Meiotic drive and genome evolution in vascular land plants

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Abstract

Meiotic drive is a deviation from Mendelian inheritance where genetic elements are preferentially inherited by the surviving egg cell. This can profoundly impact chromosome (and genome) size and structure. Across 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 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, and the three polar bodies die. 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. Here we review how meiotic drive impacts genome evolution, what we would expect to see in lineages without meiotic drive, and finally what the first homosporous plant genomes tell us about patterns of evolution concerning meiotic drive.

Introduction

Meiotic drive is a deviation from Mendelian inheritance where genetic elements are preferentially inherited by the germ line (Sandler and Novitski, 1957; Pardo-Manuel de Villena and Sapienza, 2001b). This occurs via the asymmetry of female meiosis 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 germ line (Fig 1A, Burt and Trivers, 2009; Schmerler and Wessel, 2011; Haig, 2020). In heterozygotes, a driving allele can rapidly rise to fixation by taking advantage of a functionally asymmetric meiotic spindle pole, which will be preferentially transmitted into the surviving egg cell (Pardo-Manuel de Villena and Sapienza, 2001b; Fishman and Willis, 2005; Finseth, 2023). Regardless of fitness consequences, a drive locus can become fixed in a population rapidly, sometimes within a handful of generations (e.g., Fishman and Willis, 2005). Consequently, meiotic drive can have profound impacts on the genome. 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, meiotic drive is thought to affect critical parts of the cell that would not be under selection otherwise. For example, drive can lead to increased centromere size and sequence diversity (Henikoff, Ahmad and Malik, 2001; Malik and Bayes, 2006; Zedek and Bureš, 2016; Finseth, Nelson and Fishman, 2021). Meiotic drive has been described across eukaryotes (e.g., Foster and Whitten, 1991; Lindholm *et al.*, 2016; Zedek and Bureš, 2016; Lampson and Black, 2017), but has not previously been explored as a potential mechanism for the remarkable difference in genome structure and chromosome number among vascular land plants. Meiotic drive can only occur during asymmetric meiosis—a trait of most heterosporous plants, but not homosporous plants. Therefore, meiotic drive cannot happen in homosporous lineages, and the absence of drive may be part of the reason we see such distinct genomic differences between homosporous and heterosporous plants.

Across vascular land plant lineages, there is great diversity and disparity of genome size and structure. 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). Flowering plants and some pteridophytes are heterosporous, and reproduce via separate megaspores and microspores that develop into female and male gametophytes. Female meiosis is typically asymmetric in heterosporous plants and male meiosis is symmetric (Fig. 1A, B). In contrast, most species of pteridophytes are homosporous, and they reproduce by one type of spore which germinates into a gametophyte capable of producing eggs, sperm, or both; all homosporous meiosis is symmetric (Fig. 1C). Homospory is the ancestral character state in land plants whereas heterospory is thought to have evolved as many as 11 times (Bateman and DiMichele, 1994). Importantly, the transition to heterospory is 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). An important caveat is that gymnosperms—the heterosporous seed plant lineage sister to flowering plants—have large genomes. However, they have relatively low chromosome numbers that have been fairly static over time (Li et al. in prep). Their large genome sizes are due to the accumulation of repetitive elements (e.g., Nystedt *et al.*, 2013). In addition, while gymnosperms have experienced a few potential ancient WGD events (Li *et al.*, 2015; One Thousand Plant Transcriptomes Initiative, 2019; Stull *et al.*, 2021) they may not undergo significant genome downsizing (Ickert-Bond *et al.*, 2020) and have lower rates of genome evolution relative to flowering plants (De La Torre *et al.*, 2017).

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-supported have been differences in the number of rounds of ancient whole genome duplications (WGDs) and subsequent re-diploidization (Klekowski and Baker, 1966; Wagner and Wagner, 1979; Haufler, 1987; Barker, 2013; Kinosian, Rowe and Wolf, 2022). Interestingly, homosporous and heterosporous lineages have experienced roughly the same number of rounds of WGDs, but likely different mechanisms or at least rates of diploidization (One Thousand Plant Transcriptomes Initiative, 2019; Li *et al.*, 2021; McKibben, Finch and Barker, 2024), Li et al. in prep). Following a WGD, diploidization can proceed rapidly in flowering plants via a reduction in chromosome number (dysploidy) and extensive gene deletions (Wendel, 2015; Li *et al.*, 2021). It has been proposed that pteridophytes undergo some genomic restructuring following WGDs, but their diploidization process appears to involve limited chromosome loss accompanied by gene silencing rather than deletion (Haufler, 1987; Barker, 2013), Li et al. in prep). Over the multiple rounds of WGD in their history, homosporous pteridophyte chromosome numbers have increased despite their repeated return to diploid inheritance.

