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ECOLOGICAL STRATEGIES OF AQUATIC MACROPHYTES IN THE PRIPYAT RIVER BASIN. I. A FUNCTIONAL TRAIT-BASED APPROACH WITHIN AN R–K–S FRAMEWORK: A CASE STUDY OF ALISMATACEAE

Aquatic macrophytes are key structural and functional components of freshwater ecosystems, yet their ecological strategies remain difficult to classify due to high morphological plasticity and the coexistence of multiple adaptive traits. This study synthesizes current knowledge on ecological strategies of aquatic macrophytes of the family Alismataceae in the Pripyat River basin (Eastern Europe) using a functional trait-based approach.

Based on a synthesis of published data, species were evaluated using a semi-quantitative assessment of key functional traits, including growth rate, reproductive mode, clonal capacity, morphological plasticity, and tolerance to abiotic factors. Ecological strategies were interpreted within a generalized r–K–S continuum integrating ruderal (r), competitive (K), and stress-tolerant (S) components.

The results demonstrate that the studied species occupy intermediate and overlapping positions, combining multiple strategy components rather than forming discrete types. In particular, closely related species exhibit pronounced differentiation in trait combinations, reflecting adaptation to hydrological variability and trophic conditions.

To better capture this complexity, the r–K–S framework is conceptually extended into a three-dimensional r–K–S space, where species are represented as continuous and variable regions rather than fixed points. This approach allows for the coexistence of multiple strategy components within a single species and provides a more realistic representation of ecological strategies in aquatic environments.

The proposed framework bridges classical ecological theory and modern trait-based approaches and offers potential for application in

freshwater ecosystem assessment, monitoring, and restoration.

***Keywords*:** aquatic macrophytes; Alismataceae; ecological strategies; functional traits; clonal growth; reproductive strategies; environmental gradients; Pripyat River basin.

Problem statement. Aquatic macrophytes are key components of freshwater ecosystems, performing essential structural and functional roles, including habitat formation, regulation of trophic status, nutrient cycling, and maintenance of biodiversity [1; 2; 3; 4]. Within the Styr–Horyn sub-basin of the Pripyat River basin (Eastern Europe), characterized by high hydrological heterogeneity, diversity of waterbody types, and varying degrees of anthropogenic impact, aquatic macrophytes form complex and dynamic communities. A special role in this flora is played by representatives of the order Alismatales, which encompass a wide spectrum of life forms – from submerged and free-floating to emergent species – and exhibit high morphological and ecological diversity [5; 6].

Macrophytes strongly influence the spatial organization of aquatic communities by modifying light availability, gas exchange, and sedimentation processes, and they are widely recognized as indicators of ecological status in freshwater systems [3; 7]. The relative contribution of species with different ecological strategies reflects environmental conditions, including trophic status, hydrological regime, and disturbance intensity [3; 8; 9]. A critical adaptation of aquatic macrophytes to seasonal environmental instability is the formation of specialized vegetative propagules and resting structures – such as turions, buried buds, and modified rhizomes – which ensure population persistence during periods of anoxia and low temperatures [10].

Traditional approaches to life-history strategy classification, particularly the r/K concept, have been widely applied in population ecology; however, their direct application to plants, especially aquatic species, remains limited due to the complexity of plant life forms and their high phenotypic plasticity [11; 12]. More recently, functional trait-based approaches have gained prominence, allowing ecological strategies to be interpreted along continuous gradients rather than as discrete categories [13; 14; 15]. In this study, the term "ecological strategies" is used in a broad integrative sense, combining elements of the r–K framework, CSR theory, and trait-based approaches to describe plant adaptation to environmental conditions. It is well established that the distribution of CSR strategies is governed by the balance between environmental stress and disturbance intensity [9], supporting the interpretation of plant strategies as a continuum.

Changes in trophic status have a strong impact on the composition and functional structure of macrophyte communities, often resulting in the loss of sensitive species and the dominance of opportunistic taxa [16]. In this context, the application of an extended r–K–S continuum, integrating traits of rapid colonizers, competitors, and stress-tolerant species, appears promising for the classification of aquatic macrophytes based on their functional characteristics. Unlike the classical CSR framework, originally developed for terrestrial ecosystems, the r–K–S continuum applied here allows for the simultaneous expression of colonization ability, competitive performance, and stress tolerance in aquatic plants.

