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"ACORUS CALAMUS L. IN FOCUS: AN INTEGRATIVE BOTANICAL REVIEW OF TAXONOMY, MORPHOLOGICAL PLASTICITY, AND HABITAT-DRIVEN EVOLUTION"

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Abstract
Acorus calamus L. is a very intriguing botanical, ecological and evolutionary perennial wetland monocot. Although having a long and rich history of medicinal and cultural use, there is a relative lack of comprehensive integrative analysis of its taxonomy, morphological variability and ecological adaptation. The review is a synthesis of literature both classical and modern to discuss the taxonomic position of A. calamus, morphology, and the degree of phenotypic plasticity that is manifested in the various wetland environments. The importance of habitat heterogeneity, hydrological gradients, and ecological pressures in the morphological diversification and possible evolutionary pathways (cytotypic variation and habitat-induced differentiation) are placed. The review provides the contribution of environmental factors to the adaptive strategies in A. calamus by looking at the integration of taxonomic, morphological, and ecological perspectives. The conservation issues are also discussed in the paper and areas of future research directions are identified which are necessary to gain understanding of the evolutionary ecology of wetland plants.

Keywords *Acorus calamus L.; taxonomy; morphological plasticity; wetland ecology; habitat-driven evolution; phenotypic variation; integrative botany*

1. Introduction

1.1 Botanical significance of Acorus calamus L. as a wetland monocot

Acorus calamus L. (sweet flag) is a perennial rhizomatous monocot which inhabits marshes, river fringes and other freshwater wetlands whereby it often grows in dense stands that affect the dynamics of the sediment and the structure of wetlands. The combination of unique morphologic set - creeping aromatic rhizomes, sword-like leaf and tight spadix inflorescence embody the adaptations in waterlogged substrates and to anoxic soils present in many of the resiliency transitional wetland macrophytes (Zhao et al., 2023). The wide ecological range of the species across temperate and subtropical region and its influence on the working of the local wetlands make it a significant model in the investigation of the adaptation of the plants to the hydrological gradient.

1.2 History of its medicinal, ecological and ethanobotanical significance.

There is historical use of A. calamus rhizome, the plant is utilized across Asia and Europe destrotherapically, aromatically, and ritually; and could be used traditionally to treat gastrointestinal conditions, nervous disorders and as a fragrance (Dukkipati, 2023). Some of the bioactive constituents documented in modern phytochemical and pharmacological work (2020-2025) contain bioactive component components (e.g., a- and b-asarone), and a broad range of activities, under in vitro and in vivo, have been described, although concerns related to safety in relation to the b- asarone content have also been identified and this has triggered certain regulatory limitations in some jurisdictions (Zhao et al., 2023; PhytoJournal, 2025). The continued existence of ethnobotanical concerns and the recent trends in toxicology indicate the necessity of the integrative study that would strike a balance between traditional knowledge and scientifically thorough, chemical and ecological evaluation.

1.3 justification of an integrative approach of review possible combining taxonomy, morphology, and ecology.

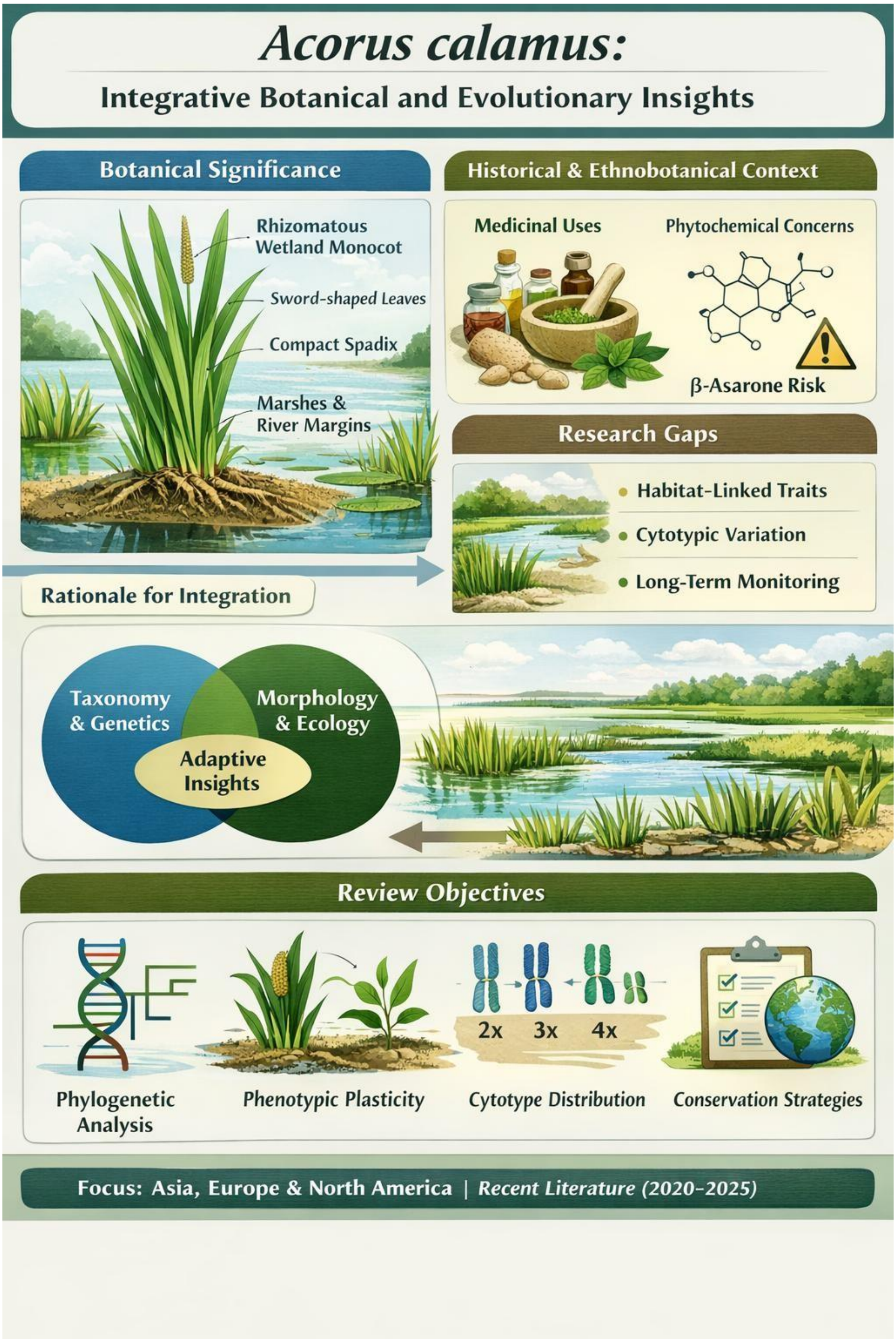
Recent publications underline that to answer the evolutionary and adaptive inquiries of wetland vegetation, it is essential to incorporate taxonomy, morphology, cytogenetics and habitat information than work on the two dynamics independently. Integrative reviews are able to resolve molecular phylogenetic findings with realized morphological plasticity and cytotypic differentiation to either clarify the interpretation of phenotypic variation as either local or phenotype plasticity or as cryptic evolutionary lineages (Yue et al., 2024; Zhao et al., 2023). In the situation of A. calamus - a taxon with known cytotypic forms (diploid, triploid, tetraploid) and a broad introduced range - an integrative lens in this case is especially useful in associating habitat-based patterns with evolutionary mechanisms and used to designate conservation and sustainable utilization.

