The architecture of sexual systems in mosses and its ecological and evolutionary consequences

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Abstract

Sexual systems in mosses depend on how antheridia and archegonia are arranged in the gametophyte, and this organization directly shapes how fertilization takes place. In this review, we bring together current knowledge and recent conceptual advances on the origin, function, and evolution of sexual systems in mosses. We first place moss reproduction in the broader context of land plant evolution, showing how gametophyte dominance, dependence on free water for fertilization, and strong desiccation tolerance influence life histories. We then survey the diversity of sexual systems, from dioicy to several forms of monoicy, and examine how the spatial distribution of antheridia and archegonia constrains fertilization processes, sexual expression, and mating opportunities. Empirical studies consistently report female-biased sex ratios, low male sex expression, and strong environmental control of phenology, particularly in dioicous species. Recent work also shows that reproductive allocation and sexual architecture covary, with higher investment in male function in systems that favour cross-fertilization over longer distances, such as rhizautoicy. Using the genus *Fissidens* as a case study, we illustrate how phylogenomic analyses can be related to habitat features, genomic evolution, and functional traits. We also discuss how climate change is likely to affect different sexual systems in distinct ways, with dioicous species and some monoicous architectures showing lower resilience and greater projected niche loss, whereas rhizautoicous systems appear less impacted among monoicous systems. Finally, we highlight key gaps in our understanding of developmental genetics, physiological costs, and macroevolutionary dynamics of sexual systems, and outline research directions to connect processes at the scale of individual buds to global patterns of biodiversity.

Keywords: bryophyte reproduction, sex ratio, reproductive allocation, climate change vulnerability, fertilization limitation.

1. Introduction

1.1 Plant reproductive strategies and their evolutionary importance

One of the main features of an organism's life-history is reproduction, which preserves lineage continuity and impacts genetic variation, and by extension, diversification and adaptation (Haig 2016; Krueger-Hadfield et al. 2024). In addition to supporting the survival of populations in changing conditions, sexual reproduction has greatly influenced the morphology, physiology, and ecology of plants throughout their evolutionary history (Leslie et al. 2021; Becker et al. 2025). Through the combined action of sexual and asexual reproduction, plants can generate new genetic combinations capable of exploiting different ecological niches, while also retaining well-adapted genotypes (Holsinger 2000; Wang 2010; Hollister et al. 2015; Islam et al. 2023). This dynamic balance between conservation and adaptation impacts the reproductive strategies we observe today (Leslie et al. 2021; Becker et al. 2025).

One of the most striking evolutionary characteristics of plants is the diversity of reproductive strategies they possess (Becker et al. 2025). From the reproductive strategies of bryophytes to those of angiosperms, the diversity observed indicates that evolution has shaped numerous adaptive solutions (De Jong and Klinkhamer 2005; dos Santos et al. 2024; Ekwealor and Fisher 2024). Specific selective pressures associated with water availability, propagule dispersal, population density, and biotic interactions have given rise to specific strategies (Bengtsson and Ceplitis 2000; Frey and Kürschner 2011), while also balancing trade-offs in population success across various environments. According to Hollister et al. (2015) and Becker et al. (2025) the evolution of these diverse reproductive systems demonstrates how plants diversified their reproductive strategies to deal with constraints imposed by resource scarcity, being sessile, and biotic stressors.

Understanding the evolution of the reproductive systems of plants helps us see the history of how ecosystems function (Alix et al. 2017). The way plants reproduce impacts patterns of gene flow, population structure, and the ability to respond to change (Burgarella et al. 2024). Studying reproductive strategies, therefore, provides a framework to link genetics, to ecology and evolution. The study of reproductive strategies lets researchers assess how these processes affect species resilience and distribution (Frey and Kürschner

2011; Stark and Brinda 2013; Burgarella et al. 2024). When researchers examine reproduction from this view, they see that reproduction is not just a way to keep life going. Reproduction also acts as a core link between genetic diversity, adaptation and evolution in the history of land plants (Becker et al. 2025).

The transition from the aquatic to terrestrial environment marked a turning point in plant evolution and reshaped how reproduction occurred (de Vries and Archibald 2018; Bowles et al. 2022; Becker et al. 2025). In aquatic environments, gametes were dispersed by water which facilitated fertilization (Fürst-Jansen et al. 2020). As plants colonized land, reproduction became difficult, because water limitation constrained the movement of gametes (Fürst-Jansen et al. 2020). Sun exposure and strong diurnal temperature fluctuations created additional stress and selected for adjusted structure and physiology. During this transition, several traits evolved, including multicellular gametangia and stronger cell walls (Renzaglia et al. 2000; Dehors et al. 2019; Artur and Kajala 2021). Plants also began producing spores coated with sporopollenin, which helped protect their reproductive tissues during dispersal (Shaw and Goffinet 2000). Another important step was the retention of the zygote within maternal tissue, a feature that increased survival during early development (Haig 2016). Together, these adjustments protected genetic material and supported sexual reproduction outside water.

During the diversification of land plants, lineages with different levels of dominance and autonomy for their sporophyte and gametophytes life stages evolved (Donoghue et al. 2021) (**Figure 1**). Rather than reflecting a simple linear progression from gametophyte-dominant to sporophyte-dominant life cycles, there is a continuum. Current phylogenetic and genomic evidence indicates that bryophytes and tracheophytes diverged from a relatively complex common ancestor (McDaniel 2021; Harris et al. 2022). In tracheophytes, the expansion and increasing structural and physiological independence of the sporophyte phase, accompanied by reduced reliance on free water for fertilization, led to the life histories evident today (Frank and Scanlon 2015; Donoghue et al. 2021). In contrast, bryophytes followed a distinct evolutionary trajectory in which the sporophyte became developmentally reduced and nutritionally dependent, while the gametophyte retained ecological and functional prominence (McDaniel 2021; Harris et al. 2022).