In addition to the dynamics of WGDs and diploidization, we propose that meiotic drive may be an important force behind differences in genome evolution across vascular land plants, specifically due to fundamental differences in meiosis related to spore production between heterosporous and homosporous plants. Traditionally defined meiotic drive can only happen with asymmetric meiosis (Sandler and Novitski, 1957; Fishman and Willis, 2005), which is well-documented in heterosporous plants (e.g., Lindholm *et al.*, 2016; Haig, 2020; Finseth, 2023). Homosporous plants have strictly symmetric meiosis, eliminating the possibility of traditionally defined meiotic drive and any genome restructuring it can cause. Other types of drive can occur in symmetric meiosis, although these processes typically occur after meiosis and are expected to have different effects on the genome (Lindholm *et al.*, 2016). Here we review how meiotic drive impacts genome evolution across vascular land plants, what genome characteristics we would expect to see in a lineage without meiotic drive, how post-meiotic drive may be influencing pteridophyte genomes, and conclude with future directions for incorporating meiotic drive into the growing body of work on plant genome evolution.

The influence of meiotic drive on heterosporous genome structure

Meiotic drive can happen by several mechanisms, including centromere and chromosome drive. These types of drive are likely important forces shaping heterosporous plant genome structure, as they can lead to drastic changes in chromosome number and karyotype morphology. For example, centromere drive causes accelerated centromere evolution despite these structures being essential to cell division (Henikoff, Ahmad and Malik, 2001; Malik and Bayes, 2006; Zedek and Bureš, 2016). Centromere drive results from competition among chromosomes to be transmitted to a gamete during asymmetric meiosis and results in selection for particular centromere morphologies (Henikoff, Ahmad and Malik, 2001; Finseth, 2023). In angiosperms, the four meiotic products are arranged in a line with the surviving cell that becomes the gamete typically at one end (Huang and Russell, 1992; Bell, 1996). Larger centromeres have a stronger kinetochore-spindle connection, resulting in the larger centromere (and attached homolog) being preferentially moved to the end of the set of meiotic products where it becomes the egg cell

(Dudka and Lampson, 2022). Competition among chromosomes to be transmitted to the egg can lead to an increase in the centromere size to increase the strength of the kinetochore-spindle connection. While this has been demonstrated in mice, the mechanism of centromere drive may be more complex in plants (Finseth, 2023). For example, centromere size is correlated with genome size and chromosome number in plants (Bennett *et al.*, 1981; Zhang and Dawe, 2012), suggesting that centromere size does not simply increase in plants due to drive. Different proteins may mediate the strength of kinetochore attachment in plants (Talbert and Henikoff, 2022; Finseth, 2023; Majka *et al.*, 2023), but additional work is needed to understand the mechanisms at play. Although the biology of centromere drive and its impacts are complex in plants, two of the best examples of centromere-associated meiotic drive–the D locus in *Mimulus* (Fishman and Saunders, 2008) and Ab10 in maize (Dawe *et al.*, 2018)–are from flowering plants.

Driving centromeres can be part of large, non-recombining regions that harbor deleterious alleles (Finseth *et al.*, 2022). This can have major negative fitness consequences in both males and females (Fishman and Kelly, 2015) and can lead to hybrid inviability between populations (Henikoff, Ahmad and Malik, 2001; Talbert and Henikoff, 2022), but also select for chromosome fusions which reduce overall chromosome number (Pardo-Manuel de Villena and Sapienza, 2001a; Lindholm *et al.*, 2016). This is most prevalent in lineages with monocentric chromosomes, where fused centromeres directly increase the strength of the centromere-spindle fiber bond (Chmátal *et al.*, 2014; Ruckman *et al.*, 2020). For example, Robertsonian translocations are preferentially transmitted in humans despite deleterious effects (Daniel, 2002; Poot and Hochstenbach, 2021; Talbert and Henikoff, 2022). Chromosomes with a derived fusion are also preferentially transmitted in *Drosophila* (Stewart *et al.*, 2019). In *Mimulus* it is thought that chromosome fissions supported by meiotic drive are responsible for chromosome number doubling, not polyploidy (Fishman *et al.*, 2014). 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, there is increased rate variation in chromosome number evolution in monocentric (compared to holocentric) insects, which could be explained by meiotic drive being present or absent depending on the lineage (Ruckman *et al.*, 2020). Chromosome fusions favored by meiotic drive could be part of how heterosporous plants cytologically downsize following WGD; the absence of meiotic drive in homosporous plants would eliminate this process as a mechanism for genome downsizing.