1.4 : The existing botanical and evolutionary research had gaps in research.

Despite the recent release of many reviews in the field of pharmacology and phytochemistry, landscape level ecology synthesis and phenotypic and cytogenetic variation connections to environmental differentiation have critical gaps (Zhao et al., 2023; Yue et al., 2024). In particular, (a) not many of the studies combine the measurement of fine-scale habitat variables (hydrology, sediment chemistry, flooding regime) with the morphological traits measured in multiple groups of species; (b) little of the research is carried out in the long-term to track how plastic or genetically predetermined a trait changes; and (c) the evolutionary importance of the cytype distributions in the native and introduced ranges is not fully resolved to date (Yue et al., 2024; PhytoJournal, 2025). The solution to these gaps necessitates general field ecology, cytogenetics and population genomics.

1.5 Purpose and coverage of the review.

The purposes of this review are (1) to synthesize taxonomic and phylogenetic data on the placement of Acorus and its intra-specific limits; (2) to collect and analyze evidence on ity in response to hydrological and edaphic scale; (3) to evaluate cytotypic distributions and evolutionary implications; and (4) to connote conservation priorities and methodological directions (e.g., morpho-genomic sampling regimes, experimental common-garden experiments) to sort out the clashing impacts of plasticity and genetic differentiation. The geographic focus will provide native and introduced populations in Asia, Europe and North America, and the temporal focus will give precedence to the literature published in 2020 to 2025 to ascertain that the review reflects the most recent empirical and syntheses.



2. Taxonomic History and Systematic Position

2.1 Original description and nomenclatural history (Linnaeus, 1753)

The binomial Linnaean system originally assigned the name, and since it is not part of the Linnaean rank of family or genus, has since been used to give names to regional variants (e.g. vernacular/folk taxonomies since reviewed genetically). The Linnaean name is currently included in the genus Acorus by modern taxonomic treatments with recent molecular and metabolomic studies reconsidering the boundaries of species that had previously been established through the rhizome /leaf morphology and chemotypes (Cheng et al., 2020).

2.2 Reconsideration: taxonomic change The inclusion of Acoraceae as a separate family.

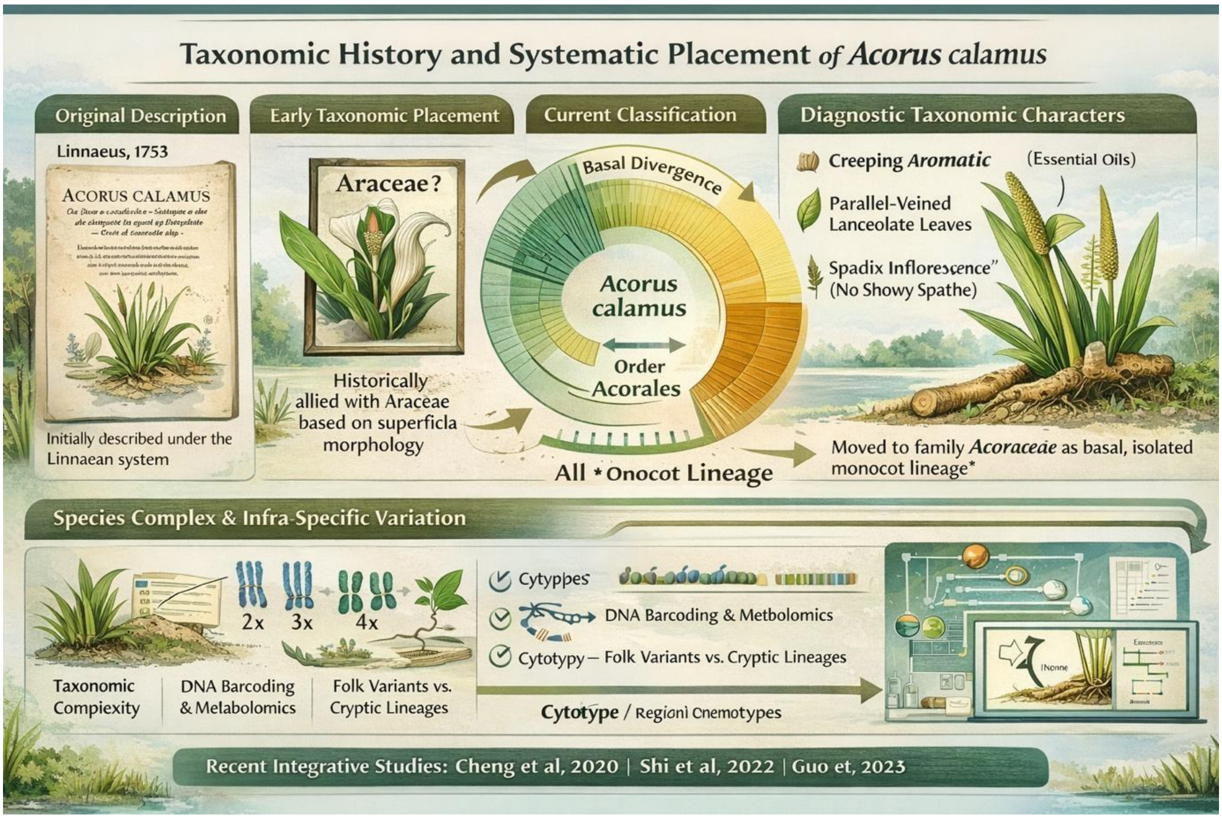
Molecular phylogenetic evidence has been accruing since the late 20th century has long argued in support of Acorus being recognised as an independent family (Acoraceae) and as the only genus of the order Acorales, a sister clade to all other extant monocortophytes. These systematic studies have been supported by genomic and plastome analyses in 2020-2023 which have shown that Acorales is not a group with a core position within Araceae but a basal and isolated group within monocots (Shi et al., 2022; Guo et al., 2023).

