The role of meiotic drive in chromosome number disparity between heterosporous and homosporous plants

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Abstract

In vascular plants, heterosporous lineages typically have fewer chromosomes than homosporous lineages. The underlying mechanism causing this disparity has been debated for over half a century. Although reproductive mode has been identified as critical to these patterns, the symmetry of meiosis during sporogenesis has been overlooked as a potential cause of the difference in chromosome numbers. In most heterosporous plants, meiosis during megasporogenesis is asymmetric, meaning one of the four meiotic products survives to become the egg. Comparatively, meiosis is symmetric in homosporous megasporogenesis and all meiotic products survive. The symmetry of meiosis is important because asymmetric meiosis enables meiotic drive and associated genomic changes, while symmetric meiosis cannot lead to meiotic drive. Meiotic drive is a deviation from Mendelian inheritance where genetic elements are preferentially inherited by the surviving egg cell, and can profoundly impact chromosome (and genome) size, structure, and number. Here we review how meiotic drive impacts chromosome number evolution in heterosporous plants, how the lack of meiotic drive in homosporous plants impacts their genomes, and explore future approaches to understand the role of meiotic drive on chromosome number across land plants.

Introduction

Across vascular land plant lineages, there is great diversity and disparity of genome size and chromosome number (Table 1). Specifically, flowering plants have smaller average nuclear genomes and lower chromosome numbers than most pteridophytes (ferns and lycophytes), a pattern that is correlated with a difference in reproductive mode (Klekowski and Baker, 1966; Wagner and Wagner, 1979; Nakazato *et al.*, 2008; Leitch and Leitch, 2013). Seed plants (including flowering plants) reproduce via separate megaspores and microspores that develop into female and male gametophytes, respectively (Fig. 1A). In these heterosporous systems, female meiosis is typically asymmetric, and male meiosis is symmetric (Fig. 2A, B). While some pteridophytes share this heterosporous system of gamete production (Pettitt, 1977; Bell, 1981), most pteridophytes and all bryophytes have a homosporous system (Fig. 1B) where symmetric meiosis leads to the production of only one type of spore, which germinates into a gametophyte that is capable of producing eggs, sperm, or both. Homospory is the ancestral state of land plants and heterospory has evolved a minimum of 11 times throughout the history of tracheophytes (Bateman and DiMichele, 1994). These transitions from homospory to heterospory are often accompanied by distinct changes in genome structure, including a decrease in chromosome number and genome size (Clark *et al.*, 2016; Carta, Bedini and Peruzzi, 2020). One exception to this pattern are gymnosperms, which are heterosporous with small chromosome numbers but unusually large genome sizes due to the accumulation of repetitive elements (e.g., Nystedt *et al.*, 2013) and few potential ancient WGD events (Li *et al.*, 2015; One Thousand Plant Transcriptomes Initiative, 2019; Stull *et al.*, 2021).

Several mechanisms have been proposed to explain the differences in genome organization between homosporous and heterosporous plants (Klekowski and Baker, 1966; Wagner and Wagner, 1979; Haufler and Soltis, 1986; Haufler, 1987; Barker and Wolf, 2010; Leitch and Leitch, 2013; Kinosian, Rowe and Wolf, 2022). The most well-studied have been differences in whole genome duplications (WGDs) and diploidization (Klekowski and Baker, 1966; Wagner and Wagner, 1979; Haufler, 1987; Barker, 2013). Recent work has shown homosporous and heterosporous lineages have roughly the same number of WGDs, but likely different mechanisms or at least different rates of diploidization and fractionation (One Thousand Plant Transcriptomes Initiative, 2019; Li *et al.*, 2021; McKibben, Finch and Barker, 2024; Z. Li *et al.*, 2024). In flowering plants, diploidization and fractionation can proceed rapidly via a reduction in chromosome number (descending dysploidy) and extensive gene deletions by ectopic recombination (Wendel, 2015; Li *et al.*, 2021). Diploidization in homosporous pteridophytes appears to involve limited chromosome loss accompanied by gene silencing rather than deletion, leading to their high chromosome numbers (Haufler, 1987; Barker and Wolf, 2010; Barker, 2013; Z. Li *et al.*, 2024) and striking intra- and intergenomic collinearity (Huang *et al.*, 2022; C. Li *et al.*, 2024). Heterosporous pteridophytes, however, have chromosome numbers akin to heterosporous angiosperms (Klekowski and Baker, 1966). The transition to heterospory might lead to smaller chromosome numbers and genomes through the dynamics of post-WGD diploidization, perhaps through fundamental changes in the symmetry of female meiosis associated with heterospory.

Female meiosis in heterosporous plants is asymmetric in terms of cell fate: of the four meiotic products, only one survives to become the egg cell and the three polar bodies do not enter the germline (Figs. 1A, 3A; (Burt and Trivers, 2009; Schmerler and Wessel, 2011; Haig, 2020). This asymmetry allows for a deviation in Medelian inheritance called meiotic drive (also referred to here as *female meiotic drive* or *true meiotic drive*), where genetic elements are preferentially transmitted to the germline specifically during asymmetric female meiosis (Sandler and Novitski, 1957; Pardo-Manuel de Villena and Sapienza, 2001b). Meiotic drive is a type of transmission ratio distortion (TRD) or non-random inheritance caused by different processes through an organism's life cycle, including meiosis, gametogenesis, fertilization, and development (Fishman and McIntosh, 2019).