The evolution of reproductive strategies in plants illustrates a set of constraints and evolutionary trade-offs between cross-fertilization, dispersal, and survival (Frank and Scanlon 2015; Lora et al. 2016; Borg et al. 2021). The increasing dominance and complexity of sporophytes and the origin of structures such as seeds, flowers, and fruits represent distinct solutions to optimize these trade-offs under contrasting environmental conditions (Artur and Kajala 2021). Species that rely primarily on cross-fertilization tend to maximize genetic variation and adaptive potential, whereas those that maintain mechanisms of self-fertilization or vegetative propagation favor persistence in stable and/or isolated environments (Reutemann et al. 2025). This diversity of evolutionary solutions shows that plant reproduction did not follow a linear path, but rather a path of braided streams, in which new traits arise, are lost, or reverse to previous states. Indeed, considering the evolutionary history of plant reproduction, bryophytes form one of its most revealing and fundamental chapters.

In a broader evolutionary context, mating systems have been widely studied across plants and animals because they strongly influence genetic diversity, population structure, and evolutionary trajectories (Glémin et al. 2006). In flowering plants, transitions between outcrossing and self-fertilization have long been recognized as important drivers of speciation, adaptation, and colonization dynamics (Tsuchimatsu & Fujii 2022). Although bryophytes differ markedly from angiosperms due to their haploid-dominant life cycle and the diversity of sexual systems (how male and female reproductive functions are distributed among individuals) they exhibit, many of the same evolutionary questions apply (Glime and Bisang 2017a). In this sense, mosses provide a valuable system for examining how ecological conditions, reproductive architecture, and mating patterns interact to shape population structure and evolutionary outcomes (Glime and Bisang 2017a, dos Santos et al. 2024).

1.2. Bryophytes illustrate key adaptations of plant reproduction for life on land

Although all extant plant lineages have been evolving for the same amount of time, bryophytes retain many features thought to resemble those of early land plants (Shen et al. 2025). Bryophytes' phylogenetic position as sister to all other land plants and the preservation of ancestral traits make them exceptional models for investigating the origins of reproductive mechanisms in land plants (Hisanaga et al. 2019). Unlike more derived

groups, bryophytes maintain a life cycle in which the gametophyte is the dominant life stage responsible for photosynthesis and reproduction (Maciel-Silva and Pôrto 2014; Haig 2016). This gametophytic dominance represents an example in which plants still depended directly on water for fertilization and are strongly constrained by micro environmental conditions of moisture and light (Shaw and Goffinet 2000). Thus, the study of bryophytes' traits can provide insight into how the first land plants adjusted their reproductive mechanisms to the constraints imposed by terrestrial habitats (Renzaglia and Garbary 2001; Hisanaga et al. 2019).

The relevance of bryophytes is not restricted to their evolutionary position but also extends to their ecological importance and physiological resilience (Lindo et al. 2013; Slate et al. 2024). These organisms play critical structural and functional roles in many ecosystems where they contribute to soil formation, stabilize water cycles, and pioneer extreme environments (Lindo and Gonzalez 2010; Ren et al. 2021; Lett et al. 2022; Slate et al. 2024). Their capacity to survive prolonged periods of desiccation illustrates a resilient strategy with important implications for reproduction (Alpert and Oliver 2002; Oliver 2005; Marks et al. 2016; Stark et al. 2017, 2022; Stark and dos Santos 2024). Spore germination, regeneration from fragments, and the production of vegetative propagules all allow bryophytes to exploit unstable niches and maintain viable populations even under adverse environmental conditions (Tiloca et al. 2022; Stark and dos Santos 2025). These mechanisms support both persistence and dispersal, reinforcing the role of bryophytes as environmental pioneers and model systems for understanding the balance between survival and reproduction.

The combination of a gametophyte-dominated life cycle and reliance on water for fertilization has shaped a suite of reproductive strategies in bryophytes that are central to understanding how plants balance reproduction and survival in variable environments (Pressel and Duckett 2019; Glime and Bisang 2017a). Features such as embryo retention, the production of resistant spores, and specialized dispersal structures illustrate evolutionary responses to water limitation in land plants (Shaw and Goffinet 2000). Among bryophytes, mosses stand out for their diversity and ecological breadth, providing an ideal system to investigate how sexual systems, reproductive modes, and environmental pressures shape reproductive success.

2. Reproduction in mosses

2.1. Life cycle and alternation of generations

The life cycle of bryophytes is characterized by a heteromorphic alternation of generations in which the haploid gametophyte is the dominant phase and the diploid sporophyte is reduced and physiologically dependent (Maciel-Silva and Pôrto 2014) (**Figure 2**). This condition contrasts with that observed in vascular plants where the sporophyte is the autonomous and dominant phase. In bryophytes, the gametophyte performs the essential functions of photosynthesis, reproduction, and supporting the sporophyte (Landberg et al. 2022; Naramoto et al. 2022). The antheridia are the male gametangia that produce flagellated antherozoids, and the archegonia are the female gametangia that produce the oospheres (Oliveira and Pôrto 2005; Haig 2016). Fertilization occurs when antherozoids swim to the archegonia, a process that requires the presence of free water (Shaw and Goffinet 2000). This dependence on liquid water imposes the strong ecological limitation restricting sexual reproduction to periods of time or microhabitats that are sufficiently moist (Stark 2002; dos Santos et al. 2020).

