reproductive mode, particularly the contrast between annual generative species of the genus *Najas* and perennial clonal species.

The integration of functional trait analysis with CSR classification and the r–K–S continuum provides a comprehensive framework for interpreting ecological strategies of aquatic macrophytes. The studied species predominantly occupy intermediate positions along the continuum, combining competitive, ruderal, and stress-tolerant components rather than forming discrete strategy types.

Clonal growth appears to be a key adaptive mechanism in Hydrocharitaceae, contributing to persistence, spatial expansion, and competitive ability in relatively stable aquatic environments. In contrast, species with dominant generative reproduction are associated with greater ecological flexibility under variable conditions.

The example of *E. canadensis* demonstrates the applicability of the proposed approach for understanding mechanisms of plant invasiveness in freshwater ecosystems. Comparison with previously studied representatives of Alismataceae further indicates that habitat specialization plays a central role in shaping functional diversity and ecological strategy patterns among aquatic macrophytes.

Overall, the study supports the interpretation of ecological strategies as continuous combinations of functional traits structured by environmental conditions. The proposed framework may serve as a useful tool for ecological assessment, monitoring, and management of freshwater ecosystems and provides a basis for future quantitative modeling of species distribution within the r–K–S space.

ЕКОЛОГІЧНІ СТРАТЕГІЇ ВОДНИХ МАКРОФІТІВ БАСЕЙНУ РІЧКИ ПРИП'ЯТЬ. ІІ. ПІДХІД НА ОСНОВІ ФУНКЦІОНАЛЬНИХ ОЗНАК У МЕЖАХ R–K–S КОНЦЕПЦІЇ: РОДИНА HYDROCHARITACEAE

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У дослідженні оцінено екологічні стратегії водних макрофітів родини Hydrocharitaceae у басейні річки Прип'ять із використанням підходу на основі функціональних ознак та визначено положення досліджених видів уздовж континууму r–K–S. Набір даних сформовано на основі опублікованих джерел і європейських баз даних функціональних ознак та включено ключові функціональні ознаки, екологічні індикаторні значення і CSR-класифікації.

Результати показали, що види Hydrocharitaceae характеризуються відносно узгодженим комплексом ознак, пов'язаних з адаптацією до повністю водного середовища, зокрема переважанням занурених і вільноплаваючих життєвих форм, високою клональністю та вегетативним розмноженням. Водночас виявлено чіткі функціональні відмінності між однорічними видами роду *Najas* з переважно генеративним розмноженням і багаторічними клональними видами. Аналіз CSR виявив домінування проміжних і змішаних типів стратегій (CR, CS), тоді як оцінка в межах r–K–S-підходу показала, що більшість видів займає проміжні положення вздовж континууму.

Такі види, як Elodea canadensis та Najas minor, характеризуються вираженими r-компонентами, пов'язаними зі здатністю до швидкої колонізації, тоді як Hydrocharis morsus-ranae демонструє збалансовану K–r-стратегію, а Stratiotes aloides – комбіновану K–S-стратегію. Високі значення питомої площі листка у досліджених видів свідчать про стратегію інтенсивного використання ресурсів, характерну для водного середовища.

Дослідження підтверджує, що екологічні стратегії видів Hydrocharitaceae доцільно розглядати як безперервні комбінації функціональних ознак, які визначаються тривалістю життєвого циклу, способом розмноження та умовами середовища. Інтеграція функціональних ознак із CSR– та r–K–S-підходами є перспективним інструментом для екологічної оцінки та інтерпретації адаптивних стратегій у прісноводних екосистемах.

Дослідження є частиною серії робіт, присвячених екологічним стратегіям водних макрофітів басейну річки Прип'ять.

Ключові слова: водні макрофіти, Hydrocharitaceae, функціональні ознаки, екологічні стратегії, CSR, r–K–S континуум, басейн річки Прип'ять

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