Female meiotic drive can have profound impacts on genome structure. In heterozygotes, a driving allele can rapidly rise to fixation within a handful of generations by taking advantage of a functionally asymmetric meiotic spindle pole and be preferentially transmitted into the surviving egg cell (Pardo-Manuel de Villena and Sapienza, 2001b; Fishman and Willis, 2005; Akera *et al.*, 2017; Finseth, 2023). The mechanisms of drive often act on entire chromosomes: meiotic drive can favor the inheritance of certain chromosomal rearrangements and morphologies, altering a species' karyotype and chromosome number (Pardo-Manuel de Villena and Sapienza, 2001a; Burt and Trivers, 2009; Fishman *et al.*, 2014; Baack *et al.*, 2015; Lindholm *et al.*, 2016; Blackmon *et al.*, 2019; Boman *et al.*, 2024). In addition, female meiotic drive can lead to increased centromere and chromosome size (Henikoff, Ahmad and Malik, 2001; Malik and Bayes, 2006; Zedek and Bureš, 2016; Finseth, Nelson and Fishman, 2021; Plačková *et al.*, 2022). Drive has been proposed as a mechanism of karyotype evolution in mammals (Pardo-Manuel de Villena and Sapienza, 2001a; Blackmon *et al.*, 2019), as well as examined in the context of symmetric and asymmetric meiosis in plants (Zedek and Bureš, 2016; Plačková *et al.*, 2024); however, it has not previously been explored as a potential mechanism for the remarkable difference in genome structure and chromosome number between heterosporous and homosporous plants.

We propose that female meiotic drive may be an important force behind differences in chromosome number evolution across land plants. In heterosporous angiosperms, chromosome number decreases by descending dysploidy following WGD (Li *et al.*, 2021; Z. Li *et al.*, 2024). Descending dysploidy occurs at a slower rate in homosporous pteridophytes, about half that of angiosperms (Z. Li *et al.*, 2024). This disparity could be explained by the presence of meiotic drive in heterosporous lineages and its absence in homosporous lineages. Meiotic drive is a known mechanism for chromosomal rearrangements to overcome a heterozygote disadvantage, and rearrangements involving the centromere would be preferentially inherited (White, 1968; Searle, 1993; Searle and de Villena, 2022). Specifically, rearrangements like Robertsonian translocations can be favored by drive and reduce overall chromosome number and could be part of how dysploidy occurs during the diploidization process (Escudero *et al.*, 2014; Searle and de Villena, 2022). Homosporous plants may go through slower post-WGD dysploid changes because they have strictly symmetric meiosis, eliminating the possibility of genome restructuring by true meiotic drive. Other types of TRD can occur in lineages with symmetric meiosis, although these processes typically occur before or after meiosis and often act on specific genotypes (Lindholm *et al.*, 2016). Here we review how female meiotic drive impacts genome evolution and chromosome number across vascular land plants (focusing on angiosperms), what genome characteristics we would expect to see in a lineage without meiotic drive (focusing on pteridophytes), how post-meiotic drive may be influencing homosporous genomes, and conclude with future directions for incorporating meiotic drive into the growing body of work on post-WGD genome evolution in plants.

The influence of meiotic drive on heterosporous genome structure

Changes in genome structure as a consequence of female meiotic drive has been described across eukaryotes (e.g., Pardo-Manuel de Villena and Sapienza, 2001a; Chmátal *et al.*, 2014; Fishman *et al.*, 2014; Blackmon *et al.*, 2019). Female meiotic drive can happen via different mechanisms during meiosis I or II, depending on which aspects of cell division are available to create preferential inheritance (Clark and Akera, 2021). The most well-studied drive mechanism is centromere drive, which has direct effects on chromosome number, shape, and size (Blackmon *et al.*, 2019; Mayrose and Lysak, 2021; Dudka and Lampson, 2022; Plačková *et al.*, 2024). In centromere drive, cell signaling during meiosis I differentiates the egg (surviving, enters the germ line) and cortical (polar body, does not enter the germline) sides of the spindle (Figs. 2A, 3A; (Akera *et al.*, 2017; Silva and Akera, 2023). Larger centromeres have a stronger kinetochore-spindle connection, resulting in the larger homologous centromere (and attached homolog) being preferentially attached to the more stable microtubules on the egg side of the spindle (Fig. 3B; (Peris *et al.*, 2009; Akera *et al.*, 2017; Dudka and Lampson, 2022). In drive systems that favor larger centromeres, chromosome fusions can be preferentially inherited, reducing overall chromosome number (Pardo-Manuel de Villena and Sapienza, 2001a; Lindholm *et al.*, 2016). For example, Robertsonian translocations are a type of chromosome fusion where two acro- or telocentric chromosomes fuse to form a new metacentric chromosome; these fused centromeres create stronger bond to the spindle fiber (Chmátal *et al.*, 2014). Therefore, Robertsonian translocations are preferentially transmitted in human female meiosis despite deleterious effects (Daniel, 2002; Poot and Hochstenbach, 2021; Talbert and Henikoff, 2022; de Lima *et al.*, 2024); similar fused chromosomes are also preferentially transmitted in *Drosophila* (Stewart *et al.*, 2019). Chromosome number evolution mediated by chromosomal rearrangements has been documented across heterosporous plants, including Brassicaceae (Lysak *et al.*, 2006; Mandáková and Lysak, 2008), Orchidaceae (Moscone *et al.*, 2007), and Podocarpaceae (Hair and Beuzenberg, 1958; Jones, 1979), with fusions being noted as a potential mechanism of genomic downsizing and chromosome number reduction following polyploidy (Jones, 1998; Mandáková and Lysak, 2018; Mayrose and Lysak, 2021). Chromosome fusions favored by meiotic drive could be part of how heterosporous plants cytologically downsize (i.e., descending dysploidy) following WGD; the absence of meiotic drive in homosporous plants would eliminate this process as a mechanism for genome downsizing.

