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Review Article

Plant Sexual Diversity: A Nexus of Evolutionary Mechanisms, Epistemic Perspectives, and Sustainability

Różnorodność płciowa roślin: na styku mechanizmów ewolucyjnych, perspektyw epistemologicznych i zrównoważonego rozwoju

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Abstract

This review examines the conceptual limits of treating plant sexuality with fixed binary classifications. The study synthesizes evidence from evolutionary biology, developmental genetics, ecology, and reproductive biology to develop a framework for understanding plant sexual organization as dynamic and context-dependent, shaped by interacting evolutionary, developmental, genetic, and environmental processes. A systematic literature review was conducted using a screening protocol, selecting 139 studies from an initial pool of 623 database records. The findings show that plant sexual systems have evolved across lineages through developmental pathways, genetic mechanisms, and reproductive strategies, while self-fertilization, hybridization, and apomixis expand reproductive organization beyond conventional sexual categories. Pollination, sexual selection, and ecological interactions demonstrate that reproductive outcomes emerge from context-dependent interactions among sexual functions, developmental processes, phenotypic traits, and environmental conditions. Historical botanical classifications reflect human-centred terminology that has shaped descriptions and interpretations of plant sexuality, illustrating how scientific categories can influence the conceptualization of biological diversity. Binary categories of sex have biological and practical value but become insufficient when treated as universally fixed across plant lineages, life-cycle stages, and dimensions of sexual organization. This review therefore proposes a plant-centred, process-oriented framework in which established binary categories retain descriptive value within defined biological contexts but are not treated as universally sufficient representations of plant sexual organization. The findings also have broader implications for environmental philosophy by showing how biological classification can remain scientifically useful while being responsive to evolutionary change, ecological complexity, and the dynamic character of living systems.

Keywords
plant sexual diversity, plant sexual systems, reproductive plasticity, biological classification, environmental philosophy, biodiversity, sustainability

Abstrakt
Niniejszy artykuł przeglądowy analizuje ograniczenia pojęciowe wynikające z ujmowania płciowości roślin w ramach sztywnych klasyfikacji binarnych. Autorzy dokonują syntezy wyników badań z zakresu biologii ewolucyjnej, genetyki rozwoju, ekologii oraz biologii rozrodu, proponując ramy interpretacyjne, w których organizacja płciowa roślin postrzegana jest jako zjawisko dynamiczne i zależne od kontekstu, kształtowane przez wzajemne oddziaływanie procesów ewolucyjnych, rozwojowych, genetycznych i środowiskowych. Przeprowadzono systematyczny przegląd literatury z zastosowaniem protokołu selekcji, w wyniku którego spośród 623 rekordów bibliograficznych wyodrębniono 139 publikacji. Wyniki wskazują, że systemy płciowe roślin ewoluowały w różnych liniach ewolucyjnych poprzez zróżnicowane szlaki rozwojowe, mechanizmy genetyczne i strategie reprodukcyjne, przy czym zjawiska takie jak samozapłodnienie, hybrydyzacja oraz apomiksja rozszerzają zakres organizacji rozrodu poza konwencjonalne kategorie płciowe. Procesy zapylania, dobór płciowy oraz interakcje ekologiczne pokazują, że efekty rozrodu wynikają z zależnych od kontekstu oddziaływań między funkcjami płciowymi, procesami rozwojowymi, cechami fenotypowymi a warunkami środowiskowymi. Historyczne klasyfikacje botaniczne odzwierciedlają antropocentryczną terminologię, która wpływała na sposób opisywania i interpretowania płciowości roślin, co pokazuje, jak kategorie naukowe mogą kształtować postrzeganie różnorodności biologicznej. Choć binarne kategorie płci mają wartość biologiczną i praktyczną, stają się niewystarczające, gdy traktuje się je jako uniwersalne i niezmienne w odniesieniu do różnych linii ewolucyjnych roślin, etapów cyklu życiowego czy poszczególnych wymiarów organizacji płciowej. W związku z tym w niniejszym przeglądzie zaproponowano perspektywę uwzględniającą specyfikę biologii roślin i zorientowaną na procesy, w której utrwalone kategorie binarne zachowują swoją wartość opisową w określonych kontekstach biologicznych, nie stanowiąc jednak uniwersalnie wystarczającego modelu organizacji płciowej roślin. Ustalenia te mają również szersze znaczenie dla filozofii środowiskowej, ukazując, w jaki sposób klasyfikacje biologiczne mogą zachować użyteczność naukową, pozostając jednocześnie otwartymi na zmiany ewolucyjne, złożoność ekologiczną oraz dynamiczny charakter systemów żywych.