Analysis of recent research and publications. In Ukrainian studies, considerable attention has been paid to the indicator value of aquatic macrophytes, community structure, and responses to anthropogenic pressure [17; 18; 19; 20; 21]. Ovcharenko Yu. & Shevchenko G. (2025) highlights anatomical and cellular features of root systems in *Sagittaria sagittifolia* and *Alisma plantago-aquatica* as key adaptations to aquatic environments, reflecting both evolutionary divergence within Alismataceae and the high developmental plasticity of aquatic macrophytes [22]. However, a systematic synthesis of ecological strategies in aquatic flora based on modern functional approaches remains insufficiently developed.

Particular interest is associated with species of the family Alismataceae, which, although represented by a limited number of species (four in the study region), contribute disproportionately to the structural and ecological distinctiveness of aquatic vegetation in the Styr–Horyn sub-basin of the Pripyat River. This region is of high importance for the conservation of wetland ecosystems in Polissia, and the ecological roles of these species are closely linked to their emergent growth forms and dependence on hydrological stability.

From a practical perspective, plant growth forms and ecological strategies have been proposed as effective response variables for assessing the outcomes of river restoration projects [23], highlighting the applied relevance of strategy-based approaches in aquatic ecology.

Despite increasing attention to the functional ecology of aquatic macrophytes, a coherent synthesis of ecological strategies within a unified trait-based framework remains lacking, particularly for

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freshwater taxa with high morphological plasticity. Existing studies have largely focused on either community composition, indicator value, or isolated functional traits, without integrating these perspectives into a consistent strategy-based interpretation. This gap is especially evident for the family Alismataceae, where closely related species exhibit substantial ecological divergence that has not been systematically analyzed in terms of functional traits and strategy continuum. In addition, the placement of species along a single r–S gradient remains conceptually problematic, as ruderal dynamics and stress tolerance represent different ecological dimensions that cannot be adequately captured within a one-dimensional continuum. Addressing this limitation requires a more flexible representation of ecological strategies.

In this context, we propose a conceptual extension of the r–K–S framework by representing plant strategies within a continuous three-dimensional space defined by stress tolerance (S), competitive ability (K), and ruderal dynamics (r). Within this space, species are interpreted not as discrete points but as volumetric regions reflecting ecological plasticity and the coexistence of multiple strategy components.

This approach contributes to bridging the gap between traditional ecological classifications and contemporary trait-based approaches in aquatic plant ecology [24; 25; 26].

Aim and of the study is to synthesize current knowledge on the ecological strategies of aquatic macrophytes of the family Alismataceae in the Pripyat River basin using a functional trait-based approach, and to evaluate the applicability of the r–K–S continuum for their classification. In addition, the study explores the potential of representing ecological strategies within a conceptual three-dimensional framework defined by stress tolerance (S), competitive ability (K), and ruderal dynamics (r).

Materials and Methods. This study is based on a synthesis of published data on the ecological and biological characteristics of aquatic macrophytes of the family Alismataceae occurring in the Pripyat River basin (Eastern Europe). The list of analyzed species was compiled for the Styr–Horyn sub-basin based on the authors' previous floristic surveys [27; 28].

The analysis included aquatic and emergent (helophytic) species of the family Alismataceae. For each species, information on key functional traits determining ecological strategies was compiled from peer-reviewed publications, monographs, and review papers on aquatic plant ecology.

The set of analyzed functional traits included growth rate, reproductive mode (sexual and/or vegetative), life cycle duration, clonal growth capacity, morphological plasticity, and tolerance to abiotic environmental factors. These traits were selected as integrative indicators of species adaptation to environmental variability.

Species were classified according to ecological strategies using a generalized r–K–S continuum, integrating characteristics of r-strategists (rapid growth and colonization of disturbed habitats), K-strategists (competitive ability and persistence in stable environments), and S-strategists (tolerance to environmental stress). The position of each species along the continuum was determined based on the combination and relative expression of functional traits reported in the literature.

Given the high phenotypic plasticity of aquatic plants, the classification was considered interpretative rather than discrete. Species were not assigned to fixed categories but positioned along a continuous gradient, allowing for intermediate strategy types (e.g., r–K, r–S, K–S).

To further generalize the results, ecological strategies were additionally interpreted within a conceptual three-dimensional space defined by the S, K, and r axes. In this representation, species were not treated as single points but as volumetric regions reflecting the variability and plasticity of functional trait expression. The position and extent of these regions were inferred from the range and relative intensity of trait values.