In addition to chromosome number, meiotic drive can cause different morphologies (meta-, acro-, or telocentric chromosomes) to be favorably inherited depending on the system, although it is unclear exactly in what stage of meiosis this occurs (Burt and Trivers, 2009; Dudka and Lampson, 2022). Chromosome morphology changes caused by meiotic drive are known to occur in mammals and fishes, where a change in the polarity of meiotic drive (i.e., which meiotic product survives, Fig. 3A) favors a specific chromosome morphology, causing rapid rearrangement of chromosome structure and number (Molina *et al.*, 2014; Blackmon *et al.*, 2019). For example, in mammals, some species have a karyotype comprising mostly metacentric chromosomes, some have mostly acro- or telocentric chromosomes, and others have a mix of both chromosome morphologies (Pardo-Manuel de Villena and Sapienza, 2001b; Burt and Trivers, 2009). Rates of chromosome evolution are slower in species with one chromosome morphology and higher in species with a mix of morphologies (Blackmon *et al.*, 2019). Meiotic drive is thought to stabilize chromosome morphology within a species, and drive can cause rapid karyotype change if the polarity of drive changes (Pardo-Manuel de Villena and Sapienza, 2001a; Blackmon *et al.*, 2019). Interestingly, most angiosperms species have only metacentric chromosomes (Stebbins and Others, 1971; Weiss-Schneeweiss and Schneeweiss, 2013), perhaps because the polarity of meiosis is weaker compared to animals (Huang and Russell, 1992). However, within some lineages like monocots, for example, karyotypes can be much more variable (Stedje, 1989; Choi *et al.*, 2008; Hamouche *et al.*, 2010; McKain *et al.*, 2012; Plačková *et al.*, 2022). Research in the Brassicaceae suggests that a karyotype comprising multiple chromosome morphologies is perhaps a transition state (Mandáková and Lysak, 2008; Lysak *et al.*, 2009; Weiss-Schneeweiss and Schneeweiss, 2013), which could be created by drive if the polarity of meiosis recently changed, perhaps following one of the many WGD in evolutionary history of the family (e.g., Lysak *et al.*, 2009; McKibben, Finch and Barker, 2024).

Other types of meiotic drive can occur via mechanisms in meiosis II, although the exact mechanisms by which this happens are unclear because the egg and polar sides of the spindle are not established through the same signalling mechanisms as is meiosis I (Clark and Akera, 2021). A neocentromere on chromosome Ab10 in maize acts during meiosis II, where the driving neocentromeres are transmitted to the outer cells of the tetrad, one of which survives to become the egg (Dawe *et al.*, 2018). In addition, cytokinesis in female meiosis is asymmetrical, with a majority of the cytoplasm remaining in the egg cell. Certain chromosomes can lag during cytokinesis of meiosis II and remain in the egg cytoplasm, similar to biased transmission of B chromosomes (Wu *et al.*, 2019; Chen, Birchler and Houben, 2022).

As mentioned previously, the mechanisms and effects of female meiotic drive are incredibly variable. One aspect of this variability is the polarity of meiotic drive, where either large or small centromere are favored depending on which meiotic product survives to become the egg (Blackmon *et al.*, 2019; Plačková *et al.*, 2024). It has been hypothesized that centromere size may mediate chromosome size, with larger centromeres associated with larger chromosomes, and vice versa (Plačková *et al.*, 2022, 2024). Indeed, centromere size has been observed to scale with chromosome size in Agavoideae (Plačková *et al.*, 2022) and grasses (Bennett *et al.*, 1981; Zhang and Dawe, 2012). This could extend to meiotic drive favoring different chromosome traits, depending on the polarity of drive. For example, there is evidence that centromere drive can favor chromosome fusions in one species of butterfly, but conserve chromosome structure by selecting against chromosome fusions in another (Boman *et al.*, 2024). In addition, in *Mimulus* it is thought that chromosome fissions supported by meiotic drive are responsible for chromosome number doubling, not polyploidy (Fishman et al., 2014). Considering that drive is variable across systems (e.g., (Lindholm *et al.*, 2016), additional work is needed to understand the mechanisms at play.

It is important to note that there are many ways in which angiosperm megasporogenesis happens (Huang and Russell, 1992; Kaur, Kathpalia and Koul, 2024), all having different types of cells develop into the megaspore resulting in variable mechanisms of meiotic drive. Indeed, a correlation between the type of sporogenesis and nuclear genome size has been made in angiosperms, where species that undergo disporic or tetrasporic megasporogenesis have larger genomes than those with monosporic sporogenesis (Bharathan, 1996). In monosporous megasporogenesis, following meiosis one of the four resulting one-nucleate cells survived to become the egg cell (Fig. 3A); in disporic megasporogenesis, one of the two resulting two-nucelate cells survives; and in tetrasporic megasporogenesis, a single four-nucleate cell survives (e.g., Haig, 1990, 2020; Drews and Koltunow, 2011). Meiotic drive would be the strongest in a monosporic system, and present but less strong in a disporic system. In tetrasporic megasporogenesis, the egg cell develops much later, and within an embryo derived from one genetic background (Yadegari and Drews, 2004); drive would act much differently and potentially be weaker than in the other two types of megasporogenesis. Interestingly, megasporogenesis in heterosporous ferns could have stronger meiotic drive than in seed plants. While 1 out of 4 potential megaspores are ultimately viable in angiosperm monosporic sporogenesis, 1 out of 32 megaspores are ultimately viable in the germ *Marsilea*. Megasporogenesis in the fern *Marsilea* produces eight tetrads of megaspores (and in each tetrad just one megaspore survives), but only one of the eight survives to maturity (Bell, 1981). Interestingly, spores are produced in a tetrad with no polarity as to which megapore survives (Bell 1985). More research of the dynamics of meiosis in heterosporous ferns and lycophytes is needed to better understand the asymmetries in these lineages.