To counteract the negative effects of centromere drive, centromere histone H3 (CenH3) is frequently under positive selection in lineages with asymmetric meiosis (Zedek and Bureš, 2016; Finseth, Nelson and Fishman, 2021). CenH3 mediates the attachment to the kinetochore and is thought to respond epigenetically in strong centromere drive systems and alter the strength of centromeres (Malik and Henikoff, 2002; Allshire and Karpen, 2008). Notably, CenH3 is under purifying selection in lineages with symmetric meiosis because no centromere drive is taking place (Zedek and Bureš, 2016). Centromere drive causes the rapid evolution of what is otherwise a conserved genetic element, and subsequently alters the genome in unique ways.

Like centromere drive, chromosome drive can also have strong effects on an organism's karyotype that results in changes to the morphology and number of chromosomes. In chromosome drive, different morphologies (meta-, acro-, or telocentric chromosomes) are favorably inherited depending on the system (Burt and Trivers, 2009; Dudka and Lampson, 2022). This is known to occur in mammals, where a change in the polarity of meiotic drive (i.e., which meiotic product survives) favors a specific chromosome morphology, causing rapid rearrangement of chromosome structure and number (Blackmon *et al.*, 2019). For example, in mammals, it is typical to have some species with a high frequency of metacentric chromosomes and others with a high frequency of acrocentric chromosomes (Pardo-Manuel de Villena and Sapienza, 2001b; Burt and Trivers, 2009). Such bimodal karyotypes within groups are less common in angiosperms, perhaps because the polarity of meiosis is relatively weak (Huang and Russell, 1992). Most angiosperms have symmetric karyotypes comprising mostly metacentric chromosomes (Stebbins and Others, 1971; Weiss-Schneeweiss and Schneeweiss, 2013). Some angiosperms, mainly monocots with large genomes, have asymmetric karyotypes with variable chromosome size and centromere positions (Stedje, 1989; Choi *et al.*, 2008; Hamouche *et al.*, 2010; McKain *et al.*, 2012). Research in the Brassicaceae suggests that an asymmetric karyotype is perhaps a transition state between two favored chromosome morphologies (Mandáková and Lysak, 2008; Lysak *et al.*, 2009). This could be created by drive if the polarity of meiosis recently changed due to a hybridization or speciation event. As part of chromosome drive, rearrangements can be preferentially transmitted by meiotic drive, as shorter chromosomes are more likely to end up in the oocyte; therefore, deletions are favored over inversions or translocations (Burt and Trivers, 2009). If one chromosome is shorter than its homolog due to gene deletion it may be preferentially inherited via chromosomal drive. This could potentially be part of why angiosperms delete genes quickly following diploidization.

In summary, centromere and chromosomal drive influence genome structure by the preferential, non-Mendelian inheritance of chromosomes with particular features. The specific traits favored by drive depend on the biological system, but some favored features include larger centromeres, diverse centromeres, particular centromere positions, a diversity of chromosome rearrangements and structure, plus smaller genomes and chromosomes. 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 variation in the potential mechanisms of meiotic drive. These include monosporic megasporogenesis, where one of four one-nucleate cells result survives; disporic megasporogenesis, where one of two two-nucelate cells survives; and tetrasporic megasporogenesis where one four-nucleate cell develops to form the embryo sac (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 less strong than in the other two types of megasporogenesis. Interestingly, megasporogenesis in heterosporous ferns could potentially have stronger meiotic drive than in seed plants. Megasporogenesis in the fern *Marsilea* produces eight tetrads of megaspores, and in each tetrad just one megaspore survives. However, of the eight total megaspores, only one survives to maturity (Bell, 1981). Instead of 1/4 of potential megaspores surviving in angiosperm monosporic sporogenesis, in *Marsilea* only 1/32 megapores are ultimately viable. Interestingly, spores are produced in a tetrad with no polarity as to which megapore survives (Bell 1985). In any case, the potential for meiotic drive may be part of the reason heterosporous plants, in particular angiosperms, have a large diversity of genome organization that evolves relatively rapidly. Competition among centromeres and chromosomes in plant lineages with meiotic drive may lead to lower chromosome numbers especially if fusions are favored in their drive systems. In contrast, the absence of meiotic drive in homosporous plants could be why we see a 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—cannot be influenced by traditionally defined meiotic drive. Female meiotic drive requires asymmetric meiosis for the preferential inheritance of certain genetic elements to the egg or megaspore. 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. 1C). 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). In these plants without meiotic drive, we expect to see relatively slow rates of centromere evolution, limited selection pressure on chromosome size and morphology, and larger genomes.