Słowa kluczowe
różnorodność płciowa roślin, systemy płciowe roślin, plastyczność reprodukcyjna, klasyfikacja biologiczna, filozofia środowiskowa, różnorodność biologiczna, zrównoważony rozwój

Introduction

The diversity of plant sexual systems challenges the assumption that biological sex can always be represented as a fixed binary. Classical evolutionary theory links sex to the transition from isogamy (gametes of similar size) to anisogamy (gametes of different sizes), providing the evolutionary basis for differentiated male and female gametic functions (Ainsworth 2015; Lehtonen et al. 2016). However, plant sexual expression extends beyond gamete type to include diverse developmental, genetic, phenotypic, and reproductive

configurations (Ah-King and Nylin 2010). These features arise at different stages of the life cycle and should not be treated as equivalent expressions of sex. A process-oriented perspective therefore views plant sexuality as emerging from interacting evolutionary, developmental, genetic, and environmental processes rather than as a fixed attribute. The evolution of heterospory (production of distinct microspores and megaspores), which arose independently in multiple vascular plant lineages and contributed to the evolutionary pathway toward seed plants, further illustrates the diversity of reproductive organization (Bateman and DiMichele 1994; Friedman 2009). This diversity is expressed at the organismal and floral levels through hermaphroditism (male and female functions in the same individual), monoecy (separate male and female flowers on the same individual), dioecy (male and female individuals), and mixed sexual systems such as gynodioecy (female and hermaphroditic individuals) and gynomonoecy (female and hermaphroditic flowers on the same individual) (Barrett 2002). Sexual functions may also be spatially or temporally separated through mechanisms such as herkogamy and dichogamy.

Sexual differentiation also occurs at different life-cycle stages across plant lineages. In bryophytes such as *Marchantia polymorpha*, it occurs in the dominant haploid gametophyte via a UV chromosome system, whereas in angiosperms the gametophyte generation is highly reduced and sexual differentiation is expressed primarily through the diploid sporophyte and floral structures (Coelho et al. 2018; Renner and Müller 2021). Thus, superficially similar sexual systems can operate within fundamentally different developmental and ploidy contexts. This diversity raises a central question: can “sex” be adequately understood through a single fixed framework across plant lineages and life-cycle stages? Historical classification further shows that biological descriptions are shaped by the conceptual frameworks available to science. Linnaeus’s Sexual System, for example, classified plants according to stamens and pistils, using explicitly gendered terminology, illustrating how historical concepts of sex influenced botanical description (Schiebinger 1993; Endersby 2009). Although contemporary taxonomy has moved far beyond the Linnaean system, binary terminology remains useful and deeply embedded in descriptions of plant reproduction.

Contemporary research further demonstrates that plant sex determination and sexual expression involve interacting genetic, developmental, hormonal, and environmental processes, as shown in species such as *Silene latifolia, Spinacia oleracea,* and *Mercurialis annua* (Cossard and Pannell 2021; Yue et al. 2023). Comparative work in animal biology similarly treats sex as developmentally and environmentally responsive and as a multidimensional biological phenomenon (Ah-King and Nylin 2010; Fausto-Sterling 2000;

McLaughlin et al. 2023; Fuentes 2025). Plants provide a distinctive context because sexual differentiation and expression can occur across alternating generations and at multiple biological levels, including gametes, gametophytes, sporophytes, flowers, and whole individuals. This evidence does not diminish the biological meaning of male and female categories; rather, it shows that the mechanisms and developmental contexts underlying sexual expression may extend beyond a fixed organism-level binary description. Such reproductive diversity influences mating patterns, genetic variation, reproductive assurance, population persistence, and applications in crop breeding and conservation.

Despite extensive evolutionary, developmental, and genomic research (Renner and Müller 2021; Fuentes 2025; Li et al. 2025), less attention has been paid to integrating this evidence with broader conceptual analyses of sex classification. The literature documents extensive variation in plant sexual systems, yet the implications of this variation for how sex is conceptualized and classified remain underexplored. This review therefore synthesizes dispersed evidence to examine how plant sexual diversity emerges through evolutionary, developmental, reproductive, and ecological processes and what this diversity implies for the conceptualization and classification of sex. Specifically, it aims to: (1) examine evolutionary transitions in plant sexual systems across deep time; (2) synthesize reproductive diversity across major plant lineages; (3) examine historical and conceptual influences, including anthropomorphic assumptions, on the classification and interpretation of plant sexuality; and (4) assess the implications of reproductive diversity for ecology, crop breeding, conservation, and adaptation to environmental change. A process-oriented understanding of plant sexual diversity provides a broader framework for evolutionary and reproductive theory while informing biodiversity conservation, crop evolution, reproductive resilience, and adaptation to environmental change.