After fertilization, the zygote is retained in the tissue of the female gametophyte and develops into a diploid embryo (Yoro et al. 2023). Although morphologically distinct, this sporophyte is physiologically dependent on the gametophyte from which it receives water and nutrients via its point of attachment (Alfayate et al. 2000; Bisang et al. 2006). The retention of the embryo and sporophyte on the maternal gametophyte are key features in the evolution of land plants as they establish a continuous link between generations and provide protection against desiccation and solar radiation (Becker et al. 2025). When mature, the sporophyte releases haploid spores through the capsule or sporangium–usually via hygroscopic mechanisms that favor passive dispersal by wind (Glime and Bisang 2017a,b).

Spore germination gives rise to a filamentous protonema, the initial stage of the gametophyte, from which the adult plants that will form new gametangia develop (Silva et al. 2009). This simple and highly efficient life cycle reflects a series of evolutionary adaptations that balance dependence and autonomy (Glime and Bisang 2017a; Becker et al. 2025). On the one hand, the need for water for fertilization limits gamete dispersal and increases the chance of population isolation (Haig 2016). On the other hand, the abundant

production of spores and the capacity for both sexual reproduction and vegetative propagation expand opportunities for colonization and support persistence (Frey and Kürschner 2011). The reproductive cycle of bryophytes synthesizes many of the main challenges and solutions that have shaped the evolution of land plant reproduction and forms the basis for understanding the variation observed in different sexual systems (Haig 2016; Glime and Bisang 2017b).

2.2. Key features of moss reproduction

Mosses exhibit a remarkable set of unique reproductive features that reflects their wide ecological distribution (dos Santos et al. 2024). Although they share the same basic pattern of gametophyte dominance observed in other bryophytes, mosses display a morphological and functional diversity unmatched among non-vascular plant groups (Shaw et al. 2011; Lueth and Reski 2023). Their gametophytes, usually erect or branched and densely aggregated, produce specialized reproductive structures, the antheridia and archegonia, which are often borne in distinct regions of the shoot and protected by modified leaves known as gametoecia (perigonia and perichaetia) (Shaw and Goffinet 2000; Godollo 2002). This structural differentiation provides greater protection for the gametes and optimizes water use during fertilization (Greene 1956; Stark 2002; dos Santos et al. 2020). As in other bryophytes, fertilization depends on suitable moisture conditions, which contributes to the strong seasonal and spatial variation in reproductive success observed in many field populations (Glime and Bisang 2017b). Species adapted to arid environments, such as *Syntrichia caninervis* Mitt. and *Bryum argenteum* Hedw., illustrate refined strategies for synchronizing reproduction with brief moisture events, highlighting the plasticity of the reproductive cycle in the face of environmental constraints (Bowker et al. 2000; Stark et al. 2010; Batista et al. 2018).

In addition to sexual reproduction, mosses have developed extensive asexual propagation strategies that support persistence and dispersal even when environmental conditions restrict fertilization and sexual reproduction (Frey and Kürschner 2011). Fragmentation of the gametophyte, regeneration of protonemata, and the production of specialized propagules such as gemmae and buds are frequent mechanisms of asexual reproduction that contribute to population maintenance and colonization of new

microhabitats (Reese et al. 2007; Maciel-Silva and Pereira de Oliveira 2017; Stark et al. 2025). This combination of sexual and asexual reproduction gives mosses (and other bryophytes) remarkable ecological flexibility, allowing them to occupy habitats ranging from moist, shaded soils to exposed rocks in dry-lands (Souza et al. 2020). Species of genera such as *Sphagnum* and *Polytrichum* exemplify contrasting extremes of this diversity. The former are strongly dependent on water-saturated environments and bear capsules that are highly efficient in explosive spore release (Sundberg 2002), whereas the latter have robust sporophytes and elaborate mechanisms for aerial dispersal (Bell and Hyvönen 2010).

3. Sexual systems

3.1. Definition and diversity of sexual systems

Sexual systems in mosses describe how male and female gametangia are organized and distributed on the gametophytes (dos Santos et al. 2024). The sexual systems directly influence how fertilization occurs and, consequently, reproductive success (dos Santos et al. 2024). In general terms, species are dioicous when each gametophyte produces only one type of gametangium (either antheridia or archegonia), or monoicous when both types of gametangia form on the same individual (Wyatt 1985). However, both dioicous and monoicous systems are further classified according to the arrangement and organization of the gametoecia (Wyatt 1985; Maciel-Silva and Pôrto 2014).