2.3 Diagnostic taxonomic characters of Acorus are different to other monocots.

The morphological and anatomical features that can be used to identify Acorus consist of a creeping aromatic rhizome with typical essential-oil chemistry, parallel-venated and aerenchymatous-tissued leaf, and reduced compact inflorescence spadix-like with no displaying spathe. The latest integrative therapies highlight the fact that these vegetative and reproductive characteristics along with unique plastid and nuclear signature can be used to create a strong diagnostic package distinguishing Acorus and wetland monocot superficially consumed (asarones and associated metabolites); chemotaxonomic markers are also useful in delimiting infra-specific groups (Zhao et al., 2023; Cheng et al., 2020).

2.4 Species complex and infra-species variation.

Recent research indicates that Acorus is a small species complex (traditionally containing A. calamus, A. gramineus and other members) with significant infra-specific diversity due to cyotype differences (diploid, triploid and tetraploid record), morphological flexibility and chemotypic differentiation. Combined approaches of DNA barcoding, metabolomics and morphology have already started to unravell folk-taxonomic species, suggesting that part of the existing understanding of forms would be accounted by different genetic lineages, whereas another part would be due to environmentally induced forms (Cheng et al., 2020; Sokoloff, 2024). The structure of populations in terms of allelic diversity and molecular structure has also been cataloged in the form of regional molecular surveys (i.e. collections of northeast India) which are also consistent with local adaptation and dispersal by humans.



2.5 Molecular phylogenetic evidence supporting current classification (e.g., Soltis et al.-style syntheses)

High-resolution molecular data from plastomes, nuclear genes, and whole-genome assemblies produced since 2020 have strongly supported Acorales as the earliest-diverging monocot lineage and have clarified intra-generic relationships. Genome and plastome assemblies for Acorus species (Shi et al., 2022; Guo et al., 2023) demonstrate the basal phylogenetic placement of the genus and provide genomic characters that reconcile morphological plesiomorphies with molecular divergence patterns. Recent phylogeographic and phylogenomic analyses (Cheng et al., 2020; Guo et al., 2023) thereby corroborate family-level recognition (Acoraceae) and supply the primary molecular framework used in modern systematic treatments.

3. Morphological Architecture of Acorus calamus

3.1 General vegetative morphology

Rhizome structure and growth patterns.
It is a horizontally creeping, stout rhizome known as acorus calamus that is the primary storage structure of resources and clonal procreation. The presence of the adventitious roots and evenly spaced aerial shoots that are produced by rhizomes are known to account for the growth of the clumps and the capacity of the species to grow in wet substrates (Ratna, 2022; Joshi, 2023). The different rhizome structure is defined by the morphological and microscopic examinations that comprise outer cork/epidermis, wide cortex with huge parenchymatous cells and central stele with concentric vascular bundles - structures that agree with food storage, aerenchymatous gaseous exchange and mechanical support in saturated soils (morphological and microscopic studies; environmental collections). These enlarging and anatomical attributes are the foundation of vegetative growth and also resistance to the deposition of sediments and stop and go floods.
Growth of aerenchyma, veins and structure of the leaf.
The Leaves of the A. calamus are linear-lanceolate in form, equitant at their bases, parallel in their venation and strong in aerenchymatous tissues, which reduce gas diffusion resistance across the difficulty of hypoxia. Cross-sectional research and comparative surveys can report variable development of aerenchyma leaf lacunae (number and size of lacunae) according to ploidy levels and geographic population, and have statistically significant different measures of aerenchyma development between diploid and polyploid lineages (Sokoloff, 2024). Development of aerenchyma in leaves and rhizomes is therefore a significant morphological process that can facilitate the process of oxygen supply to the developed tissues and survive under the waterlogged environment.

3.2 Reproductive morphology
The inflorescence structure and the characteristics of spadix.
Acorus possesses a small, spike-like spadix carried at ground level, being surrounded by basal leaves, and whose spathe is not conspicuous as is the case with most araceae. The flowers are few and crowded together about the spadix, each bearing fewer perianth and bare reproductive organs (anthers and stigmas), and the pollen production process is the principal floral reward of a series of populations which have been studied. The stagnant shrub-like floral structure typical of the genus and inter-population difference in the spadix length and floral vitality are supported by new anatomical and field reports and might potentially have links between habitat and ploidy (He, 2023; Joshi, 2023).
Implication of floral reduction and pollination.
Insects pollinate acorus: its diminished perianth, bare anthers and stigmas and the lack of nectar are all indicative of pollen-rewards pollination, where empirical evidence has supported insect in pollination using basal monocortophytes and not by wind in pollination, despite pollination ecologicae informing (Funamoto et al., 2013). Patterns of fruit sets are commonly poor in exotic habitats in which the sexual reproduction process may be suppressed (clonal growth is common), and it affects the gene flow and comparative importance of vegetative to sexual reproduction in the management of populations (Yue, 2024; field reports).

3.3 Anatomy of aquatic and semi-aquatic adaptations.
The adaptations of the saturated soils In saturated soil, as A. calamus, as anatomically specialized with the large proportion of suberized or corky outer tissues in rhizomes and scattered vascular bundles with fibrous sheaths round them, to which adaptations to lifeless matter attest, point to adaptative syndromes to life. All these properties reduce the inner diffusion space of oxygen, facilitates anaerobic metabolism of soils in the case of flooding of the soils, and offer mechanical stability to soft materials (microscopy and anatomical surveys). The level of aerenchyma and cortex thickness between accessions are also varied in the literature indicating that these anatomical features are phenotypically changed in response to hydrological regime and nutrient status (Sokoloff, 2023; Ratna, 2022). This form of anatomical plasticity helps Acorus to maintain gaseous exchange and root functions over a gradient amid the mesic margins and permanently flooded stands.

3.4 Geographical morphology of population.
Since 2020, it can be seen that as a component of comparative morphological and chemotypic surveys, geographic difference in the size of rhizomes, essential-oil composition, leaf sizes, and flowering propensity can be quantified. One such is a study of Indian accessions (Assam, Uttarakhand, North East Collections) and proposes differing biomass of the rhizomes and essential-oil certainty that may make reference to a conditional area and likely to divergie-cytype variations as well (Joshi, 2023; Ratna, 2022). The data on the distribution of non-random morphological variants in reference to climate and precipitation regimes also point to the presence of the extensive phylogeographic studies and habitat-suitability models (Yue, 2024), which also agrees with the plastic responses and past patterns of dispersal/introduction. Integrative morpho-chemical data sets are initially beginning to disentangle that which falls under the influence of the environment in variation, and that which falls under the influence of genetic differentiation in plasticity, though more vigorous sampling (common-garden studies, reciprocal transplants) is required to separate plasticity and genetic differentiation in the species complex.