In summary, meiotic drive can influence genome structure by the non-Mendelian inheritance of chromosomes with larger centromeres, and chromosome number by inheritance of chromosomal rearrangements involving and strengthening centromeres. The potential for meiotic drive may be part of the reason why heterosporous plants, in particular angiosperms, have a large diversity and relatively rapid evolution of genome structure and organization. Competition among centromeres and chromosomes in plant lineages with meiotic drive may lead to lower chromosome numbers especially if fusions or larger centromeres and chromosomes are favored in their drive systems. In contrast, the absence of meiotic drive in homosporous plants may explain the comparative lack of diversity and slower evolution in their genome structure and organization such as largely stable and high chromosome numbers over time.

Meiotic drive and symmetric meiosis

In contrast to the genomes of the heterosporous angiosperms, the genomes of plants with symmetric meiosis—namely homosporous pteridophytes and bryophytes—cannot be influenced by female meiotic drive. Homosporous pteridophytes have a unique kind of symmetric meiosis, different from that of male meiosis in heterosporous plants. In leptosporangiate ferns, spores are produced via four rounds of mitosis and one round of meiosis (Fig. 2C). In eusporangiate ferns, hundreds of spores are produced in tetrads via one round of meiosis, akin to male meiosis in heterosporous plants (Brown and Lemmon, 2001). Sporogenesis in bryophytes is also symmetric; however, unlike pteridophytes, some bryophytes have sex chromosomes, which could lead to alternate mechanisms of TRD (e.g., Presgraves, Severance and Wilkinson, 1997; Fedyk, Bajkowska and Chętnicki, 2005). In these plants without true meiotic drive, we expect to see slower chromosomal change, limited selection pressure on chromosome size and morphology, and larger genomes. In addition, post-WGD diploidization is fundamentally different in lineage with symmetric meiosis compared to those with asymmetric meiosis; diploidization in plants with symmetric meiosis likely involves gene silencing and fractionation, without major structural changes to the genome (Haufler, 1987; Barker and Wolf, 2010; Marchant *et al.*, 2022; C. Li *et al.*, 2024; Z. Li *et al.*, 2024).

Previous work has shown that centromere drive is absent in lineages with symmetric meiosis (Zedek and Bureš, 2016; Plačková *et al.*, 2024). Evidence for this comes from molecular evolutionary analyses of histones, in particular CenH3, which is often rapidly evolving with signals of positive selection in lineages with asymmetric meiosis, but evolutionarily constrained and under purifying selection in organisms with symmetric meiosis (Zedek and Bureš, 2016; Finseth, Nelson and Fishman, 2021; Plačková *et al.*, 2024). Centromere histones are thought to be rapidly evolving to counteract the changes caused by centromere drive; thus, rapid histone evolution is not expected or observed in lineages with symmetric meiosis because centromeres are conserved in the absence of meiotic drive (Zedek and Bureš, 2016; Plačková *et al.*, 2024). Comparing the evolution of CenH3 between heterosporous and homosporous pteridophytes would reveal if this pattern held across all lineages with asymmetric meiosis.

The absence of meiotic drive in homosporous plants means no possibility for the preferential inheritance of certain karyotypes, chromosome morphologies, or rearrangements (Burt and Trivers, 2009), and could be part of the reason why homosporous pteridophytes have relatively stable chromosome structures (Wagner and Wagner, 1979; Bomfleur, McLoughlin and Vajda, 2014; Clark *et al.*, 2016), uniform chromosome sizes (Manton, 1950; Wagner and Wagner, 1979; Nakazato *et al.*, 2008; Clark *et al.*, 2016), and relatively slow rates of chromosome number evolution (Z. Li *et al.*, 2024). The size range variation in homosporous fern chromosomes is only 31-fold, compared to 1300-fold in heterosporous angiosperms (Clark *et al.*, 2016). It has been hypothesized that this stability and uniformity is due to a limit on the amount of genetic material in each chromosome (Liu *et al.*, 2019), but also may come from the lack of meiotic drive influencing chromosome morphological change (Plačková *et al.*, 2024). Despite the extensive research on pteridophyte cytology (e.g., Manton, 1950; Klekowski and Baker, 1966), limited information has been published on their chromosome morphology. We surveyed the literature for pteridophytes chromosome morphology data, finding only ten studies describing eleven taxa and a broad range of chromosome morphologies (Table 2). Further studies on homosporous and heterosporous pteridophyte chromosome morphology and karyotype structure, ideally in a phylogenetic context, are needed to understand what processes are influencing these traits.

Transmission ratio distortion can operate in organisms with symmetric meiosis, but these types of TRD occur post-meiotically, and so are different from true meiotic drive (Sandler and Novitski, 1957; Pardo-Manuel de Villena and Sapienza, 2001b; Fishman and Willis, 2005). One example of post-meiotic drive is spore drive, which results from competition between spores containing different haplotypes, often called killer and alternative haplotypes (Raju, 1994; Grognet *et al.*, 2014; Harvey *et al.*, 2014; Lindholm *et al.*, 2016). Spore drive is best characterized in ascomycete fungi, where the spores are packaged together in an ascus. The proximity of spores in an ascus allows for a “killer” haplotype to kill or disable neighboring spores with an alternate or “target” haplotype. Similar spore production occurs in pteridophytes and bryophytes with spores packaged in a sporangium. Spore drive has not been tested in ferns, but reductions in spore numbers within a sporangium has been observed across populations of homosporous ferns (Barker and James Hickey, 2006; A. L. Grusz, Pers. Ob.) which suggests it could occur. In addition, dispersal can also influence spore drive, with drive being more prevalent if spores do not travel far from one another (Lindholm *et al.*, 2016). The majority of fern spores disperse only a few meters from the parent plant (Conant, 1978; Rose and Dassler, 2017), but because ferns produce vast numbers of spores, some do travel great distances (e.g., Tryon, 1970). The greater distance that spores disperse from one another, the smaller the potential effect from spore drive (Lindholm *et al.*, 2016).