Within these categories, there are structural variations that reflect different degrees of proximity between the sexes (Stark and Brinda 2013). In dioicous species, male gametoecia (perigonia) and female gametoecia (perichaetia) always occur on separate plants (Bisang and Hedenäs 2005). Male plants may be similar in size to females or reduced; in some cases, when males are smaller and grow as epiphytes on the leaves of female plants, the system is called phyllodioicous, pseudoautoicous, or dwarf male (Hedenäs and Bisang 2011; Rosengren and Cronberg 2015). In monoicous species, the gametoecia occur on the same plant but in different arrangements (Figure 3) (Glime and Bisang 2017a). In the synoicous system, male and female gametangia are mixed in a single gametoecium (Wyatt 1985; Maciel-Silva and Pôrto 2014). In the paroicous system, they occur in the same gametoecium but with male gametangia adjacent to the female ones (Wyatt 1985; Maciel-Silva and Pôrto 2014). In the gonioautoicous system, the female gametoecium is located at

the apex of the shoot, whereas the male gametoecia are produced in the leaf axils of the same individual (Wyatt 1985; Maciel-Silva and Pôrto 2014; dos Santos et al. 2020). The cladautoicous system is characterized by male and female gametoecia occurring on distinct branches that remain connected to a main axis (Wyatt 1985; Maciel-Silva and Pôrto 2014; dos Santos, Pôrto, Bordin, et al. 2023). Finally, in the rhizautoicous system, which is considered functionally dioicous, male and female gametoecia are borne on separate shoots that are connected by rhizoids (Wyatt 1985; Stark and Delgadillo 2001; dos Santos et al. 2018) (Figure 3). These variations represent different levels of integration and proximity between the sexual organs and imply distinct strategies of fertilization and dispersal. These structural categories describe the spatial arrangement of the sexes, but they do not fully capture how reproduction actually occurs within populations.

Although sexual systems in mosses are traditionally defined by the spatial distribution of gametangia (e.g., dioicy and monoicy), their ecological and evolutionary consequences are better understood when considered alongside mating systems and reproductive modes (Haig 2016). Traits such as self-fertilization rates, levels of outcrossing, and the relative importance of clonal versus sexual reproduction are particularly relevant because they influence how populations persist, maintain genetic diversity, and respond to environmental conditions (Glime and Bisang 2017b). Bryophytes are especially notable for their capacity for clonal growth and fragmentation, which can allow populations to persist and spread even when sexual reproduction occurs only sporadically (Longton 1997; Mishler 1988; Newton and Mishler 1994). Yet sexual reproduction remains essential, not only because it generates new genetic combinations, but also because it promotes long-distance dispersal through spores (Longton and Miles 1982; Longton 2006). In parallel, empirical studies integrating demographic and genetic approaches have shown that clonal traits and mating patterns can strongly shape population sex ratios and reproductive success (McLetchie and Puterbaugh 2000). Together, these lines of evidence suggest that a fuller understanding of reproductive strategies in moss populations depends on integrating morphological sexual systems with estimates of mating patterns and clonal propagation.

The diversity of sexual systems among mosses is remarkable and reflects both the deep phylogenetic history and more recent adaptations of different lineages (Wyatt 1985).

Dioicous species, which are predominant in many genera, tend to exhibit higher genetic variability and sexual specialization, but face reproductive limitations in environments where male and female gametophytes rarely occur in sufficient proximity for fertilization (Bawa and Beach 1981; McDaniel and Perroud 2012). Monoicous species, in contrast, have greater reproductive autonomy and are often favored in unstable environments where population density is low or irregular (Maciel-Silva et al. 2012). This diversity of sexual arrangements reflects a dynamic balance among genetic, ecological, and demographic factors that shape the reproductive success of moss populations (McDaniel and Perroud 2012).

4. Reproductive strategies and challenges associated with sexual systems

4.1 Sex expression patterns and sex-ratio biases

Empirical studies in mosses frequently report female-biased sex ratios, low levels of male expression, and strong environmental control of reproductive phenology, patterns that are particularly pronounced in dioicous species (Bisang and Hedenäs 2005). Dioicous and monoicous sexual systems generate very different patterns of sex expression in mosses (Haig 2016). In dioicous species, the physical separation of males and females makes fertilization more environmentally sensitive, which in turn selects against male sex expression under suboptimal conditions (McLetchie 1992). As a result, many males never express sex in the field despite being genetically present, leading to what appears to be strongly female-biased populations (Shaw and Beer 1999). In contrast, monoicous mosses tend to express sexual structures more regularly, presumably because antheridia and archegonia occur on the same individual, which supports fertilization and makes fertilization more reliable (Bisang and Ehrlén 2002; Glime and Bisang 2017b).

Secondary sexual dimorphisms also play a role in sex ratios and spatial segregation of the sexes. In *Ceratodon purpureus*, a well-studied dioicous species, males show lower stress tolerance and higher mortality, leading to extremely female-biased sex ratios (Shaw and Beer 1999). In *S. caninervis*, male expression is even more restricted, occurring only in slightly moister microsites, which leads to phenotypic sex ratios of up to 17:1 female to male, despite genetic sex ratios close to 2:1 female to male (Bowker et al. 2000; Shortlidge et al. 2017). In *B. argenteum*, the pattern is similar: males rarely express gametangia and

reproduction depends largely on clonal growth (dos Santos et al. 2023, dos Santos et al. 2026). Together, these examples show how dioicy reinforces phenotypic male rarity and strong phenotypic female bias in many systems. On the other hand, monoicous mosses often display the opposite trend. Because both gametangia develop on the same gametophyte, they can produce sporophytes more frequently and with reduced constraints on the timing and proximity required for successful fertilization (Haig 2016; Glime and Bisang 2017b). By extension, because access to the opposite sex is less restricted, sexual expression is less sensitive to fine-scale temporal and environmental variation and monoicous mosses tend to maintain more consistent reproductive cycles, which, together with efficient clonal propagation, can enhance their persistence and colonization potential. Overall, these contrasts indicate that dioicy is associated with limited sexual reproduction and persistent phenotypic female bias, whereas monoicy promotes more stable sexual expression and higher fertilization success.