Functional trait expression was evaluated using a semi-quantitative ordinal scale based on literature data and expert assessment. Qualitative categories were converted into numerical values for visualization and comparative analysis: Low – 1, Low-Moderate – 1.5, Moderate – 2, Moderate–High – 2.5, High – 3.

Scoring was based on the frequency of trait descriptions and consensus across multiple literature sources.

AI-based tools (ChatGPT, OpenAI) were used to support data visualization, structuring of results, and language refinement [29]. All core scientific content was developed by the authors.

Results and Discussion

Conceptual approaches to ecological strategy classification. The concept of ecological strategies has a long history in ecology. The r/K selection theory was originally formulated by MacArthur and Wilson and further developed in subsequent studies [11; 30]. An alternative framework was proposed by Grime, who distinguished three primary plant strategies: competitors (C), stress-tolerators (S), and ruderals (R) [12]. These concepts have evolved into modern functional ecology, where plant strategies are interpreted through measurable morphological,

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physiological, and life-history traits [13; 15].

For aquatic macrophytes, the application of these frameworks has specific limitations. Plant responses to environmental changes – such as eutrophication, hydrological disturbance, and light availability – are determined by complex combinations of functional traits rather than discrete strategy types [3; 7]. Consequently, most species exhibit intermediate strategies, supporting the use of continuum-based approaches (Table 1).

Table 1

Comparison of approaches to the classification of ecological strategies

Approach	Conceptual basis	Key characteristics	Limitations (for aquatic plants)	Relevance to this study
r/K selection theory	Population ecology; trade-off between reproduction and competition	r-strategists: rapid growth, high reproductive output, colonization of disturbed habitats; K-strategists: competitive ability, stable populations	Oversimplified for plants; does not account for morphological plasticity and clonal growth	Provides a general ecological framework; partially applicable
CSR theory (Grime)	Plant ecology; trade-offs among competition (C), stress tolerance (S), and ruderal strategy (R)	Three primary strategies and their combinations (C, S, R); linked to stress and disturbance gradients	Originally developed for terrestrial plants; limited direct application to aquatic environments	Useful for interpreting plant adaptive strategies
Functional trait-based approach	Trait ecology; analysis of measurable plant characteristics	Strategies inferred from combinations of traits; supports continuum-based interpretation	Requires comprehensive trait data; interpretation may vary	Forms the core methodologi cal basis of this study
Generalize d r–K–S continuum	Integrative framework combining population and trait-based approaches	Strategies interpreted as a continuous gradient integrating r, K, and S components	Conceptual (less standardized); depends on trait selection	Applied in this study to classify aquatic macrophytes

The proposed conceptual framework (Fig. 1) integrates r/K selection theory, CSR theory, and the functional trait-based approach. Within this framework, species strategies are interpreted as positions within a continuous multidimensional space defined by combinations of functional traits and their responses to environmental gradients.

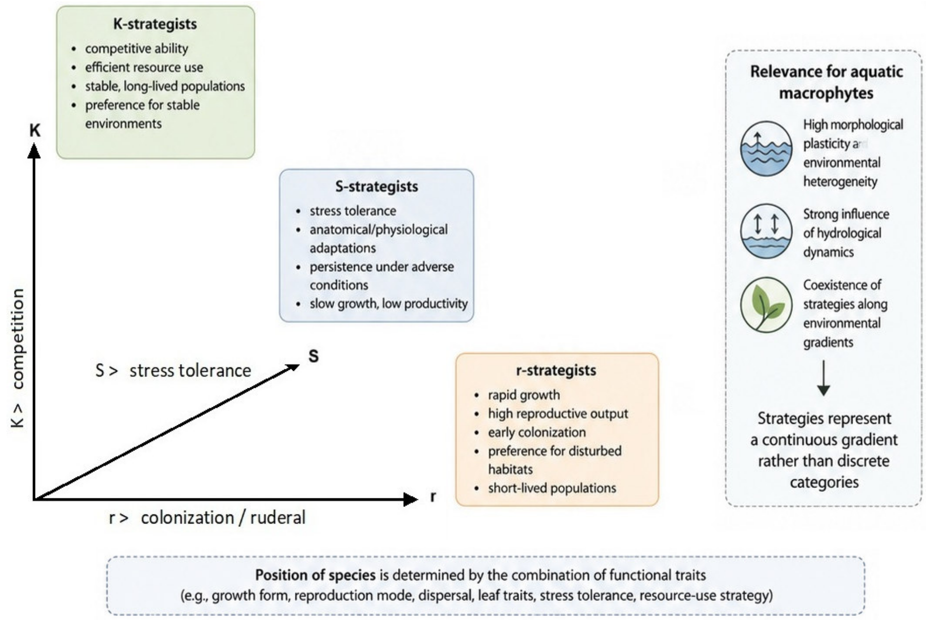

Fig. 1. Conceptual representation of the three-dimensional r–K–S strategy space for aquatic macrophytes. The axes correspond to ruderal (r), competitive (K), and stress-tolerant (S) components. This framework extends traditional two-dimensional models by allowing the simultaneous expression of multiple strategic components within species