Another example of post-meiotic drive is male drive, which occurs when a drive locus kills sperm with a target locus (e.g., Taylor, 1994; Presgraves, Severance and Wilkinson, 1997). Similar to spore drive, one genotype will kill the an alternate genotype regardless of the fitness consequences (Rice, 2013; Lindholm *et al.*, 2016). There is limited research on fern sperm competition, but observational studies have described competition in the archegonium before sperm meet the egg (Lopez-Smith and Renzaglia, 2008). Further work is needed to understand competition and potential male drive among sperm of homosporous plants, as well as in other flagette plants.

Because of fundamental differences in meiosis, meiotic drive cannot happen in homosporous pteridophytes in the same way as in heterosporous plants. TRD can still influence the genomes of homosporous plants by removing certain genotypes but likely does not shape the genome in the same ways as true meiotic drive. Several homosporous pteridophyte genome assemblies are now published (Fang *et al.*, 2021; Huang *et al.*, 2022; Marchant *et al.*, 2022; Yu *et al.*, 2023; C. Li *et al.*, 2024), giving us insight into plant genome structure in the absence of female meiotic drive. Perhaps most striking is that these species have highly conserved intra- and intergenomic synteny over millions of years (Huang *et al.*, 2022; C. Li *et al.*, 2024); the same is true for hornworts (Schafran *et al.*, 2025). An exception is *Ceratopteris richardii*, which has a rate of fractionation rivaling many angiosperm species (Nakazato *et al.*, 2006; Marchant *et al.*, 2022), but the mechanisms causing this rapid diploidization are unclear. Broad patterns in homosporous pteridophytes suggest that, while genic diploidization and fractionation occur, there are limited mechanisms for cytologically restructuring the genome following WGD.

Conclusions and future work

Here we describe how meiotic drive may be a potential mechanism behind the disparity in genome architecture among land plants, specifically influencing chromosome number and structure of heterosporous plants. Other types of TRD can occur in homosporous lineages, but not true meiotic drive, as sporogenesis is symmetric. Although the symmetry of meiosis has not been explicitly explored in the context of homosporous plants, other authors have noted that genome evolution is likely dependent on the mechanics of meiosis (e.g., Burt and Trivers, 2009; Lindholm *et al.*, 2016; Kinosian, Rowe and Wolf, 2022; Finseth, 2023). Pteridophytes are an ideal system to study the effects of drive on genome structure, as there are sister lineages with asymmetric and symmetric meiosis in both ferns and lycophytes. Here we discuss a few ways to investigate how drive or other types of transmission ratio distortion might affect homosporous vascular land plant genomes.

Consistent with the absence of meiotic drive, past studies have shown that homosporous ferns have strong Mendelian inheritance (Andersson-Kottö, 1927; Dedera and Werth, 1987). Ferns have relatively low gene densities compared to flowering plants (Rabinowicz *et al.*, 2005; Wolf *et al.*, 2015), perhaps because of a lack of meiotic drive selecting for genome downsizing or, alternatively, pseudogenization caused by transposons in ferns (Lisch, 2013). Long terminal repeat retrotransposon (LTR-RT) have a high birth but low death rate in homosporous ferns, with the inverse occurring in heterosporous lycophytes (Wang *et al.*, 2021; Yu *et al.*, 2023). Older LTR-RTs are associated with larger haploid nuclear genome size in pteridophytes (Baniaga and Barker, 2019). The exact role of transposons in unclear in pteridophytes, but more research is warranted, especially because transposons are known to be associated with meiotic drive (Eickbush, Young and Zanders, 2019; Vogan *et al.*, 2021). In addition, the expansion of different gene families as well as the rate of meiosis gene evolution is greater in heterosporous angiosperms than in homosporous pteridophytes, suggesting that different selection pressures, perhaps one of those being meiotic drive, are acting on meiosis in heterosporous lineages (Dhakal, Wolf and Harkess, 2024; Z. Li *et al.*, 2024). Building on these observations, future work could look more explicitly for evidence of TRD in homosporous plants and investigate the mechanics of homosporous meiosis.

Finding natural examples of meiotic drive can be challenging, as a driving locus is often rapidly fixed in a population, and therefore undetectable. However, these can reemerge following a hybridization event, or even be part of hybrid sterility (Lindholm *et al.*, 2016). An example of this is in yellow monkeyflowers, where hybrids between *Mimulus guttatus* and *M. nasutus* exhibit strong female meiotic drive and the driving locus is nearly fixed in only a handful of generations (Fishman *et al.*, 2001; Fishman and Willis, 2005; Finseth, Nelson and Fishman, 2021). Testing for such cryptic drive systems could be a potential avenue of research in pteridophytes, specifically in those with known hybrid sterility. Pteridology has a rich history of work on hybrid species, including studies on the model system *Ceratopteris* (e.g., Hickok, 1973; Hickok and Klekowski, 1974). Genomic resources available for *Ceratopteris* (Nakazato *et al.*, 2006; Marchant *et al.*, 2022) would make testing for drive in a hybrid mapping population feasible (e.g., Fishman and Willis 2005). It will also be important to look at TRD and sex chromosome drive in bryophytes. Segregation distortion of loci and biased sex ratios have been detected in the moss *Ceratodon* (McDaniel, Willis and Shaw, 2007), but less is known about hornworts and liverworts.