In many mosses, post-germination processes further amplify these differences. In dioicous species such as *Drepanocladus lycopodioides* (Brid.) Warnst., adult sex ratios reflect not only reduced male expression but also higher male mortality during growth (Bisang and Hedenäs 2005; Hedenäs and Bisang 2011; Rosenstiel et al. 2012). Studies on mosses with dwarf-males also show that male rarity can arise from establishment filters, asymmetries in spore germination, or differential survival, reinforcing male vulnerability in dioicous systems (Hedenäs and Bisang 2011; Rosengren and Cronberg 2015). Taken together, the comparison between sexual systems reveals a consistent pattern: dioicous mosses show low male sex expression, greater environmental sensitivity in males, and female biased sex ratios, while monoicous mosses exhibit more stable sex expression, higher fertilization, and more balanced sex ratios.

4.2 Reproductive allocation

Pre-zygotic reproductive allocation (proportion of biomass allocated to reproductive organs relative to vegetative tissues) offers a useful way to understand how sexual systems influence life-history strategies and secondary sexual dimorphisms, because it reveals how much each sex invests before fertilization (Bazzaz et al. 2005). *Aloina bifrons* (De Not.) M. Fleisch. is a rhizautoicous moss, and Stark and Brinda (2013) showed that males invest far

more than females in pre-zygotic structures. This pattern mirrors that observed in other dioicous mosses, where male shoots tend to experience higher reproductive costs than females, defined as the negative effects of current reproductive investment on future growth, survival, or reproduction (dos Santos et al. 2024). Based on this observation, the authors drew an analogy with angiosperms and proposed a broader hypothesis, as the spatial distance between antheridia and archegonia increases, from synoicy to dioicy, reproductive allocation to male function should also increase. At the time, this idea was largely theoretical and *A. bifrons* was one of the first empirical indications that monoicous species with physically separated sex organs could show dioicous-like allocation patterns (Stark and Brinda 2013).

This prediction was later tested explicitly in *Fissidens* by dos Santos et al. (2023), who compared rhizautoicous, cladautoicous, and gonioautoicous species. Their results confirmed the structural gradient proposed earlier: rhizautoicous species showed the highest male reproductive allocation, consistent with the strong pre-zygotic constraints imposed by their spatial architecture, and similar to the pattern described for dioicous mosses, whereas cladautoicous species exhibited predominantly female allocation, and gonioautoicous species showed no consistent bias. These outcomes demonstrate that pre-zygotic allocation is closely associated with the spatial architecture of the sexual system rather than simply the number of sexes per shoot. In other words, monoicous systems can behave like dioicous systems when the distance between antheridia and archegonia increases (Glime and Bisang 2017b).

Taken together, studies on *A. bifrons*, *Fissidens* spp., and dioicous mosses refine a long-standing idea first articulated by Wyatt (1985): sexual architecture not only governs fertilization opportunities but also shapes how plants distribute resources between male and female functions before the zygote is formed. Rhizautoicous and dioicous systems cluster at one end of this gradient, characterized by high male investment and strong reproductive costs for the male function (Horsley et al. 2011; Stark and Brinda 2013; dos Santos, Bordin, et al. 2023). In contrast, more compact monoicous systems, such as gonioautoicy, minimize these spatial and physiological constraints, resulting in more balanced allocation patterns across the sexes (Glime and Bisang 2017b). This comparative perspective suggests that sexual systems form a continuum rather than a dichotomy, with reproductive allocation emerging as one of the clearest consequences of that structural variation.

4.3 Seasonality

Across the studies, it becomes clear that sexual systems strongly influence how mosses respond to seasonal shifts in moisture. In dioicous species, the greater difficulty in achieving synchrony between separate male and female shoots makes reproductive activity more sensitive to rainfall patterns. This pattern appears consistently in field studies, where sexual maturation is concentrated during wet months and declines sharply during drier periods (Pôrto and de Oliveira 2002; Maciel-Silva and Válio 2011). A similar trend is evident in rhizautoicous mosses: although they are formally monoicous, male and female ramets function independently, and fertilization occurs only within narrow seasonal windows (dos Santos et al. 2020). Broader surveys also support this idea. Zander (1979) showed that dioicous taxa exhibit longer and more variable periods of sporophyte maturation, a pattern that likely reflects delayed and irregular fertilization events caused by the need for precise environmental synchrony between spatially separated sexes. In contrast, monoicous species tend to maintain steadier reproductive activity because the proximity of gametangia reduces moisture limitations and allows development to proceed more continuously through the year (Pôrto and de Oliveira 2002; Stark 2002).

The timing of gametangial development also differs in predictable ways across sexual systems. Dioicous species often show greater fluctuation in antheridial development and higher sporophyte abortion, patterns linked to the strong environmental sensitivity of male maturation and successful fertilization (Stark 2002; Maciel-Silva et al. 2016). Rhizautoicous systems highlight this sensitivity even more clearly. In these mosses, antheridia begin development earlier than archegonia, take longer to mature, and respond sharply to small shifts in moisture, which narrows the effective window for fertilization (dos Santos et al. 2020). Monoicous species with closely associated gametangia, such as synoicous and paroicous systems, face fewer of these constraints. Because male and female organs develop side by side, temporal coordination is less demanding, resulting in shorter and more predictable seasonal windows of sporophyte formation. Zander (1979) documented this pattern across multiple taxa, and the work of Stark (1985) on *Forsstroemia* supports the same conclusion: when gametangia occur close together, reproductive cycles

tend to be more continuous; when they are spatially separated, reproductive timing becomes more variable.