Previous work has shown that centromere drive is not present in lineages with symmetric meiosis (Zedek and Bureš, 2016). Evidence for this comes from molecular evolutionary analyses of histones, in particular CenH3. In lineages with asymmetric meiosis, CenH3 is often rapidly evolving with signals of positive selection, but evolutionary constrained and under purifying selection in organisms with symmetric meiosis (Zedek and Bureš, 2016; Finseth, Nelson and Fishman, 2021). This is thought to be a result of centromere histones rapidly evolving to counteract the changes caused by centromere drive. Rapid histone evolution is not expected or observed in lineages with symmetric meiosis because centromeres are conserved in the absence of meiotic drive. It is not yet possible to analyze the centromeres of homosporous fern and lycophyte genomes because they have proven difficult to detect in these large and repetitive genomes (F.-W. Li, Pers. Com). If centromere drive occurs in any of these species, we would expect to see large, diverse, and potentially growing centromeric regions with rapid evolution of centromere histones (Malik and Bayes, 2006; Zedek and Bureš, 2016).

The absence of centromere or chromosome drive in homosporous plants means no preferential inheritance of certain karyotypes, chromosome morphologies, or rearrangements (Burt and Trivers, 2009). This 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 (Li et al. in prep). 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 resulting in little selection pressure on various features of their chromosomes. Despite the extensive research on pteridophyte cytology (e.g., Manton 1950), limited information has been published on their chromosome morphology. From this small dataset (Table 1), we see several taxa with mostly acrocentric chromosomes. Although it is hard to draw meaningful conclusions without more data, it is worth noting that in some lineages with meiotic drive, Robertsonian translocations lead to the fusion of acrocentric chromosomes to form metacentric chromosomes with increased centromere size and strength (Daniel, 2002; Dudka and Lampson, 2022). The frequency of acrocentric chromosomes reported here may be evidence that meiotic drive is indeed not happening in homosporous ferns and lycophytes. 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.

Although meiotic drive may not occur in homosporous plants, other types of drive can operate in organisms with symmetric meiosis. These types of transmission ratio distortion occur post-meiotically, and so are different from the classical definition of 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. This has been characterized in fungi, and occurs when a particular haplotype kills spores with an alternative haplotype (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 haplotype. Similar spore production occurs in pteridophytes 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 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). Studies have shown that 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 spores disperse from one another, the less selective pressure for spore drive (Lindholm *et al.*, 2016), although no studies to date have looked at this type of spore competition in ferns and lycophytes.

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 another genotype regardless of the fitness consequences (Rice, 2013; Lindholm *et al.*, 2016). There is limited research on fern sperm competition, but observational studies note 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 other plant lineages with flagellate sperm.

Because of fundamental differences in meiosis, meiotic drive cannot happen in homosporous pteridophytes in the same way as in heterosporous plants. Post-meiotic drive can still influence the genomes of homosporous plants by removing certain genotypes but likely does not shape the genome in the same ways as 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; Li *et al.*, 2024), giving us insight into what plant genome structure looks like without 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; Li *et al.*, 2024). An exception is *Ceratopteris richardii*, which has a rate of fractionation rivaling many angiosperm species (Nakazato *et al.*, 2006; Marchant *et al.*, 2022). Broad patterns in homosporous pteridophytes suggest that, while genic diploidization occurs, there are limited mechanisms for cytologically restructuring the genome following WGD. Thus, meiotic drive may be important for reducing chromosome number and the extensive rearrangements observed following polyploidy in flowering plant genomes compared to those of ferns and lycophytes.