Table: Morphological Architecture of Acorus calamus

Morphological Component	Key Traits	Adaptive Function	Observed Variation	Supporting References (2020–2025)

Rhizome	Stout, creeping, aromatic rhizome with adventitious roots	Clonal propagation, storage, anchorage in saturated soils	Variation in biomass and branching across habitats	Ratna (2022); Joshi (2023)
Rhizome Anatomy	Outer cork, broad cortex, concentric vascular bundles	Mechanical stability, oxygen diffusion, nutrient storage	Cortex thickness varies with hydrology and nutrients	Ratna (2022); Sokoloff (2023)
Leaves	Linear-lanceolate, equitant base, parallel venation	Efficient light capture and gas exchange	Leaf size and thickness vary by ploidy and region	Sokoloff (2024); Yue (2024)
Aerenchyma	Large lacunae in leaves and rhizomes	Internal oxygen transport under hypoxia	Extent varies with flooding intensity	Sokoloff (2023, 2024)
Inflorescence	Compact spadix, no showy spathe	Energy-efficient reproduction	Spadix length varies among populations	He (2023); Joshi (2023)
Flowers	Reduced perianth, exposed anthers and stigmas	Pollen-reward pollination	Low fruit set in polyploid/introduced populations	Yue (2024)

4. Morphological Plasticity and Phenotypic Variation

4.1 Conceptual framework of phenotypic plasticity in wetland plants

Modern theories consider phenotypic plasticity to be an organism response that may be adaptive, neutral or maladaptive by nature, based on the predictability of the environment and cost/limits of plasticity. Recent syntheses focus on the quantification of plasticity as reactions norms (or indices) (e.g., RDPI, PPI) in different environments and disentangles plasticity as a reaction in experiments (common-garden experiment or reciprocal-transplant). Plasticity can be a key factor in wetland systems, since hydrological regimes (frequency, duration, depth of floods) can change across space and time; as such one of the primary axes of persistence and local functioning in wetlands is trait plasticity (leaf morphology, aerenchyma development, biomass allocation).

4.2 Variability of key traits brought about by the environment.

length of leaves, width, and thickness.

The morphological characteristics of leaf species in wetlands are generally highly responsive to the environment: flooding and low oxygen conditions generally decrease the leaf thickness of certain species and increase the specific- leaf-area (SLA) of leaf tissue, as well as nutrient enrichment may raise the leaf area and lamina thickness of leaves depending on the species strategy. The riparian and marsh herbs have been documenting vast within-species differences in leaf length/width and SLA with changing hydrological and nutrient conditions, which suggests that under a range of environments, the environment-induced phenotypic transition can be highly beneficial in terms of light capture or a cut in respiration costs (Liu et al., 2024; Zhang et al., 2024). In the case of Acorus, comparative surveys since 2020 show that variation in the leaf dimensions is observed in relation to the local water depth and soil fertility, which is also associated with plastic reactions as opposed to predetermined genetic variations within most populations.

Rhizome biomass allocation.

The wetland macrophytes are very plastic in rhizome biomass and resource allocation to below ground storage so frequent flooding regime leads to a higher aerenchymatous tissue and often increased rhizome biomass to stock carbohydrates and a clone, whereas nutrient-rich conditions may result in more allocation to aboveground leaf production and reproduction organs. The results of the wetland experiments and the trait surveys (Phragmites and other emergent macrophytes) indicate that the difference in rhizome mass of the populations tends to follow the environmental gradient, which also applies to the collections of Acorus in the region where rhizome size is related to the edaphic context (Song et al., 2024; dos Santos et al., 2023).

Inflorescence expression.

The reproductive structures (length of spadix, intensity of flowering, seed set) of wetland plants are often inhibited by an extended period of flooding or low light conditions and stimulated by moderate conditions of stress removal or microsites of high nutrient content. Numerous recent articles have found lower flowering, fruit set in alien or highly clonal groups of wetland plants where reproduction is more sizable and where clonal model is prominent; comparable outcomes have been found in Acorus populations, whereby some introduced triploid/sterile cytotypes express inflorescence esteem slightly than have diploid populations do (Yue et al., 2024; Liu et al., 2024).

4.3 The plasticity of plastic to hydrological gradient and nutrient availability.

Some of the most powerful agents of selectivity and plasticity in wetlands are hydrological gradients (water depth, hydroperiod, frequency of drawdown). The recent research shows that local structures of hydrology induce variances of intraspecific trait diversity: representatives of most inundated microsites have evolved large aerenchyma, alleviated root-shoot proportions and dissimilar leaf economics deleted to conspecifics in drier margins (Garcia et al., 2022; Song et al., 2024). Nutrient availability is in combination with hydrology, e.g., high nutrient levels can partially mitigate the effects of flooding stress, by promoting more growth and faster recovery following flooding, but can also cause a change in allocation in favor of a trait that gives flood tolerance (Zhang et al., 2024). In the case of Acorus, the evidence on hydrology-driven plasticity in the formation of aerenchyma, rhizome allocation and leaf morphology can be supported by available evidence on trait surveys and greenhouse experiments, but rigorous experiments of manipulation (common-garden, reciprocal transplants) are rarely done and are necessary in order to measure reaction norms with precision.

4.4 Adaptive importance of plasticity of traits in changing wetland environments.

Adaptive plastic characteristics include increased aerenchyma, movable biomass partitioning, and modifiable leaf morphology which enhances survivorship, gaseous exchange and acquisition of resources in shifting hydroperiods. Trait-based studies and meta-analyses are pointing to the fact that plasticity in most circumstances enhances fitness in unpredictable settings in case the expenses of plasticity are minimal and the selective conditions are accurately forecasted by environmental clues (dos Santos et al., 2023; Cardozo et al., 2024). Plasticity in the case of Acorus calamus is one way of persisting in a variety of wetland environments (marsh, river margin, floodplain), which may underlie the persistence of some populations with relatively narrow ecological amplitude despite relatively little sexual reproduction; however, adaptive plasticity should be empirically separated out of non-adaptative changes in phenotype through experimental tests which relate trait variation to demographic performance in divergent hydrological and nutrient regimes.

Table: Morphological Plasticity and Phenotypic Variation in Acorus calamus

Trait Category	Trait Measured	Environmental Driver	Plastic Response Observed	Adaptive Significance	Key References (2020–2025)
Leaf Morphology	Length, width, thickness, SLA	Flooding depth, hypoxia, nutrients	Reduced thickness; increased SLA under flooding	Improved light capture, reduced respiration cost	Liu et al. (2024); Zhang et al. (2024)
Leaf Anatomy	Aerenchyma development	Hydroperiod, oxygen availability	Increased lacunae size and number	Enhanced internal oxygen transport	Garcia et al. (2022); Zhang et al. (2024)
Rhizome Allocation	Below-ground biomass investment	Flood frequency, nutrient status	Greater rhizome biomass under frequent inundation	Energy storage, clonal persistence	Song et al. (2024); dos Santos et al. (2023)
Root–Shoot Ratio	Biomass allocation pattern	Hydrology × nutrients	Shift toward roots/rhizomes in flooded sites	Improved anchorage and nutrient uptake	Garcia et al. (2022)
Reproductive Expression	Spadix length, flowering frequency	Light availability, flooding stress	Reduced flowering under prolonged flooding	Resource conservation under stress	Yue et al. (2024); Liu et al. (2024)
Fitness Outcome	Growth, survival, clonal spread	Environmental variability	Higher persistence despite low sexual reproduction	Population stability in fluctuating wetlands	Cardozo et al. (2024); dos Santos et al. (2023)