Differences in phenology across sexual systems also extend to dichogamy at the onset of development. In many dioicous and rhizautoicous mosses, male organs initiate development earlier than female ones, without necessarily persisting longer, a pattern that appears to reflect both the high developmental cost of producing antheridia and their greater sensitivity to fluctuating moisture (Stark 2002; dos Santos et al. 2020). Monoicous species, however, often show the opposite trend. Protogyny is common and tends to promote cross-fertilization even when the sexes are in proximity (Longton and Miles 1982; Stark 1997). Together, these findings suggest that the organization of the sexual system shapes the entire reproductive calendar. Dioicous (including monoicous rhizautoicous) populations tend to be limited by seasonal water unavailability, while monoicous ones are more flexible and may be able to reproduce more continuously (Stark 2002; Maciel-Silva et al. 2012).

5. Evolution of sexual systems in a phylogenetic perspective: the case of the genus *Fissidens*

5.1. Phylogeny and patterns of *sexual* system evolution

Recent phylogenetic studies have advanced our understanding of the evolution of sexual systems in mosses and have made it possible to explore how ecological and morphological traits diversified over time (Pressel and Duckett 2019). One example is the work of Budke et al. (2022), who analyzed morphological and reproductive evolution in the genus *Fissidens* (Fissidentaceae, Bryophyta) using genomic data from more than 400 loci. This Budke et al. (2022) study revealed a strong phylogenetic signal for sexual systems, indicating that dioicy and monoicy are evolutionarily conserved traits, but with multiple transitions among lineages. The lack of a consistent directional trend suggests that these processes are subject to frequent reversals and are modulated by ecological and historical conditions, with no consistent evolutionary bias toward either system. More broadly, this pattern is consistent with the view that plant reproductive systems are evolutionarily labile, with repeated shifts among sexual and asexual reproduction, outcrossing and inbreeding, and

monoicous and dioicous states across lineages (Barrett 2013, Krueger-Hadfield et al. 2024). In this sense, plants, including bryophytes and angiosperms, provide powerful systems for investigating how reproductive strategies evolve, persist, and sometimes revert under changing ecological and historical conditions (Boquete et al. 2023, Bisang et al. 2025). The results of Budke et al. (2022) demonstrated a positive correlation between sexual system and habitat moisture level, with dioicous species more frequently associated with humid environments. This pattern supports the hypothesis that dioicy is favored where water availability facilitates sperm transport and reduces fertilization limitation. Under such conditions, dioicy can provide adaptive advantages by promoting obligate outcrossing and higher genetic diversity, rather than maximizing reproductive efficiency per se, whereas monoicy tends to be favored in seasonal or dry habitats, where proximity between gametangia enhances reproductive success (Stark 1983, dos Santos et al. 2025).

The greater reproductive flexibility observed in monoicous mosses may also be interpreted in the context of reproductive assurance, a concept widely discussed in plant reproductive biology (Villarreal & Renner 2013). In angiosperms, the ability to reproduce through self-fertilization has long been considered advantageous in situations where mates or pollinators are scarce, a pattern summarized in Baker's Law (Baker 1959, 1967). Although the reproductive biology of bryophytes differs substantially from that of flowering plants, similar ecological principles may apply when sexual partners are spatially or temporally limited.

These findings are consistent with classic studies emphasizing the central role of water in bryophyte fertilization and the context-dependent benefits of dioicy under high moisture availability (McQueen 1985; Muggoch and Walton 1997; Crum 2001). Thus, the ecological patterns observed in Fissidens reflect evolutionary trade-offs in which genetic variability, reproductive efficiency, and ecological persistence are differentially prioritized across sexual systems, in agreement with trends documented in other mosses (Crawford et al. 2009; McDaniel et al. 2013; Villarreal and Renner 2013).

The phylogenetic analysis of *Fissidens* reinforces that the evolution of sexual systems is closely tied to the ecological interactions of the group. The coexistence of multiple sexual states in different lineages and the recurrent transitions between monoicy and dioicy

indicate a non-directional evolutionary pattern driven by environmental pressures and by morphological and physiological constraints (Wang et al. 2021). These findings suggest that factors such as water availability, and gametophyte morphology interact to shape reproductive patterns (Shaw et al. 2011; Wang et al. 2021; dos Santos et al. 2025). The case of *Fissidens* also illustrates how phylogenomic approaches that integrate morphological, ecological, and genetic data can reveal the forces driving sexual diversity in bryophytes and, more broadly, in land plants (Huttunen et al. 2012).

6. Climate change, sexual systems, and resilience

Bryophytes respond quickly and predictably to climate change because they are highly dependent on external water and are sensitive to fluctuations in temperature and humidity (Gignac 2001; Stark et al. 2011; He et al. 2016). Even small shifts in microclimate can alter their physiology by reducing photosynthesis, disrupting water balance, and increasing the metabolic cost of recovery after desiccation, as documented in species exposed to warming temperatures or reduced moisture (Wagner et al. 2013; Číhal 2023). This sensitivity results in altitudinal and latitudinal range shifts, as shown by herbarium-based analyses indicating that many species are migrating toward cooler regions under warming scenarios (Bergamini et al. 2009). Moreover, the increase in evapotranspiration expected for future climates heightens the risk of water stress, particularly because mosses rely entirely on ambient conditions to gain and lose water and lack internal mechanisms for regulating hydration (He et al. 2016). Consequently, climate change directly affects the physiology, spatial distribution, and community stability of bryophytes, with implications for their persistence in warming ecosystems.