A post-meiotic TRD mechanism that could be happening in homosporous plants is spore drive. In fungi, spores are affected by drive when a certain genotype kills an alternative genotype. Considering the large number of spores produced within a sporangium by both eusporangiate and leptosporangiate lineages, the ingredients for spore drive are present. DNA expression studies have identified spore drive systems, revealing that the driving element can lethally target specific genes (Urquhart and Gardiner, 2023). A consistent reduction in spore number per sporangium in leptosporangiate ferns has been observed (Barker and James Hickey, 2006; A. L. Grusz, Pers. Ob.), suggesting something may be happening during sporogenesis to reduce spore number. Additional work counting spores could better characterize this pattern. If more concrete patterns of spore reduction are observed and connected to a spore drive system, the model fern *Ceratopteris* could help understand the genetic mechanisms for homosporous spore drive.

Other processes outside of meiotic and related drive systems could affect chromosome number and genome size. Population size can be a greater force on chromosome number than meiotic drive in Carnivora: smaller populations had greater variation in chromosome number than large populations (Jonika *et al.*, 2024). Another hypothesis for the evolution of chromosome number is the minimum interaction theory, which postulates smaller chromosomes are selected to reduce reciprocal translocation; consequently, chromosome number will increase as more chromosomes are needed to contain the genome (Imai *et al.*, 1986). Exploring ecology and natural history in homosporous plants could be another avenue to understand their distinct genome organization outside of meiotic drive. It is well-established that the rate of molecular evolution is higher and genome size is smaller in plants with shorter life cycles, compared to those with longer life cycles (Cavalier-Smith, 2005; Smith and Donoghue, 2008). There is also a correlation between vascular structure (i.e., the presence or absence of tracheids) and genome size (Cavalier-Smith, 2005). Heterosporous ferns (Salviniales) and *Selaginella* have tracheids and small genome sizes, but gymnosperms and the heterosporous lycophyte *Isoëtes* lack tracheids and have large genomes (Cavalier-Smith, 1978; Leitch *et al.*, 2005). Comparing life history and genome traits in a phylogenetic context could help tease apart complex interactions between these variables.

The proliferation of a selfish element is key in female meiotic drive and TRD systems, yet the mechanisms by which this occurs are incredibly varied (Burt and Trivers, 2009; Lindholm *et al.*, 2016; Saupe and Johannesson, 2022). Female meiotic drive is potentially a mechanism behind the rapid diploidization and downsizing following WGD in heterosporous plants. TRD in pteridophytes and bryophytes is probably distinct from true meitoic drive in angiosperms, fungi, or animals. The absence of meiotic drive would help explain large and stable genomes, uniform chromosome sizes, relatively static chromosome numbers following WGDs, as well as the current challenges with assembling centromeres in homosporous fern and lycophyte genomes. Although almost certainly only one piece of the puzzle, researching meiotic drive in homosporous plants is important to broaden our understanding of the unique genomes of this lineage.

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Table 1. Genome traits and potential types of meiotic drive for land plants.

Group	**Average Genome size (1C)**	**Average Haploid Chromosome Number (n)**	**Average Inferred rounds of WGD**	**Asymmetric meiosis**	**Potential types of drive**	**Citations**
Angiosperm	4.4	15.99	3.5	Yes	Centromere, chromosome, female meiotic drive	(Klekowski and Baker, 1966; One Thousand Plant Transcriptomes Initiative, 2019; Pellicer and Leitch, 2020; McKibben, Finch and Barker, 2024; Z. Li *et al.*, 2024)
Gymnosperm	15.51	11.69	1.63	Yes	Centromere, chromosome, female meiotic drive	(Rice *et al.*, 2015; One Thousand Plant Transcriptomes Initiative, 2019; Pellicer and Leitch, 2020; Z. Li *et al.*, 2024)
Heterosporous pteridophyte	1.01	13.62	2.4	Yes	Centromere, chromosome, female meiotic drive	(Klekowski and Baker, 1966; Pellicer and Leitch, 2020; Z. Li *et al.*, 2024)
Homosporous pteridophyte	15.13	57.5	2.82	No	Spore drive, other non-meiotic TRD	(Klekowski and Baker, 1966; Pellicer and Leitch, 2020; Z. Li *et al.*, 2024)
Bryophytes	0.72	10.23	2.28	No	Spore drive, other non-meiotic TRD, sex chromosome drive	(Klekowski and Baker, 1966; Pellicer and Leitch, 2020; Z. Li *et al.*, 2024) N. Patel, unpublished data)

Table 2. Published descriptions of chromosome morphology for homosporous and heterosporous pteridophytes.

Taxon	**Reproductive mode**	**Chromosome morphology**	**Citation**
Claytosmunda claytoniana	homosporous	acrocentric, very few metacentric	(Tatuno and Yoshida, 1967)
Osmundastrum cinnamomeum	homosporous	acrocentric, very few metacentric	(Tatuno and Yoshida, 1967)
Plenasium banksiaefolium	homosporous	acrocentric, very few metacentric	(Tatuno and Yoshida, 1967)
Hymenophyllum barbatum	homosporous	acrocentric, some metacentric	(Tatuno and Takei, 1969)
Asplenium incisum	homosporous	acrocentric, very few metacentric	(Tatuno and Kawakami, 1969)
Pteris	homosporous	acrocentric	(Kawakami, 1971)
Regnellidium diphyllum	heterosporous	Submetacentric and subtelocentric	(Kuriachan, 1994)
Selaginella	heterosporous	Metacentric, telocentric	(Takamiya, 1993; Marcon, Barros and Guerra, 2005)
Danaea	homosporous	submetacentric	(Benko-Iseppon, Rodrigues and da Fonsêca, 2000)
Acrostichum	homosporous	subtelocentric	(Marcon, Barros and Guerra, 2003)
Doryopteris triphylla	homosporous	telocentric	(Neira *et al.*, 2017)