1. Materials and Methods

A systematic literature review of plant sexuality was conducted following PRISMA guidelines (Tricco et al. 2018). The search strategy comprised two conceptual blocks: terms describing plant sexual organization and terms capturing evolutionary, developmental, reproductive, ecological, and plasticity-related dimensions. Searches were conducted in Web of Science, Scopus, PubMed, JSTOR, and Google Scholar using database-specific adaptations of the core string: (“plant sexuality” OR “plant sex” OR “sexual system” OR “sex expression” OR “unisexual” OR “hermaphrodite” OR “monoecy” OR “dioecy” OR “gynodioecy” OR “androdioecy”) AND (“evolution” OR “development” OR “reproduction” OR “pollination” OR “ecology”

OR "plasticity"). This strategy was designed to capture diverse dimensions of plant sexuality while retaining sexual organization as the central focus. Inclusion criteria comprised peer-reviewed, English-language, full-text articles; conference proceedings, dissertations, notes, and errata were excluded. Records were screened by title and abstract, followed by full-text assessment. The search yielded 623 records; after removal of 180 duplicates, 443 were screened, 201 were assessed in full text, and 62 were excluded for being unrelated to plant sexuality (n = 25), non-peer-reviewed (n = 9), lacking substantive focus on reproductive systems (n = 21), or providing insufficient methodological detail (n = 7), leaving 139 studies for qualitative synthesis (Fig. 1).

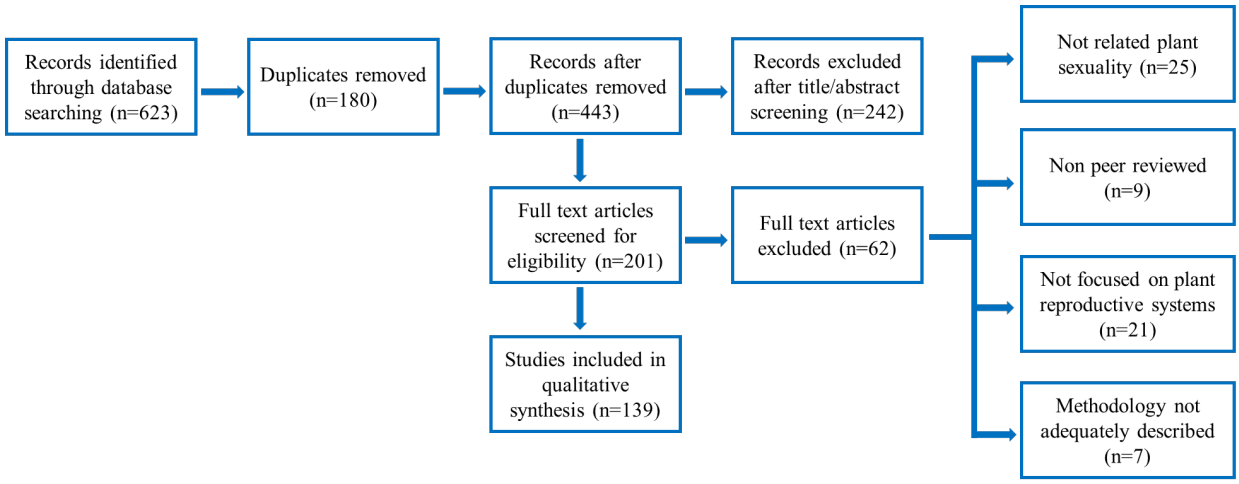


Figure 1. PRISMA workflow depicting study identification, screening, and inclusion for rethinking sexual diversity in plants: Evolutionary biology to epistemic transformation and sustainability. Source: Author's own elaboration.

The included studies were thematically coded by comparing their research questions, objectives, biological systems, mechanisms, and principal findings. Recurring codes were iteratively consolidated into eight broader thematic domains and specific subthemes. Although individual studies frequently addressed more than one dimension of plant sexuality, each study was assigned to the thematic domain representing its primary analytical focus to provide a non-overlapping distribution of the literature. The thematic framework and study allocation are presented in Table A1 (Appendix).