The possible effects of climate change on various bryophyte sexual systems become evident when comparing the responses of dioicous and monoicous species under warming and future climate projections. In *Polytrichastrum alpinum* (Hedw.) G.L. Sm., a dioicous Antarctic moss, passive warming reduced oxidative stress indicators and increased photosynthetic efficiency; however, these physiological gains did not translate into higher sporophyte production, indicating that spatial separation of the sexes continues to constrain fertilization even under elevated thermal conditions (Shortlidge et al. 2017). In contrast, monoicous species occurring in the same plots showed a marked increase in sporophyte

production under warming, confirming that close proximity of male and female gametangia enhances reproductive success across environmental contexts (Shortlidge et al. 2017). This contrast mirrors broader patterns reported in dos Santos et al. (in review), where niche-model projections indicate that dioicous *Fissidens* species are likely to lose over 50% of their climatically suitable area even under optimistic scenarios. This projected decline is consistent with reduced reproductive opportunity under warming, strong fertilization limitation, and consequently reduced sexual recruitment, although clonal propagation may partially buffer population persistence in dioicous species. By comparison, monoicous systems may exhibit greater demographic and biogeographic tolerance to climate change primarily through higher reproductive assurance via sexual reproduction, rather than enhanced physiological stress tolerance. Although rhizautoicous taxa are morphologically classified within monoicy, the spatial separation of male and female organs often results in functional dynamics like dioicous species, which may influence patterns of persistence and reproductive success (dos Santos et al., in review). Together, these studies indicate that sexual system architecture is a strong predictor of bryophyte vulnerability to climate warming by shaping fertilization success and interacting with clonal (asexual) reproduction to influence population persistence and large-scale distributional responses.

7. Final considerations

In summary, sexual systems are not merely reproductive categories, but dynamic reproductive phenotypes that both shape and are shaped by ecological context. Environmental conditions can influence which reproductive strategies persist in populations, while sexual architecture in turn affects fertilization dynamics, population persistence, and evolutionary trajectories in mosses. When we compare the two main systems, dioicous and monoicous, the physical distance between the sexes becomes a key ecological factor. Dioicous species tend to occupy wetter and more stable habitats because fertilization depends heavily on sustained moisture, while monoicous species are more common in unpredictable or highly variable environments where keeping gametangia close together increases the chances of successful reproduction. Each system carries its own set of trade-offs that contribute to population persistence. Despite progress in recent years, we still know surprisingly little about the genetic mechanisms that regulate sexual differentiation, how

each system allocates resources during development, or how physiological strategies vary across ecosystems. Breakdowns or instability in sex-determination systems may also provide valuable opportunities to investigate the genetic basis of dioicy and the mechanisms underlying transitions between sexual systems (Haig 2016). In addition, advances in genomic and transcriptomic approaches now make it possible to examine patterns of gene expression associated with sex determination and reproductive function (Božović et al. 2024, Hisanaga 2024). Such approaches may allow empirical tests of classic predictions about sex-linked genes in haploid dioecious organisms, such as those proposed by Bull (1978), and could help clarify how genetic regulation interacts with patterns of reproductive allocation. Even so, broad-scale patterns are starting to emerge. Studies on *Fissidens*, for example, show that the distribution of sexual systems can be shaped by water availability and functional traits. Ultimately, examining sexual systems in mosses gives us more than a description of how these plants reproduce. It offers a framework for understanding why certain lineages are more resilient or more vulnerable to climate change and how environmental conditions have long structured bryophyte diversity.

Author contributions

WLS conceived the study, conducted the literature review, analyzed the data, and wrote the manuscript. ASM, FP, and RM contributed to the revision of the manuscript and provided important intellectual input and corrections.

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Figures Legends

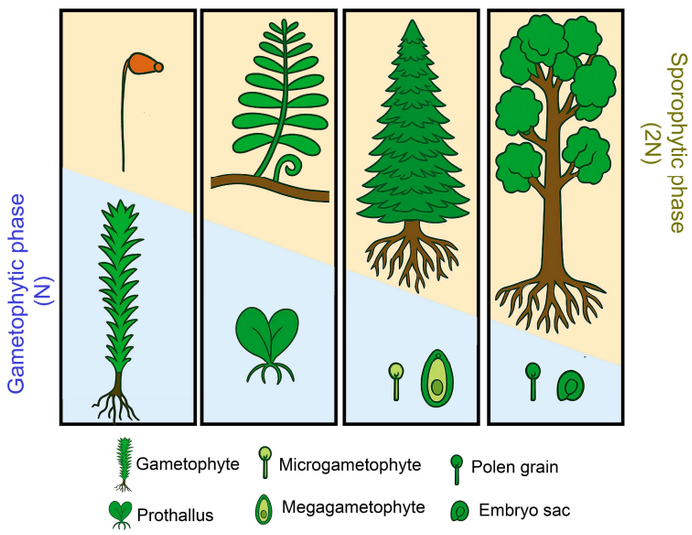

Figure 1 - Alternation of generations in land plants illustrating a general evolutionary shift toward reduced gametophyte expression and increasing sporophyte dominance. In bryophytes, the haploid gametophyte (N) constitutes the dominant, free-living phase of the life cycle. In pteridophytes, the gametophyte remains independent but is smaller and less conspicuous. In seed plants, including gymnosperms and angiosperms, the sporophyte is fully dominant, whereas gametophytes are strongly reduced and physiologically dependent, occurring as the pollen grain (microgametophyte) and the embryo sac (megagametophyte).