In contrast to traditional two-dimensional representations, this framework is further conceptualized as a three-dimensional space defined by stress tolerance (S), competitive ability (K), and ruderal dynamics (r). This representation allows ecological strategies to be visualized as continuous distributions rather than fixed positions, reflecting the multidimensional nature of plant adaptation.

Functional traits and ecological characteristics of Alismataceae species. To evaluate ecological strategies, representative species of the family Alismataceae occurring in the Styr–Horyn sub-basin of the Pripyat River were selected. Previous studies have identified four species in the

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region: *Alisma gramineum, A. lanceolatum, A. plantago-aquatica*, and *Sagittaria sagittifolia*. Among them, *A. gramineum* and *A. lanceolatum* are relatively rare (single localities; <20% of plots) and restricted to specific physiographic regions, whereas *A. plantago-aquatica* and *S. sagittifolia* are widespread (60–80% of plots) across all regions. All species belong to emergent or amphibious ecological groups. According to Dubyna et al. (1993), species of *Alisma* are generally classified as ruderal (R), whereas *S. sagittifolia* shows a combined CSR strategy [17].

A synthesis of literature data allowed the identification of key functional traits determining species strategies (Table 2).

Table 2

Functional traits in relation to ecological strategies of the studied species

Species	Main functional traits	Ecological adaptations and strategy features	References
A. gramineum	Moderate growth; predominantly seed reproduction; pronounced morphological plasticity (submerged and terrestrial forms); reduced leaf blade area in submerged forms	High tolerance to rapid water-level fluctuations; typical of unstable shallow-water habitats; low competitive ability with a tendency toward stress tolerance (S-strategy)	[31; 32; 33]
A. lanceolatum	Moderate growth; seed and vegetative reproduction; moderate morphological plasticity	Tolerance to water-level fluctuations; occurrence in shallow-water and periodically exposed substrates; moderate competitive ability; tendency toward intermediate (C–S) strategy	[32; 33; 34]
A. plantago-aquatica	Rapid vegetative growth; heterophylly; tuberous rhizome; high seed production; well-developed aerenchyma	High plasticity to hydrological regime; tolerance to eutrophic conditions; capacity for rapid recolonization; ability to maintain occupied space; tendency toward mixed r–K–S strategy	[32; 33; 34]

Continuation of the table 2

S. sagittifolia	Moderate growth; vegetative reproduction (tubers, clonal growth); heterophylly; high morphological plasticity	Tolerance to hypoxia (aerenchyma formation); occurrence in unstable and disturbed habitats; capacity for spatial dominance through clonal growth; high competitive ability; tendency toward competitive strategy (K) with ruderal features	[22; 33]

The analyzed species differ markedly in their trait combinations. *Alisma gramineum* is well adapted to fluctuating environmental conditions but shows limited competitive ability and does not effectively displace co-occurring species, reflecting a stress-tolerant strategy. *A. lanceolatum*, in turn, displays intermediate traits, combining moderate plasticity with both sexual and vegetative reproduction. *A. plantago-aquatica* demonstrates high ecological plasticity and mixed strategy features, while *S. sagittifolia* exhibits strong clonal growth and competitive ability, enabling spatial dominance.

Position of species along the r–K–S continuum. The strategy types reported by Dubyna et al. (1993) [17] were used as an initial reference and subsequently reinterpreted within a continuous r–K–S framework based on functional trait analysis (Table 3).

Table 3

Generalized assessment of ecological strategies of Alismataceae species based on their position along the r–K–S continuum; qualitative categories were converted into numerical scores (values are given in parentheses)

Species	r	K	S	Group
A. gramineum	Low (r = 1)	Low–Moderate (K= 1.5)	High (S = 3)	S
A. lanceolatum	Moderate (r = 2)	Moderate (K = 2)	Moderate (S= 2)	K–S
A. plantago-aquatica	High (r = 3)	Moderate–High (K= 2.5)	Moderate–High (S = 2.5)	r–K–S
S. sagittifolia	Moderate (r = 2)	High (K = 3)	Moderate (S = 2)	K

While existing classifications [17] assign species to discrete

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strategy types, the present analysis shows that these strategies are more accurately represented as continuous and overlapping positions along the r–K–S gradient. This shift from discrete classification to a continuous framework enables a more nuanced interpretation of ecological strategies, particularly among closely related aquatic species.