2. Results and Discussion

2.1. Evolution and Diversity of Plant Sexual Systems

2.1.1. Diversity and evolutionary pathways of plant sexual systems

Plants exhibit extensive sexual diversity, including hermaphroditism, monoecy, dioecy, and mixed

systems such as gynodioecy and gynomonoecy (Barrett 2002). Rather than representing fixed categories, these systems have undergone repeated transitions across angiosperm lineages, with hermaphroditism remaining widespread and dioecy evolving independently in numerous lineages (Charlesworth 2006; Renner 2014; Dorken et al. 2017). The evolution of dioecy can proceed through different pathways, including transitions through gynodioecy or monoecy, as male and female reproductive functions become increasingly separated among individuals. Such transitions are influenced by interactions among mating-system dynamics, sex allocation, inbreeding avoidance, and mechanisms that modify the spatial or temporal expression of sexual functions, including self-incompatibility, dichogamy, and herkogamy (Barrett 2010; Dufay et al. 2014; Sabath et al. 2016). At the life-cycle level, heterospory represents a major evolutionary reorganization of sexual differentiation. Sexual differentiation also varies across major plant lineages and their contrasting life-cycle architectures. In bryophytes, sexual differentiation is predominantly expressed in the haploid gametophyte, whereas in seed plants the gametophytic phase is highly reduced and develops within specialized reproductive structures (Coelho et al. 2018; Renner and Müller 2021). Collectively, these patterns show that plant sexual systems arise through repeated evolutionary transitions and are expressed within diverse developmental and life-cycle contexts across lineages.

2.1.2. Distribution and lineage-specific patterns

Across plant lineages, sexual systems vary in how male and female reproductive functions are distributed among flowers, individuals, and populations. Dioecy is common in bryophytes, whereas gymnosperms include both monoecious conifers and independently evolved dioecious lineages such as cycads and *Ginkgo* (Leslie et al. 2012; McDaniel et al. 2013). Angiosperms exhibit particularly high diversity in sexual systems; hermaphroditism predominates, but monoecy, dioecy, gynodioecy, and gynomonoecy have evolved repeatedly across families (Barrett 2002; Käfer et al. 2017). These distributions indicate that sexual-system evolution is shaped by lineage history, life-cycle organization, and recurrent evolutionary transitions rather than a single trajectory. While traditional categories remain useful for describing specific reproductive configurations, treating them as universal models can oversimplify variation across lineages and life-cycle stages. Collectively, these lineage-level patterns show that plant sexual organization is evolutionarily dynamic and dependent on life-cycle context, providing a basis for examining how developmental mechanisms, genomic regulation, and reproductive plasticity further diversify sexual organization.

2.2. Developmental Pathways, Genomics and Plasticity of Plant Sexual Expression

2.2.1. Ontogeny and evolution of plant unisexuality

Plant unisexuality arises through distinct developmental pathways, linking floral ontogeny with the repeated evolution of separate-sex systems. Secondary unisexuality (Type I) involves the initiation of both stamens and carpels, followed by selective abortion of one sexual function, whereas primary unisexuality (Type II) results from early suppression or differentiation of floral organ primordia (Diggle et al. 2011; Jabbour et al. 2022). These pathways have evolved repeatedly across angiosperm lineages, indicating that similar sexual phenotypes can arise through different developmental mechanisms (Sabath et al. 2016; Sauquet et al. 2017). Unisexuality is therefore not a single developmental condition but an outcome of alternative ontogenetic routes that modify the timing and extent of male and female reproductive development. Because reproductive development recurs throughout the plant life cycle, sexual expression can vary across developmental stages, providing a developmental basis for context-dependent sexual expression (Barrett 2002; Diggle et al. 2011).

2.2.2. Genomics, developmental regulation and environmental plasticity

Plant sexual expression arises from dynamic interactions among genomic programs, hormonal pathways, developmental processes, and environmental cues (Guo et al. 2019). Sex-determining regions and young sex chromosomes have evolved independently across angiosperms, underscoring the evolutionary lability of the genetic mechanisms underlying separate-sex systems (Renner and Müller 2021). These genomic regions may harbour key regulatory elements for sex determination, as illustrated by the Y-chromosome-encoded OGI small RNA, which targets the autosomal MeGI gene in persimmon (Akagi et al. 2014). Downstream regulatory networks, including ethylene-mediated signalling in cucurbits, can influence floral sexual development, as shown by the CsEIN2–CsEIN3–CsERF31 pathway that regulates female-flower development in cucumber (Li et al. 2025). These regulatory networks contribute to context-dependent variation in floral sex expression (Rodriguez-Granados et al. 2022). Thus, genomic and genetic mechanisms provide a developmental framework whose phenotypic expression is modulated by hormonal, developmental, and environmental interactions.

2.3. Reproductive Flexibility and the Limits of Conventional Sexual Categories

2.3.1. Self-Fertilization and the organization of male and female reproductive functions

Self-fertilization illustrates the flexibility of plant reproductive organization by allowing male and female reproductive functions to contribute to reproduction within the same individual. Recurrent evolutionary transitions from outcrossing (allogamy) to selfing (autogamy) can provide reproductive assurance when mates or pollinators are scarce while conferring the transmission advantage associated with self-fertilization (Barrett 2002). Repeated shifts from self-incompatibility to self-compatibility further demonstrate that mating systems are evolutionarily dynamic (Lucek et al. 2025). Importantly, self-fertilization does not erase the biological distinction between male and female gametic functions; rather, it shows that these functions need not be distributed among individuals or depend on mating. By decoupling gametic functional differentiation from separate individual bodies, self-fertilization shows that individual-level sex categories do not encompass the full diversity of plant reproductive organization. In haploid-dominant plant lineages, intragametophytic selfing extends this principle to the gametophytic phase, allowing gametes produced by a single gametophyte to fuse and produce diploid progeny that are homozygous at each locus (Otto and Marks 1996).