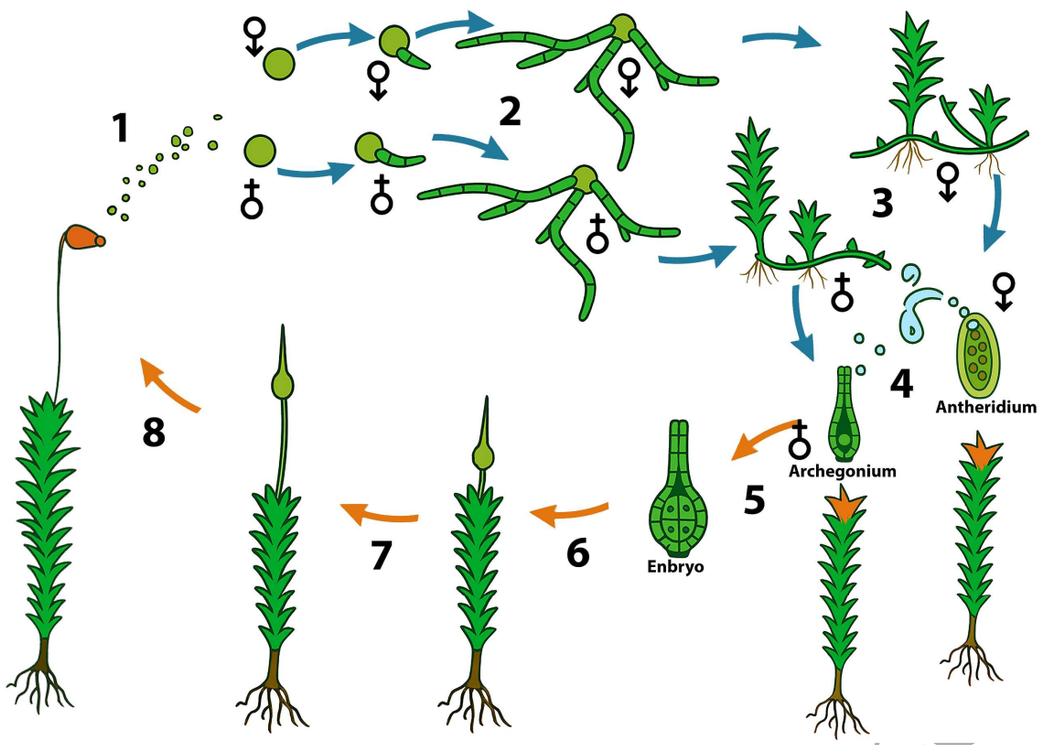

Figure 2 - Reproductive life cycle of bryophytes. Haploid spores produced by meiosis within the sporophyte capsule are released into the environment and germinate to form the protonema. The protonema subsequently gives rise to male and female gametophores, on which gametangia differentiate. Antheridia produce flagellated sperm, whereas archegonia each contain a single egg cell. Fertilization is dependent on free water and results in the formation of a diploid zygote, which develops into an embryo and a young sporophyte attached to the gametophyte. As the sporophyte matures, it differentiates into foot, seta, and capsule, within which meiosis produces a new generation of spores, completing the alternation of generations.

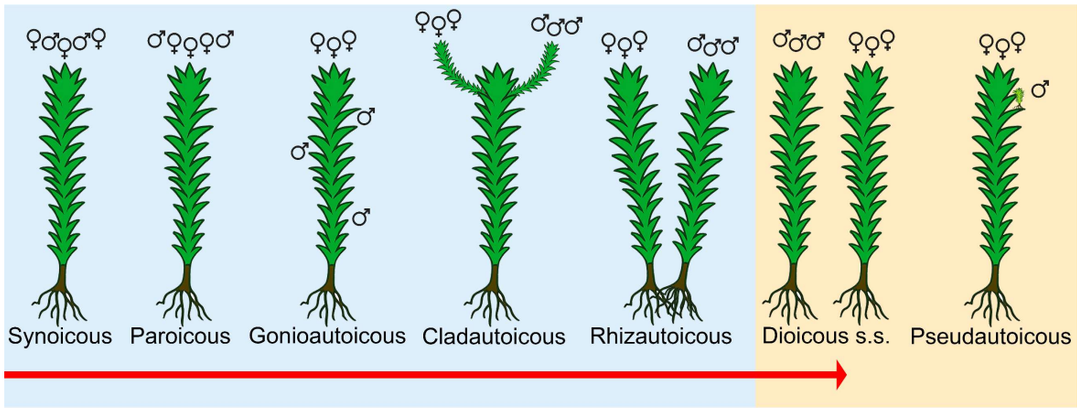

Figure 3 - Sexual systems in mosses arranged along a gradient of increasing spatial separation between male and female functions. Monoicous systems (blue) include a range of gametangial arrangements on the same gametophyte: synoicous, with antheridia and archegonia occurring together within a single gametoecium; paroicous, in which male and female gametangia are separate but closely associated; gonioautoicous, characterized by a terminal perichaetium and perigonia formed in leaf axils; cladautoicous, with sexes segregated into different branches of the same individual; and rhizautoicous, where male and female shoots are spatially separated but remain connected by rhizoidal structures. Dioicous systems (yellow) include the dioicous sensu stricto condition, with distinct male and female plants, as well as pseudoautoicous systems, in which reduced male gametophytes ("dwarf males") develop epiphytically on female individuals. The red arrow indicates increasing sexual segregation.

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