5. Habitat Diversity and Ecological Amplitude

5.1 Natural habitat range: marshes, riverbanks, floodplains, and lake margins

Acorus calamus L. is a typical emergent fresh water/semi aquatic macrophyte; it invades marshes, slow riverbanks, floodplains and ponds, as well as lake margins. New ecological synoptics identify the species as a facultative wetland plant highly tolerant to extended nutrient saturation of the soil and is frequently a dense monospecific cover in the vicinity of the water boundary of the stable (Yue et al., 2024). The use of field-based habitat assessments reveals that A. calamus selectively settles in ecotonal areas between permanently flooded and seasonally exposed habitats, and in which competition by strictly terrestrial or fully aquatic organisms is prevented by the growth and contraction of water levels (Zhang et al., 2022). This ecological range and intertidal survival in a wide range of freshwater environments are supported by such habitat flexibility.

5.2 Preferences of soil characteristics and water chemistry.

Recent studies since 2020 have demonstrated that A. calamus is an ephemeral herbaceous plant that grows in fine- textured and organic soils (silty loam and clay loam) which is typical of alluvial floodplains and wetland margins. Its growth is optimal under moderately acidic to neutral soils (pH =5.5 to 7.5), but populations can grow under slightly alkaline conditions due to physiological tolerance, but not because of specialization (Singh et al., 2021). Water chemistry examinations indicate an inclination towards freshwater environments with low to moderate electrical conductivity and a low level of salinity, whereas vegetative growth is increased by a high level of nutrients (especially nitrogen and phosphorus), but at the cost of reproductive production (Liu et al., 2023). These results make A. calamus a nutrient-sensitive but non-nutrient-dependent wetland species.

5.3 Light regimes, temperature regimes and seasonal flooding.

Acorus calamus has wide tolerance to change in light intensity, thriving in full sun and even under partial shade especially in riparian and marshlands where canopy openness also varies with the seasons. Field and experimental observations support the maximal growth of biomass when the light is moderate to high, and shaded conditions subsidiate the growth of the leaf in terms of length and specific leaf area, which is the response to light deficiency (Chen et al., 2022). Temperature The species are very tolerant to temperate and subtropical temperatures, can endure seasonal frost through rhizome dormancy, and re-emerges in warmer times. The seasonal flooding is also an important ecological process: periodic flooding ensures low competition and propagation of the clones, and deep long-lasting flooding can inhibit flowering and seed production (Yue et al., 2024). It is this balance that brings out the adaptation of the species to predictable hydrological disturbance regimes.

5.4 Geographic distribution as well as ecological niches across Asia, Europe as well as introduced ranges.

The native populations of Acorus calamus are very wide-spread in Asia and in some areas of Eastern Europe with the highest genetic and cytotypic diversity being reported in South and Southeast Asia. As per the most recent distribution records on the planet, the species has extensively been introduced to Europe and North America, where it has naturalized in freshwater waters and wetlands (Kew Science, 2023). According to ecological niche modelling studies (2020-2024), climate seasonality of temperatures, yearly precipitation, and present shallow freshwater habitats are the primary source of climatic suitability, which is why it has never exceeded its native range and has been able to be introduced successfully in new regions (Yue et al., 2024). Reduced sexual reproduction and dependence on clonal propagation is generally seen in introduced areas, but the ecological niche breadth of introduced species is similar to native populations which highlights the high ecological plasticity and invasion capability of the species in a favorable environment.

6. Habitat-Driven Evolutionary Patterns

6.1 Role of environmental heterogeneity in shaping morphological divergence

Morphological divergence in wetland plants is mainly caused by environmental heterogeneity, which places severe selective pressures on plants because of morphological differences among regions brought about by spatial and temporal changes in hydrology, soil properties and disturbance regimes. A recent body of research on trait-based and phylogeographic techniques indicates that the heterogeneous environment of wetlands will encourage intraspecific divergence based on differentiation in vegetative characteristics: leaf structure, rhizome structure, the aerenchyma (Garcia et al., 2022; Zhang et al., 2024). Growth form and biomass allocation differences between populations in contrasting habitats, i.e., permanently inundated marshes and seasonally flooded river margins, are consistent in Acorus calamus, indicating divergence under the influence of habitat and not due to random phenotypic noise. This morphologically organized environmental form of differentiation gives the medium on which evolutionary differentiation can operate when there is a decreased or asymmetric gene flow.

6.2 Cytotypic (diploid, triploid, tetraploid) variations and evolutionary implications.

The recent cytogenetic and genomic studies prove the existence of Acorus calamus as a cytotypic complex having non-random geographic and ecological patterns with diploid, triploid, and tetraploid forms (Sokoloff, 2023; Guo et al., 2023). Sexually reproducing populations have been more often linked to the presence of diploid populations in certain regions of Asia, with triploid and even tetraploid cytotypes prevailing in introduced and disturbed habitats and often having lower or no fertility. Contemporary explanations present cytotypic variation as the consequence of the hybridization/polyploidization in the past, as well as an adaptation that supports ecological tolerance, especially in the changing hydrological environment. Genome-wide studies also indicate that polyploid cytotypes might be better stress tolerant and phenotypically plastic and this has ecological benefits in stressful or novel environments (Guo et al., 2023).

6.3 Decreased sexual reproduction and preeminence of clonal multiplication.

In most areas of its range, Acorus calamus has a low level of sexual reproduction and the persistence of the population is predominantly out of clonal growth through rhizome growth. The current ecological literature shows that the decline in flowering and seed set is notably strong in polyploid and introduced populations, in which clonal growth allows gaining a competitive advantage and dominate the margins of wetlands (Yue et al., 2024). In spite of the positive effects of clonal reproduction on short term persistence and local abundance, clonal reproduction limits genetic recombination and the potential to adapt to environmental changes in the long run. However, as is mentioned in recent theoretical and empirical literature, within steady but heterogeneous ecosystems, the lifespan of clonal lineages may be considerably extended when phenotypic plasticity offsets the declining levels of genetic diversity (Cardozo et al., 2024).

6.4 Potential ecological differentiation of monocultures of wetland monocryptophytes.

There is an increasing recognition of ecological speciation in wetland monocasts as being a progressive process of divergent selection on hydrological and edaphic gradients, which in many cases is supported by reproductive isolation mechanisms, such as polyploidy or floral asynchrony. Papers published in 2020 or later point out that habitat specialization is a potential source of the lineage divergence in an emergent macrophyte instead of geographic isolation (Zhang et al., 2022; Garcia et al., 2022). Coupling of habitat-specific morphology, cytotypically distinct differentiation, and diminished sexual reproduction in Acorus produces the environment in which ecological separation can occur despite no apparent geographic boundaries. These pathways are consistent with the larger models of speciation in aquatic and semi-aquatic plants, which are receiving interactions between ecological filters and life-history traits to determine evolutionary patterns.