2.3.2. Apomixis and alternative reproductive pathways beyond conventional sexual reproduction

Apomixis is a reproductive pathway in which embryo formation occurs without the conventional sequence of meiosis and fertilization, enabling offspring production while maintaining substantial genetic continuity with the maternal genotype (Hörandl 2010). Facultative apomictic systems may retain both sexual and apomictic pathways, showing that alternative reproductive modes can coexist within the same lineage (Xue et al. 2024; Yao et al. 2023). Beyond apomixis, hybridization and reticulate evolutionary processes provide additional routes for gene exchange between divergent lineages, generating novel genetic combinations (Rieseberg and Willis 2007). Together, these pathways demonstrate that plant reproduction can be reorganized across evolutionary and developmental contexts rather than following a single obligatory sequence linking meiosis, fertilization, and offspring production.

2.4. Reproductive Strategies, Ecological Interactions and Evolutionary Diversification

2.4.1. Pollination strategies, mating systems and plant diversification

Pollination strategies shape plant reproductive success by influencing pollen transfer, mating patterns,

gene flow, and reproductive isolation (Ollerton et al. 2011; Barrett and Harder 2017). Mating systems arise from dynamic interactions among floral traits, pollinator behaviour, and environmental conditions, producing substantial variation in selfing and outcrossing within and among populations (Barrett and Harder 2017; Whitehead et al. 2018). Generalized pollination systems tend to facilitate broader pollen movement, whereas pollinator specialization restricts effective pollen transfer and, under specific ecological conditions, reinforces reproductive isolation among sympatric taxa (van der Niet and Johnson 2012). Highly specialized adaptations, such as sexual deception in *Ophrys* and resting-site mimicry in *Serapias*, further illustrate how floral traits and pollinator behaviour interact to shape reproductive outcomes (Inda et al. 2012; Schiestl 2015). Pollination thereby links male and female reproductive functions to ecological context, moving beyond static sexual categories to reveal reproduction as an environment-dependent process. By modulating pollen flow, interspecific pollen transfer, and reproductive barriers, pollination interactions connect variation in mating systems with floral divergence, speciation, and angiosperm diversification (Kay and Sargent 2009; Moreira-Hernández and Muchhala 2019).

2.4.2. Sexual Selection, ecological constraints and context-dependent reproductive success

Sexual selection in plants operates through differential reproductive success before and after pollination, encompassing competition for pollination opportunities, pollen competition, pollen–pistil interactions, and variation in siring success (Beekman et al. 2016; Minnaar et al. 2019). The pathway from pollen production and transfer to fertilization contains multiple stages at which reproductive success is filtered, linking male function to pollinator behaviour, pollen competition, and the ecological conditions of mating (Barrett and Harder 2017; Minnaar et al. 2019). Pollinator-mediated selection likewise interacts with abiotic and resource conditions, demonstrating that reproductive traits are shaped by the combined effects of biotic interactions and environmental context rather than by pollinators alone (Sletvold et al. 2017; Sletvold 2019). These processes make reproductive success inherently context-dependent: the relative success of male and female functions varies with pollinator activity, resource availability, mating opportunities, and the traits of interacting organisms. Sexual selection thus provides a process-based framework for understanding how ecological interactions translate variation in reproductive traits into differential reproductive success, with consequences for floral divergence and reproductive isolation (Beekman et al. 2016; Moreira-Hernández and Muchhala 2019).