Conclusions and future work

Here we have covered 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 drive can occur in homosporous lineages, but not meiotic drive, as traditionally defined, because sporogenesis is symmetric. Although the symmetry of meiosis has not been explicitly discussed before 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). 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. The rate of evolution of meiosis related genes 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 these lineages (Li et al. in prep). As expected with the absence of meiotic drive, CenH3 does not appear to be rapidly evolving in ferns and lycophytes (Zedek and Bures 2016), but the analysis combined homosporous and heterosporous genera with a mixture of symmetric and asymmetric meiosis. More focused molecular evolutionary analyses of CenH3 and other proteins in heterosporous versus homosporous plants would provide further insight into the pattern. In addition, there is a positive correlation between long terminal repeat retrotransposon (LTR-RT) insertion time with haploid nuclear genome size in pteridophytes, as well as a notable difference in insertion time between homosporous and heterosporous plants (Baniaga and Barker, 2019). LTR-RTs 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). Transposons are known to be associated with meiotic drive, although the exact transmission mechanisms depend on the system (Eickbush, Young and Zanders, 2019; Vogan *et al.*, 2021). Building on these observations, future work could look more explicitly for evidence of drive or transmission ratio distortion in homosporous plants and investigate the mechanics of homosporous meiosis.

Finding natural examples of meiotic drive can be challenging, as a driving or target 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). While the drive mechanism would likely not be the same in pteridophytes as in flowering plants, detecting transmission ratio distortion in pteridophytes would be insightful and help create a path for future work.

A drive 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 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 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 in vascular plants. Population size can be a greater force on chromosome number than meiotic drive. For example, 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 (Imai *et al.*, 1986). Under minimum interaction theory, chromosome numbers are predicted to increase as more chromosomes are needed to contain the genome. Exploring ecology and natural history in homosporous plants is also 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). 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). 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 gymnsperms 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 meiotic drive systems, yet the mechanisms by which this occurs are incredibly varied (Burt and Trivers, 2009; Lindholm *et al.*, 2016; Saupe and Johannesson, 2022). Therefore, if meiotic drive occurs in pteridophytes it is probably distinct from 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 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. 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

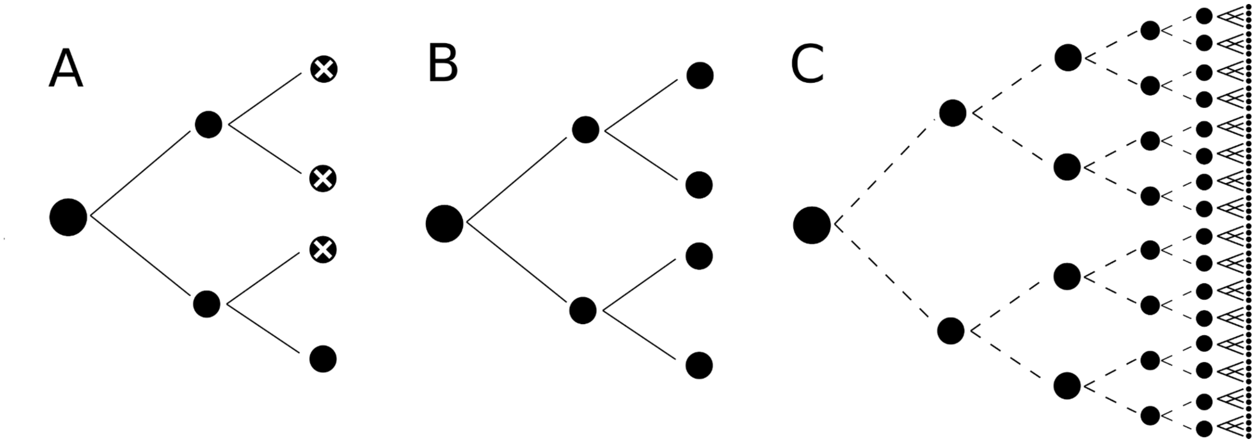

Figure 1. Examples of different types of meiosis. In each panel, the far left circle depicts the sporocyte, and succeeding divisions proceeding to the right. Solid lines indicate meiosis and dotted lines indicate mitosis. A) Heterosporous female meiosis, where only one meiotic product survives (can be on either top or bottom) and the remaining three polar bodies die; 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.

Glossary

Transmission ratio distortion - unequal inheritance of parental alleles in the offspring population

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

Spore drive - typically occurring in fungi, one haplotype will kill the alternative haplotype.

Male drive - biased transmission which occurs during or after male meiosis. This 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 important functionally 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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