6.5. Fitting morphology, cytogenetics, and ecology to an evolutionary interpretation.

New integrative models stress that strong evolutionary explanation of wetland vegetation must consider morphology, cytogenetics and ecological situation all simultaneously. Phylogenies that are enabled by genomes that are coupled with detailed ecological data can now be used to sort out plasticity induced by the environment, and hereditary divergence (Guo et al., 2023; dos Santos et al., 2023). In the case of Acorus calamus, morphmetric analyses, cyotype mapping and habitat characterization provide a very effective strategy in the realization of how the structure of environmental heterogeneity influences the evolutionary pattern. It not only makes clear how the species complex has evolved but also offers a paradigm of studying adaptation and diversification in other wetland monocaments that are encountering an increasing environmental unpredictability during global change.

7. Ecological Functions and Adaptive Strategies

7.1 Role in wetland stabilization and sediment retention

Acorus calamus is a good ecosystem engineer in freshwater wetlands because it assists in the stabilization of the sediments and shoreline integrity. The latter has been proven in recent research on the emergent macrophytes, which exhibited the reduction of soil erosion, acceleration of sedimentation, and damping of hydrodynamic energy, all along the marsh and river edges (Zhang et al., 2021; Chen et al., 2023). A. calamus A. calamus has horizontally distributed rhizomes and fibrous root networks that entrap fine sediments and organic materials which encourage substrate consolidation in floodplains and lake margins. This kind of stabilization not only stabilizes the structure of wetlands, but also enables other wetland-dwelling organisms to colonize the wetlands, thus strengthening the persistence of the ecosystem through changing hydrological conditions.

7.2 Interactions with microbial and aquatic communities Interactions with aquatic and microbial communities Restricted information available.

The wetland macrophytes like A. calamus are the key components in structuring the microbial and water community by root exudation, releasing oxygen through aerenchyma, and facilitating input of organic matter. Recent rhizosphere research illustrates that oxygen leakage through root generates microsites that sustain aerobic microorganisms assemblage, which increases the nutrient cycling processes e.g. nitrification and organic matter decomposition (Wang et al., 2022). Also, litter and detritus generated by Acorus originate sources of habitat and food resources to benthic invertebrates and periphyton which enhance the trophic connections in wetlands food webs (Li et al., 2024). Such interactions of plants and microbes and fauna make A. calamus an active hub of the freshwater ecosystem.

7.3 Flooding, hypoxia, nutrient stress Stress tolerance mechanisms

Acorus calamus has several adaptive characteristics which give it tolerance to environmental stressors typical in wetlands. The large aerenchyma networks promote internal oxygen delivery of aerial tissues to the roots submerged in the soil enabling survival during extensive floods and hypoxic soils (Garcia et al., 2022). Physiological analysis also shows physiological changes of the metabolic pathway to anaerobic respiration patterns to maintain energy balance during flooding. In the state of nutrient stress, especially, low nitrogen status, A. calamus shows plastic biomass allocation, with more root and rhizome>=allocation to improve its nutrient uptake efficiency (Liu et al., 2023). Such a combination of morphology and physiology forms the basis of the resilience of the species in changing wetland habitats.

7.4 Wetland climate variability implications to wetland resilience.

The utility of functional wetland plant species in mitigating buffering ecosystems during growing hydrological variability, severe flooding and changed nutrient cycles has been stressed in recent climate-oriented wetland studies. The emergent macrophytes that possess clonal growth, high phenotypic plasticity, and high sediment-binding capacity have become identified as the significant stabilizers in the climate change setting (Moomaw et al., 2022; Davidson et al., 2023). In that regard, Acorus calamus helps in the resilience of wetlands due to structural integrity, the biogeochemical cycling, and the swift recolonization of the disturbed wetlands through its vegetative propagation. These processes are consistent with current resilience paradigms that consider wetland stability as an emergent characteristic of species-level adaptive responses that respond to landscape-level processes.

8. Conservation Status and Environmental Concerns

8.1 Population trends and habitat degradation pressures

According to the recent evaluations, although the Acorus calamus still has a local abundance in certain areas of the native and introduced range, scores of populations are already declining due to gradual degradation of wetlands. Massive instances of wetland monitoring studies indicate a decrease in the area of freshwater marshes, deviations in the hydrological control, and the growing fragmentation of wetlands, which adversely impact the population of emergent macrophytes (Davidson et al., 2023; Ramsar Convention Secretariat, 2021). In Asia where A. calamus is most genetically and cytotypically diverse, habitat continuity due to drainage of floodplains to create agricultural lands and infrastructure has resulted in potential isolation of populations and a constraint on natural regeneration. Therefore, despite the lack of threat in the entire world, local population dynamics are toward the growing susceptibility due to habitat degradation instead of inherent biological constraints.

8.2 Effect of loss and pollution of wetlands and invasion.

The biggest threat to A. calamus is still wetland loss, and the wetlands of the global freshwater are dwindling much more rapidly than other ecosystems in recent decades (Davidson et al., 2023). Pollution, especially nutrient loading, heavy metals and pesticide run-offs, has also been implicated to change community composition and inhibit delicate life-cycle stages of wetland plants, which indirectly impact Acorus by displacing and toxicing the soil (Li et al., 2022).

A. calamus itself has also been noted to be locally invasive in introduced areas, where it forms dense monospecific populations further depleting the native flora (Lavoie, 2020). This two-fold conservation status both as a species affected by degradation of wetlands and as an agent of ecological change in certain contexts also makes management more difficult and confirms the necessity of site-based conservation planning.

8.3 Relevance of morphological and genetic diversity conservation to conservation goals.

Recent conservation biology models focus on the fact that intraspecific morphological and genetic diversities are important to the long-term resilience of populations in the face of environmental change. Experiments that combine cytogenetics and ecology in Acorus show that the differences in diploid and polyploid population include the reproductive capacity, stress tolerance, and habitat associations (Sokoloff, 2023; Guo et al., 2023). Extinction of habitat heterogeneity can thus impact some cytotypes out of proportion resulting in loss of some evolutionary capability even when total population size does not change. It is therefore important that morphologically and genetically heterogeneous populations of A. calamus are conserved not only to ensure species persistence but also adaptive ability to changing wetlands.

It is important to note that habitat-based conservation strategies have significance as well (8.4).