2.5. Historical Classification, Anthropomorphism and Conceptual Assumptions

2.5.1. Legacy of plant sexual categories

The classification of plant sexuality has been shaped by historical, cultural, and linguistic frameworks that organized diverse reproductive systems into specific conceptual categories (Schiebinger 1993; Subramaniam and Bartlett 2023). The Linnaean Sexual System offers a foundational example, classifying plants according to stamens and pistils and using explicitly gendered terms such as “male,” “female,” and “marriage” (Schiebinger 1993). Although contemporary plant systematics no longer follows this framework, its legacy shows that scientific categories reflect prevailing conceptual assumptions and do not necessarily capture the full diversity of biological organization. At the same time, binary and dichotomous classifications remain practically valuable in plant identification because readily observable, relatively stable morphological characters enable efficient field identification without requiring molecular analysis. Their continued use therefore reflects diagnostic utility and accessibility rather than necessarily implying that plant sexual organization is universally binary. The diversity of hermaphroditic, monoecious, dioecious, gynodioecious, and other mixed reproductive systems further illustrates the limits of treating plant sexuality with a single categorical scheme (Renner 2014). Recent scholarship likewise calls for approaches to plant reproduction that move beyond conventional assumptions about sex and reproductive organization (Subramaniam and Bartlett 2023). Thus, the significance of sexual categories lies not in their inherent invalidity, but in recognizing that their explanatory value depends on the biological level, reproductive process, and context in which they are applied.

2.5.2. Anthropomorphism and conceptual assumptions

The use of human-centred terminology in plant sexuality reflects a historical tendency to interpret botanical reproductive structures through concepts derived from human sex and gender (Schiebinger 1993; Subramaniam and Bartlett 2023). Although such terminology can be useful for description, conflating levels of sexual organization may obscure distinctions among gametic sex, reproductive function, sexual phenotype, and sexual system (Pannell 2023). This does not imply that contemporary botanical classifications are inherently anthropomorphic; rather, it highlights how inherited terminology can shape interpretations of biological variation. In plants, where reproductive functions can be combined, separated, or expressed across different temporal and spatial scales, these distinctions are particularly important (Barrett 2010; Pannell 2023).

These distinctions also provide a basis for comparative biology, in which scholarship on sexual diversity emphasizes that sex and sexual variation require analysis across multiple biological dimensions rather than a single categorical framework (Lewis and Sharpe 2023).

2.6. Plant Sexual Diversity in Comparative and Epistemological Perspective

2.6.1. Plant sexual diversity and the critique of fixed binary models

Plant sexual organization is better understood as multidimensional and context-dependent rather than as a single fixed organismal attribute (Renner and Müller 2021). In *Marchantia polymorpha*, sex is determined in the dominant haploid gametophyte via a U/V chromosome system, whereas in angiosperms, sexual differentiation occurs primarily in the diploid sporophyte through reproductive structures (Coelho et al. 2018; Renner and Müller 2021). This contrast shows that a single organism-level model is insufficient across plant lineages. Within sporophytic lineages, sex organization also varies between genetically structured systems and environmentally responsive expression, as illustrated by sex-chromosome differentiation in *Silene latifolia* and plastic, "leaky" sex expression in *Mercurialis annua* (Cossard and Pannell 2021; Yue et al. 2023). Such evidence indicates that sex expression is not uniformly fixed but can vary with developmental and ecological context. Crucially, recognizing plant sexual diversity does not negate the biological distinction between anisogamous male and female gametic functions; rather, it shows that these functions are not always adequately represented by mutually exclusive, organism-level sexual categories.

2.6.2. Comparative perspectives from animal biology and developmental systems

Comparative animal research has challenged static conceptions of sex by treating sex and sex-associated traits as reaction norms shaped by developmental and environmental contexts (Ah-King and Nylin 2010). More recent multivariate approaches treat sex as a composite of interacting biological dimensions, recognizing that gamete type, chromosomal inheritance, physiology, morphology, and behaviour need not be perfectly coupled (McLaughlin et al. 2023). Broader comparative scholarship emphasizes biological diversity and variation in sex and the implications of these patterns for biological research and education (Lewis and Sharpe 2023; Sharpe et al. 2023). Related scholarship also emphasizes that binary assumptions about sex and gender can become analytically limiting when developmental, relational, and contextual dimensions are considered (Fausto-Sterling 2025). Evolutionary studies show that traits associated with one sex can evolve in the other through processes such as cross-sexual transfer, illustrating that sex-associated traits are not

necessarily evolutionarily confined to one sex (Anderson and Falk 2023). A recent synthesis emphasizes that biological sex encompasses multiple interacting dimensions and that binary classifications, while biologically grounded in some contexts, have limits as comprehensive representations of sexual variation (Fuentes 2025). This comparison does not imply biological equivalence between plant and animal sexual systems; rather, it highlights that the explanatory scope of sex categories depends on the biological dimension, developmental context, and reproductive conditions under consideration.

2.7. Implications of Plant Sexual Diversity for Ecology, Agriculture and Sustainability

Recognizing plant reproductive diversity has practical implications for maintaining population viability, improving crop performance, and strengthening the capacity of plant populations and agricultural systems to respond to environmental change.