Figures

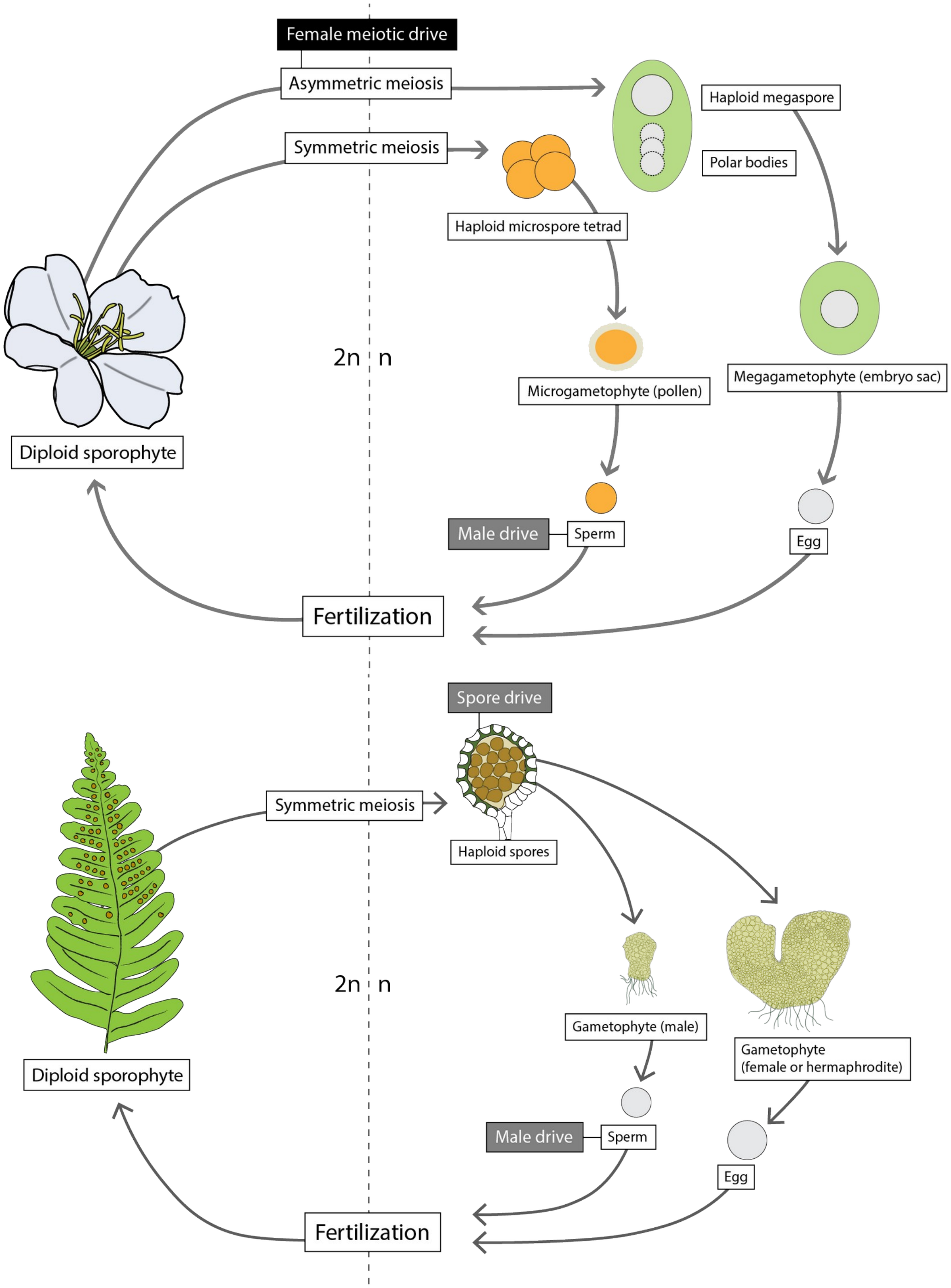

Figure 1. Life cycles of heterosporous (top) and homosporous (bottom) land plants. Locations of female meiotic drive and other types of transmission ratio distortion are denoted in black and gray boxes, respectively.