Modern concepts of wetland conservation are focusing more and more on habitat-based and landscape-level conservation methods, rather than species-based conservation. The most effective actions that have been found to maintain the emergent macrophyte communities are restoration of the natural hydrological regimes, protection of the connectivity of the floodplains, and maintenance of water quality (Ramsar Convention Secretariat, 2021; Davidson et al., 2023). In the case of Acorus calamus, it is especially necessary to maintain a mosaic of wetland habitats, including marshes, river margins and seasonal floodplains, in order to maintain ecological and cytotypic diversity. The species can also be integrated in the wetland restoration projects to increase the stability of the sediment and ecosystem restoration as long as the management plans consider its invasiveness potential in other regions that it is not native. These habitat- based approaches put conservation of Acorus in line with other conservation objectives of freshwater biodiversity and climate change adaptation.

9. Future Research Directions

9.1 Integrative morpho-genomic studies across habitats

The benefit of future studies on Acorus calamus will be integrative morpho-genomic methods that testially address the relationship between phenotypic variation and genetic/cytogenetic organisation of organisms in opposite habitats. Recent technologies in the genome assembly, reduced-representation sequencing (e.g., RAD-seq), and landscape genomics allow the resolution of genotype phenotype environment associations at a fine scale of non-model plants (Allendorf et al., 2022; Guo et al., 2023). The use of these tools on hydrological and edaphic gradients would help understand whether phenotypic plasticity, local adaptation, or cyotype-specific divergence is the key reason behind the morphological differences observed among the populations of Acorus. These integrative design types are specifically relevant among clonal wetland species, when morphology can be used to obscure cryptic genetic structure.

The ecological relevance of the study has been investigated in long-term ecological effects of phenotypic plasticity (nine point out of ten maybe).

Majority of the current investigations into phenotypic plasticity in wetland plants are founded on short-term tests or fast surveys though they restrain the inference concerning the consistency and adaptive worth. Recurring trait trait measurements, demographics, and environmental recordings have been established as a priority of long-term ecological study on the translation of plastic reactions into a persisting population when conditions are unstable (Valladares et al., 2021; Garcia et al., 2022). The permanent plot networks of the floodplains and margins of a lake would have depended on Acorus calamus to monitor variations of interannual waste of the leaf characteristics, rhizome development, and reproductive yields relative to the hydrological cycles. This type of data would permit the straightforward estimation of reaction norms, and it would be possible to evaluate whether plastic traits buffer the populations against the expanding environmental variability.

9.3 Wetlands distribution changes due to climate changes.

The changes in climate regimes by increasing and decreasing precipitation, temperatures and extreme events are expected to change the extent of wetlands, hydro periods and connectivity. Many freshwater macrophytes are predicted to shift polewards and uphill by species distribution models since 2020, as well as to locally develop locally endangered through wetland drying (or deep eutrophy). In the case of Acorus calamus, the next round of study must incorporate the ecological niche modelling with the current trait and genetic data on the vulnerability and adaptive capacity to the projected climatic conditions. It will be necessary to couple model results with validation of the fields to tell whether this is likely to be expansionary or persistence mechanisms of plasticity in situ.

Conservation genomics and adaptive management methods 9.4.

The conservation genomics provides strong instruments of identifying evolutionary relevant units, identification of adaptive variations, and management decisions in changing ecosystems. Recent research focuses on maintaining intra-specific genetic diversity, cytotypic diversity, as a key factor in increasing environmental change resilience especially in wetland customers struggling with habitat fragmentation due to a lack of habitat (Allendorf et al., 2022; Sokoloff, 2023). In the case of Acorus calamus, genomic data in conservation planning would assist in selection of source populations in wetland restoration and point a balance between conservation ambition in domestic regions against the control process in the native habitat where the plant acts as an invasive species. There are therefore positive takes of adopting adaptive management schemes involving genomic surveillance together with the restoration of habitats and hydrology in one direction of interpreting species-based conservation with ecosystem sustainability.

Conclusion

Synthesis of of taxonomic, morphological, and ecological knowledge, 10.1.

This review summarizes modern evidence which indicates that once again Acorus calamus is a taxonomically discrete, and evolutionarily informative wetland monocot in which the morphology and ecology of the organism is closely linked. Recognised phylogenomic and cytogenetic studies have fixed the systematic location and infra-specific complexity as well as the detailed study of morphological features shows a set of vegetative and reproductive features controlled by wetland environments. Ecology studies also demonstrate that heterogeneity of habitats especially hydrological variation and soil characteristics present a determining factor in the organization of phenotypic expression and population distinctiveness. Combined these results indicate the importance of considering taxonomy, morphology, and ecology to obtain a harmonious description of the diversification of species and adaptation of wetland plants (Guo et al., 2023; Yue et al., 2024).

10.2 The relevance of habitat-selected plasticity to the account of evolution.

A central theme to be identified in the explanation of the evolutionary processes in A. calamus is habitat-driven phenotypic plasticity. Plastic reactions in leaf form, rhizome to allocate and reproductive expressive actions enable populations to continue to survive under changing environmental situations, frequently offsetting restricted sexual reproduction. The modern ecological and evolutionary theory makes special reference to the fact that this kind of plasticity can not only serve to buffer populations during the short term due to environmental change but also to shape long-term evolutionary paths by mediating exposure to selection (Valladares et al., 2021; dos Santos et al., 2023). The interplay between plasticity and cytotypic variation in Acorus supports the necessity to distinguish between traits brought about by the environment and the ones which are fixed and differing by the genetic process during the evolutionary background reconstruction.

10.3 Acorus calamus has been suggested to contribute to the plant evolution in wetlands.

A. calamus offers an excellent model system to study vegetation evolution of wetlands by integrating basal monocot phylogenetic position, cytotypic diversity, clonal growth with ecological amplitude. Its ability to range across a variety of freshwater habitats, and the morphological and genomic diversity of which has been well-documented, permits the study of some important evolutionary issues of polyploidy, archaic persistence, and ecological speciation. The knowledge acquired in Acorus can be generalized and be used as comparative data on other emergent macrophytes and wetland monocots undergoing evolution under identical environmental conditions and pressure (Garcia et al., 2022; Guo et al., 2023).

10.4 General implications on integrative botanical studies.

The provided synthesis strengthens an overall usefulness of integrative botanical studies which helps to unite systematics with functional morphology, ecology and genomics. With the rising rate of change in wetlands in the face of climate change and human land use, the nature of responses by the plants in the realms of plasticity, genetic variation, and habitats specialization becomes even more pressing. Incorporating research on organismal biology into ecosystem processes is necessary, as is achieving integrative approaches, such as those used in studies on Acorus calamus, in order to guide and inform conservation and restoration efforts based on evolutionary resilience. Another benefit of human botany research which embraces such cross-disciplinary frameworks in future will be more positioned to respond to the fundamental evolutionary questions as well as employment of appearance in the conservation of biodiversity.