2.7.1. Reproductive diversity, ecological resilience and conservation

Variation in plant sexual and mating systems shapes opportunities for reproduction, gene flow, genetic variation, and reproductive assurance at the population level (Barrett 2002; Charlesworth 2006). These effects are especially important when pollinator availability, mating opportunities, or population connectivity are reduced, because reproductive systems differ in their capacity to sustain reproduction under such conditions (Ågren and Sletvold 2025). Conservation should therefore consider not only species presence and abundance but also reproductive characteristics that contribute to population viability and genetic diversity. Maintaining viable reproductive systems and the ecological interactions that support reproduction can strengthen population persistence under environmental disturbance.

2.7.2. Crop evolution, breeding and food security

Plant reproductive diversity has important consequences for crop evolution and breeding because self-fertilization, outcrossing, hybridization, male sterility, and apomixis provide distinct pathways for generating, reshuffling, or preserving genetic variation (Barrett 2002; Munoz-Sanz et al. 2020). Self-fertilization provides reproductive assurance when mates or pollinators are limited, whereas outcrossing and hybridization increase opportunities for recombination and novel genetic combinations (Barrett 2002). These contrasting reproductive pathways have consequently shaped crop diversification and breeding strategies (Munoz-Sanz et al. 2020). Apomixis is particularly relevant because it enables embryo development without the normal sequence of meiotic reduction and fertilization and can preserve maternal genotypes across generations,

although many apomictic systems still require fertilization for endosperm development (Hörandl 2010). Apomixis offers the potential to fix hybrid performance across generations, linking the manipulation of reproductive pathways to breeding efficiency, yield stability, and longer-term food security.

2.7.3. Climate adaptation and sustainability

Plant reproductive responses to environmental change shape the capacity of populations and crops to sustain reproduction and maintain adaptive potential under changing conditions. Plant sex expression reflects interactions among genetic regulation, hormonal signalling, developmental processes, and environmental cues, with the relative contributions of these factors varying among species (Renner and Müller 2021; Li et al. 2025). This plasticity is especially relevant under climate change, as shifts in temperature, water availability, phenology, and pollinator interactions alter reproductive development and success (Martén-Rodríguez 2025). Climate adaptation and conservation strategies should therefore account for reproductive traits and ecological interactions that influence population persistence and adaptive capacity. Maintaining reproductive capacity and the environmental and biotic conditions that sustain it can strengthen the ability of plant populations and crops to respond to changing climates.

2.8. Challenges of Fixed Binary Sex Categories and Pathways Forward

Binary categories have a legitimate biological basis and remain useful for describing gametic functions and specific reproductive systems. However, their explanatory scope is limited when treated as universally fixed across plant lineages, life-cycle stages, and reproductive contexts. The evidence reviewed here supports distinguishing among gametic sex, sexual function, sexual phenotype, sexual system, and reproductive mode rather than treating these dimensions as interchangeable. Moving beyond rigid binary frameworks therefore requires defining their biological scope and integrating evolutionary, developmental, genetic, and ecological perspectives. Future research and science education should use diverse plant examples to show how scientific categories can remain useful while accommodating biological variation. The way forward is not to replace binary categories but to apply them more precisely within a broader understanding of plant reproductive diversity.

From a broader philosophical perspective, this distinction also illustrates the limits of scientific classification as a representation of living systems. Biological categories are indispensable tools for description and communication, but their explanatory value depends on how closely they correspond to the

complexity of the phenomena they describe. Plant sexual diversity shows that categories that are useful at one biological level may become insufficient when extended across different life-cycle stages, developmental processes, or reproductive systems. This supports a view of biological classification as context-sensitive and open to revision when empirical diversity exceeds the explanatory scope of established categories.

This perspective also has implications for environmental philosophy. Understanding biological diversity requires attention not only to the number of species or genetic variants, but also to the diversity of biological processes through which living organisms develop, reproduce, and respond to changing environments. Plant reproductive diversity therefore provides an example of how ecological complexity can challenge overly simplified representations of nature. Recognizing such complexity can contribute to more adequate interpretations of biodiversity, ecological resilience, and conservation, while encouraging approaches to sustainability that remain attentive to the dynamic and relational character of living systems.

2.8.1. Limitations of the study

This review is limited by its interdisciplinary, literature-based approach and uneven empirical coverage of evolutionarily labile reproductive systems. Although evolutionary and developmental perspectives are relatively well represented, genomic regulation and environmental influences on sex expression remain rapidly developing areas. The evaluation of fixed binary frameworks is interpretive but grounded in the scientific literature reviewed here. These limitations highlight the need for further empirical, comparative, and interdisciplinary research on the ecological, evolutionary, and conceptual dimensions of plant reproductive diversity.