The relative positions of the studied species within the r–K–S continuum are illustrated in Fig. 2 and are based on semi-quantitative trait assessment.

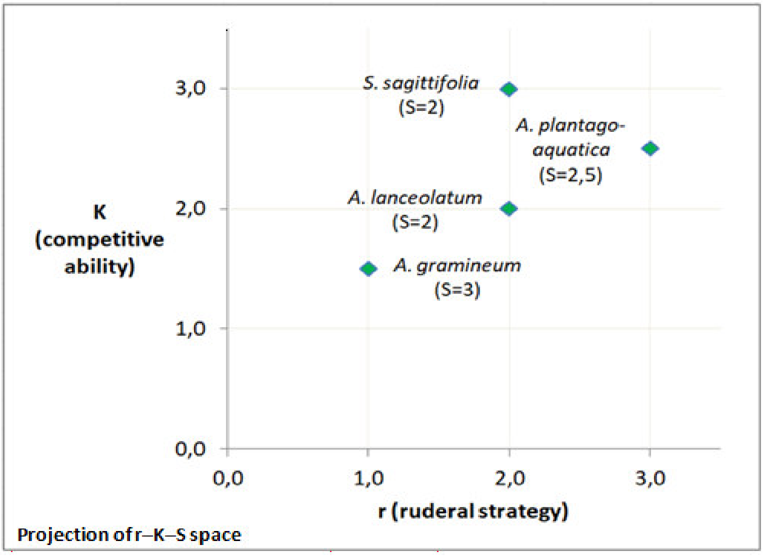

Fig. 2. Two-dimensional projection of species positions within the three-dimensional r–K–S strategy space based on semi-quantitative functional trait assessment. The horizontal axis represents the ruderal component (r), and the vertical axis reflects competitive ability (K), while stress tolerance (S) is indicated in parentheses. The projection illustrates species distribution along a multidimensional continuum of ecological strategies

When interpreted within a three-dimensional r–K–S space, these positions represent not fixed points but regions of variation, reflecting the plasticity of trait expression under different environmental conditions. The species occupy partially overlapping regions, particularly along the K–S axis, which indicates their adaptation to hydrologically variable habitats.

Most species combine multiple strategic components. For example, *A. plantago-aquatica* integrates r-, K-, and S-traits, while *S. sagittifolia* is characterized by strong competitive ability combined with ruderal features. This supports the interpretation of ecological strategies as a continuous multidimensional space rather than a set of discrete categories.

Applicability of the functional trait-based approach. The analysis demonstrates that the studied species form a continuous spectrum of ecological strategies, ranging from stress-tolerant forms to competitively dominant and ruderal types. Accordingly, the distinction into discrete groups is conditional, as most species exhibit combinations of traits associated with different strategies.

These findings are consistent with contemporary functional ecology, which emphasizes that plant responses are determined by trait combinations rather than fixed categories [13; 15]. Classical frameworks such as r/K selection theory [11; 30] and CSR theory [12] only partially capture this complexity, particularly for aquatic plants.

In this context, the functional trait-based approach applied in this study allows species to be interpreted within a three-dimensional r–K–S space defined by resource acquisition, competitive ability, and stress tolerance. Within this framework, species are positioned along continuous gradients rather than assigned to discrete types, which enables the identification of intermediate and mixed strategies.

The inclusion of the stress-tolerance (S) component is particularly important for aquatic macrophytes, as it reflects adaptation to fluctuating hydrological conditions. At the same time, the separation of ruderal and stress-tolerant components into independent axes resolves the limitations of one-dimensional gradients, where such strategies are artificially opposed.

The generalized r–K–S continuum proposed in this study thus serves as an integrative framework that reflects the ecological specificity of aquatic plants. Its extension into a three-dimensional space enhances its explanatory power by allowing the simultaneous representation of multiple strategic components within a single species.

The methodological novelty of this approach lies in combining the adapted r–K–S continuum with a trait-based analysis and its interpretation within a multidimensional space. Unlike classical models, this framework does not constrain species to fixed positions but allows the coexistence of different strategy components, providing a more realistic representation of plant adaptation in dynamic freshwater environments.