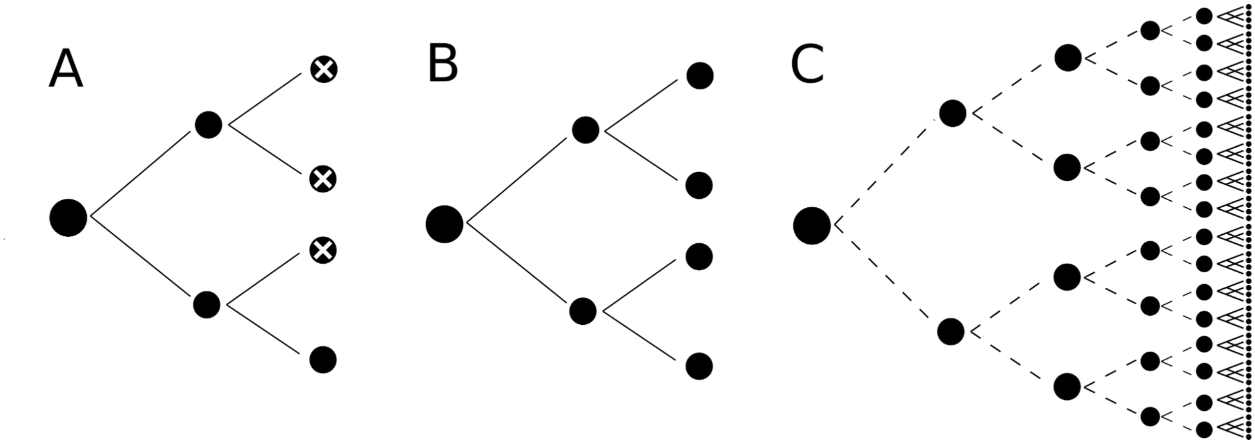

Figure 2. Examples of different types of meiosis. In each panel, the far left circle depicts the sporocyte, and succeeding divisions proceeding to the right. Solid lines indicate meiosis and dotted lines indicate mitosis. A) Heterosporous female meiosis, where only one meiotic product survives and the remaining three polar bodies die (can be either top or bottom, resulting from the cell on the chalazal or micropylar end surviving, see Fig. 3A) ; B) Heterosporous male meiosis, where all meiotic products survive; C) Leptosporagiate sporogenesis where 64 spores are generated through four rounds of mitosis and one round of meiosis; all spore survive.

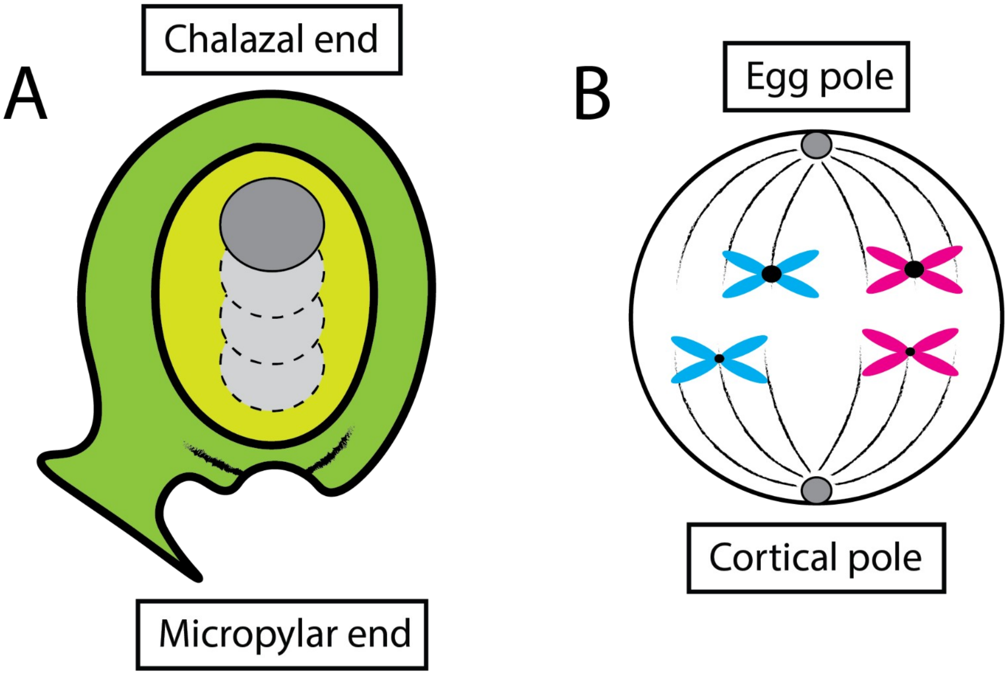

Figure 3. A) Organization of megasporogenesis in a heterosporous ovule, the cell on the chalazal end often survives, but alternatively the cell on the micropylar end can become the egg. B) Centromere drive, where larger centromeres are preferentially transmitted to the egg pole in meiosis I (anaphase I is depicted); the egg pole is often associated with the chalazal end of the ovule (see panel A), and the cortical side the micropylar end.

Glossary

Transmission ratio distortion - non-random inheritance of parental alleles in the offspring population, occuring before, during, or after meiosis.

Meiotic drive - non-random inheritance of alleles, chromosomes, or other genome structures specifically during asymmetrical meiosis.

Spore drive - observed in ascomycete fungi where spores are packages together in an ascus, a spore with the "killer" haplotype will kill spores with the alternative haplotype, particularly in when spores are in close proximity.

Male drive - biased transmission that occurs during or after male meiosis; typically involves an allele that kills certain sperm cells.

Sporogenesis - the generation of a spore cell by meiosis (in heterosporous plants) or mitosis (in homosporous plants)

Megasporogenesis - creation of spores that will develop into a female gametophyte (megagametophyte)

Microsporogenesis - creation of spores that will develop into a male gametophyte (megagametophyte)

Homosporous - an organism that produces one type of spore. This spore develops into a gametophyte which can produce male and/or female gametes.

Heterosporous - an organism that produces two types of spores. These are the mega- and microspores, which develop into gametophytes capable of producing eggs or sperm, respectively.

Pteridophyte - a plant classified as a fern or lycophyte. This group is paraphyletic but is functionally important because all taxa are seedless vascular plants.

Leptosporangiate fern - ferns that produce sporangia with a long stalk that arise from a single epidermal cell. Their spore production proceeds from a single spore mother cell through four rounds of mitosis and one round of meiosis to form 64 spores.

Eusporangiate fern - ferns that produce sporangia with a short or no stalk that arise from several epidermal cells. Hundreds to thousands of spores are produced in each sporangium via meiosis.

Metacentric - a chromosome with the centromere positioned in the middle, with both arms being the same length.

Acrocentric - a chromosome with the centromere close to one end, with one arm being much longer than the other.

Telocentric - a chromosome where the centromere is at one end, causing there to be effectively only one arm rather than two.

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