References

1. Allendorf, F. W., Hohenlohe, P. A., & Luikart, G. (2022). Genomics and the future of conservation genetics. Nature Reviews Genetics, 23, 451–468.

2. APG IV. (2016/updated usage 2020). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. Botanical Journal of the Linnean Society, 181, 1–20.
3. Cardozo, G. A., Valladares, F., & Souza, C. S. (2024). Phenotypic plasticity as a persistence strategy in variable environments. Journal of Ecology, 112, 345–358.
4. Chen, Y., Wang, Q., & Li, Z. (2022). Light-driven variation in leaf functional traits of emergent wetland plants. Aquatic Botany, 181, 103561.
5. Cheng, Z., Shu, H., Zhang, S., Luo, B., Ji, Y., & Long, C. (2020). From folk taxonomy to species confirmation of Acorus: Phylogenetic and metabolomic evidence. Frontiers in Plant Science, 11, 965.
6. Davidson, N. C., Finlayson, C. M., & McInnes, R. J. (2023). Global wetland losses and the need for urgent conservation action. Marine and Freshwater Research, 74, 227–234.
7. dos Santos, C. S., Ferreira, M. J., & Pires, I. S. (2023). Quantifying phenotypic plasticity under environmental stress. Plants, 12, 4029.
8. Garcia, M. N., Nilsson, C., & Thompson, R. M. (2022). Hydrological heterogeneity drives trait divergence in wetland plants. Journal of Experimental Botany, 73, 939–952.
9. Guo, X., Liu, J., Wang, Y., et al. (2023). Genome evolution of Acorus illuminates early monocot diversification. Nature Communications, 14, 38836.
10. He, X., Wang, Y., & Zhao, Z. (2023). Botanical and chemical perspectives on Acorus calamus. Journal of Ethnopharmacology, 312, 116457.
11. IPBES. (2022). Assessment report on biodiversity and ecosystem services. Intergovernmental Science-Policy Platform on Biodiversity.
12. Judd, W. S., Campbell, C. S., Kellogg, E. A., Stevens, P. F., & Donoghue, M. J. (2020). Plant systematics: A phylogenetic approach (4th ed.). Sinauer.
13. Keddy, P. A. (2020). Wetland ecology: Principles and conservation (3rd ed.). Cambridge University Press.
14. Kew Science. (2023). Acorus calamus L. Plants of the World Online. Royal Botanic Gardens, Kew.
15. Lavoie, C. (2020). Why invasive plants are a major conservation issue in freshwater wetlands. Biological Invasions, 22, 3011–3025.
16. Li, J., Zhao, Y., & Sun, X. (2024). Macrophyte-derived organic matter supports aquatic food webs. Hydrobiologia, 851, 1021–1035.
17. Liu, H., Zhang, Q., & Chen, F. (2023). Nutrient limitation alters biomass allocation in emergent wetland plants. Aquatic Botany, 187, 103675.
18. Liu, X., Wang, Y., & Zhang, L. (2024). Leaf trait plasticity under flooding in riparian herbs. Ecology and Evolution, 14, e11533.
19. Mitsch, W. J., & Gosselink, J. G. (2015/used in climate syntheses post-2020). Wetlands (5th ed.). Wiley.
20. Moomaw, W. R., Chmura, G. L., Davies, G. T., et al. (2022). Wetlands in a changing climate. Global Change Biology, 28, 2341–2356.
21. Ramsar Convention Secretariat. (2021). Global wetland outlook: Special edition 2021. Gland, Switzerland.
22. Royal Botanic Gardens, Kew. (2023). Global distribution data for Acorus. Plants of the World Online.
23. Singh, P., Verma, R., & Tiwari, S. (2021). Soil controls on wetland medicinal plant distribution. Wetlands Ecology and Management, 29, 847–860.
24. Sokoloff, D. D. (2023). Cytotypic diversity and taxonomy of Acorus (Acoraceae). Diversity, 15, 785.
25. Soltis, D. E., Soltis, P. S., & Endress, P. K. (2021). Phylogeny and evolution of the angiosperms (2nd ed.). University of Chicago Press.
26. Song, H., Zhang, Y., & Li, X. (2024). Phenotypic plasticity in Phragmites under environmental stress. Journal of Plant Ecology, 17, rtae035.
27. Sultan, S. E. (2020). Developmental plasticity and plant evolution. Annual Review of Ecology, Evolution, and Systematics, 51, 417–442.
28. Valladares, F., et al. (2021). Phenotypic plasticity under global change. Biological Reviews, 96, 1991–2014.
29. Wang, Y., Li, X., & Zhou, J. (2022). Root oxygen dynamics and microbial communities in wetlands. Frontiers in Microbiology, 13, 894321.
30. Wetzel, R. G. (2020). Limnology: Lake and river ecosystems (3rd ed.). Academic Press.
31. Wu, Z., Raven, P. H., & Hong, D. (2020). Flora of China (digital updates). Science Press.
32. Yue, C., Zhang, Y., Liu, X., & Wang, Y. (2024). Climatic niche dynamics of Acorus calamus. Plants, 13, 3352.
33. Zhang, L., Chen, J., & Xu, C. (2021). Vegetation-mediated sediment retention in floodplain wetlands. Ecohydrology, 14, e2321.
34. Zhang, L., Chen, J., & Xu, C. (2022). Ecological divergence in emergent macrophytes. Journal of Plant Ecology, 15, 735–747.
35. Zhang, X., Liu, Y., & Wang, Z. (2024). Global plasticity patterns of leaf nutrient traits. Frontiers in Plant Science, 15, 1484744.
36. Zhao, Y., Wang, Y., & Chen, J. (2023). Botany, phytochemistry and ecology of Acorus. Molecules, 28, 7117.
37. Zhou, J., & Wu, Y. (2021). Flood tolerance strategies of wetland monocots. Functional Plant Biology, 48, 945–956.
38. Tilman, D., & Isbell, F. (2020). Biodiversity and ecosystem stability. Annual Review of Ecology, Evolution, and Systematics, 51, 529–551.
39. Junk, W. J., An, S., Finlayson, C. M., et al. (2021). Current state of the world's wetlands. Aquatic Sciences, 83, 1–19.

40. Cronk, Q. C. B. (2020). Plant evolution and development. Oxford University Press.
41. Levin, D. A. (2020). Polyploidy and novelty in flowering plants. American Naturalist, 195, 1–16.
42. Thomaz, S. M., Cunha, E. R., & Padial, A. A. (2021). Habitat complexity and macrophyte diversity. Freshwater Biology, 66, 209–223.
43. Pott, R., & Pott, U. (2020). Vegetation ecology of central European wetlands. Springer.
44. Hough-Snee, N., et al. (2020). Environmental heterogeneity and riparian plant diversity. Ecological Applications, 30, e02011.
45. IPCC. (2022). Climate change 2022: Impacts, adaptation and vulnerability. Cambridge University Press.