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Overall, this approach offers a basis for integrating classical ecological theory with functional trait analysis and can be applied to broader sets of aquatic plant species.

Practical implications. The proposed functional trait-based framework and r–K–S continuum, together with its conceptual extension into a three-dimensional r–K–S space, provide a useful tool for assessing the ecological status of freshwater ecosystems through macrophyte communities. By linking species strategies to environmental gradients, this approach can support monitoring of eutrophication, hydrological alterations, and anthropogenic disturbances.

Representing species strategies as continuous and potentially overlapping regions enhances the ability to capture ecological plasticity and improves the sensitivity of assessments compared to discrete classifications. The framework also offers a basis for predicting vegetation responses to environmental change and for selecting indicator species in ecological assessments.

Furthermore, the approach can be applied in river and wetland restoration projects to evaluate ecosystem recovery and guide management decisions.

Conclusion. This study demonstrates that ecological strategies of aquatic macrophytes of the family Alismataceae in the Pripyat River basin are more adequately interpreted within a continuous r–K–S framework rather than as discrete categories. Functional trait analysis revealed clear differentiation among closely related species, reflecting their adaptation to environmental gradients, particularly hydrological variability and trophic conditions.

The results support the representation of ecological strategies as a multidimensional space rather than a single continuum. Extending the r–K–S framework into a conceptual three-dimensional space enables species to be described as dynamic combinations of ruderal, competitive, and stress-tolerant traits, capturing their ecological plasticity and context-dependent responses.

Clonal growth, reproductive flexibility, and morphological plasticity emerge as key mechanisms shaping strategy formation in aquatic plants, emphasizing the importance of functional traits in explaining species ecological behavior.

The proposed trait-based perspective provides an integrative framework linking ecological theory with species-level functional variation and offers practical potential for application in freshwater ecosystem assessment, biomonitoring, and management.

Further research should expand this approach to broader taxonomic groups and community-level patterns in order to advance the understanding of functional diversity and ecosystem functioning in aquatic environments.

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ЕКОЛОГІЧНІ СТРАТЕГІЇ ВОДНИХ МАКРОФІТІВ БАСЕЙНУ РІЧКИ ПРИП'ЯТЬ. І. ПІДХІД НА ОСНОВІ ФУНКЦІОНАЛЬНИХ ОЗНАК У МЕЖАХ R–K–S КОНЦЕПЦІЇ: ПРИКЛАД РОДИНИ ALISMATACEAE

Водні макрофіти є ключовими структурними та функціональними компонентами прісноводних екосистем, однак їхні екологічні стратегії залишаються складними для класифікації через високу морфологічну пластичність і поєднання численних адаптивних ознак. У цій роботі узагальнено сучасні уявлення про екологічні стратегії водних макрофітів родини Alismataceae у басейні річки Прип'ять (Східна Європа) із використанням підходу, що базується на функціональних ознаках.

На основі синтезу літературних даних види оцінено за допомогою напівкількісного аналізу ключових функціональних ознак, зокрема швидкості росту, способів розмноження, здатності до клонального розростання, морфологічної пластичності та толерантності до абіотичних чинників. Екологічні стратегії інтерпретовано в межах узагальненого континууму r–K–S, що інтегрує рудеральну (r), конкурентну (K) та стрес-толерантну (S) компоненти.

Отримані результати свідчать, що досліджені види займають проміжні та перекриваючі позиції, поєднуючи кілька компонентів стратегії, а не утворюючи окремі типи. Зокрема, близькоспоріднені види демонструють виражену диференціацію за комбінаціями ознак, що відображає адаптацію до гідрологічної мінливості та трофічних умов середовища.

Для кращого відображення цієї складності концепцію r–K–S розширено до тривимірного простору r–K–S, у якому види представлені не як фіксовані точки, а як безперервні варіабельні області. Такий підхід допускає співіснування кількох стратегічних компонентів у межах одного виду та забезпечує більш реалістичне відображення екологічних стратегій у водному середовищі.

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Запропонована модель поєднує класичну екологічну теорію та сучасні підходи, які ґрунтуються на функціональних ознаках, та має потенціал для застосування в оцінці, моніторингу та відновленні прісноводних екосистем.

Ключові слова: водні макрофіти; Alismataceae; екологічні стратегії; функціональні ознаки; клональний ріст; стратегії розмноження; екологічні градієнти; басейн річки Прип’ять.

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