2.8.2. Novel integrative contributions of the present study

The principal contribution of this review is a plant-centred framework that distinguishes among gametic sex, sexual function, sexual phenotype, sexual system, and reproductive mode across lineages and life-cycle stages. By integrating evolutionary, developmental, genomic, reproductive-ecological, and historical perspectives, the review links plant sexual diversity to broader questions of biological classification and knowledge production. Rather than rejecting binary categories or replacing them with another universal model, the review clarifies their scope and limits across reproductive contexts. This synthesis offers a more precise understanding of plant sexual diversity while preserving the descriptive value of established categories.

Conclusion

Plant sexual diversity shows that no single fixed binary model can adequately represent reproductive organization across all plant lineages, life-cycle stages, and reproductive contexts. This does not invalidate binary distinctions when they accurately describe gametic sex or specific reproductive systems; rather, it underscores the need to distinguish among gametic sex, sexual function, sexual phenotype, sexual system, and reproductive mode. Across the evidence reviewed, these dimensions are shaped and coordinated by evolutionary, developmental, genetic, and environmental processes, yielding diverse, context-dependent patterns of reproductive expression. The review therefore advances a plant-centred, process-oriented framework that preserves the descriptive value of established sexual categories while clarifying their biological scope and limits. Moving beyond a simple binary-versus-non-binary opposition offers a more precise basis for understanding plant reproduction and informs evolutionary research, classification, science education, crop breeding, conservation, and adaptation to environmental change.

More broadly, the findings also have an interpretative significance for environmental philosophy. Plant sexual diversity demonstrates that the living world cannot always be adequately represented through fixed and universally applied classificatory schemes. Scientific categories remain necessary, but their use should remain sensitive to biological context, evolutionary change, and ecological complexity. In this sense, a process-oriented understanding of plant reproduction contributes not only to biological knowledge but also to a more nuanced conceptualization of biodiversity and the dynamic character of nature, with implications for conservation and sustainability.

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Appendix

Table A1. Summary of included studies categorized by major themes and key focus areas

The table summarizes the 139 studies included in the review across eight thematic domains. For each domain, it presents the main subthemes, the number of studies assigned to that domain, and the principal focus areas identified during thematic synthesis. Each study was assigned to one primary domain to provide a non-overlapping overview of the literature.

Theme	Subtheme	No. of Studies (n = 139)	Key Focus Areas
1. Evolution and Diversity of Plant Sexual Systems	• Diversity and evolutionary pathways of plant sexual systems • Distribution and lineage-specific patterns	23	Diversity and evolution of plant sexual systems; evolutionary transitions and pathways; lineage-specific patterns; life-cycle organization and diversification.
2. Developmental Pathways, Genomics and Plasticity of Plant Sexual Expression	• Ontogeny and evolution of plant unisexuality • Genomics, developmental regulation and environmental plasticity	25	Developmental pathways of sexual expression; genetic, genomic, and hormonal regulation; environmental influences; developmental plasticity.
3. Reproductive Flexibility and the Limits of Conventional Sexual Categories	• Self-fertilization and the organization of male and female reproductive functions • Apomixis and alternative reproductive pathways beyond conventional sexual reproduction	21	Self-fertilization and reproductive-function reorganization; hybridization; sexual–apomictic coexistence; alternative reproductive pathways; genetic continuity.
4. Reproductive Strategies, Ecological Interactions and Evolutionary Diversification	• Pollination strategies, mating systems and plant diversification • Sexual selection, ecological constraints and context-dependent reproductive success	19	Pollination and mating strategies; sexual selection; ecological constraints; context-dependent reproductive success; gene flow, reproductive isolation, and evolutionary diversification.
5. Historical Classification, Anthropomorphism and Conceptual Assumptions	• Legacy of plant sexual categories • Anthropomorphism and conceptual assumptions	17	Historical classification of plant sexuality; gendered and anthropomorphic interpretations; inherited conceptual assumptions; changing frameworks for interpreting reproductive diversity.
6. Plant Sexual Diversity in Comparative and Epistemological Perspective	• Plant sexual diversity and the critique of fixed binary models • Comparative perspectives from animal biology and developmental systems	15	Multidimensional organization and expression of sex; comparative perspectives from animal biology and developmental systems; explanatory scope and limits of fixed binary models; implications for biological classification.
7. Implications of Plant Sexual Diversity for Ecology, Agriculture and Sustainability	• Reproductive diversity, ecological resilience and conservation • Crop evolution, breeding and food security • Climate adaptation and sustainability	16	Ecological resilience and conservation; crop evolution and breeding; food security; climate adaptation; reproductive resilience; sustainability.
8. Challenges of Fixed Binary Sex Categories and Pathways Forward	• Limitations of the study • Novel integrative contributions of the present study	3	Conceptual limitations of fixed binary frameworks; integrative approaches to plant sexual diversity; implications for future comparative and interdisciplinary research.