

Polyploid Speciation

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Key Points

- Ploidy describes the number of genomic copies carried within a cell: one (haploidy), two (diploidy), or more than two (polyploidy).
- Polyploidy has contributed to the rich diversity of life, with ancient polyploidization events (paleopolyploidy) inferred to have occurred early in the evolution of angiosperms, teleost fishes, vertebrates, and yeast, along with numerous recent events (neopolyploidy).
- Increases in ploidy (polyploidization) cause a suite of phenotypic changes and create a reproductive barrier between a newly formed species and its parents, due to the reduced fitness of hybrid offspring with unmatched chromosome sets (e.g., triploids).
- While polyploidization is a mechanism that facilitates speciation, this reproductive barrier is often incomplete, with gene flow augmenting genetic variation in newly formed polyploid populations.
- There is strong evidence that polyploidization facilitates the evolution of new (polyploid) species from their diploid parental species (“Type I Polyploid Speciation”).
- There is, however, mixed evidence about how polyploidy impacts speciation and extinction rate of lineages that descend from a polyploidization event (“Type II Polyploid Speciation”).
- Phylogenetic analyses indicate that polyploid plant species tend to diversify slower than their diploid relatives.
- Using genomic data to date paleopolyploidization events suggests that polyploid lineages may increase diversification in some lineages of plants, although causality is challenging to determine.

Glossary

Allopolyploid - A polyploid formed by the combination of genomes from two different species.

Autopolyploid - A polyploid formed by the combination of genomes from within a single species (from the same or different parental individuals).

Diploid - Having two sets of each chromosome. For example, humans are diploid (the majority of our cells have two sets of chromosome, one from each of our parents).

Diversification rate - The net rate at which a group of species grows in number. The diversification rate equals the speciation rate minus the extinction rate.

Haploid - Having one set of each chromosome (as found in the eggs and sperm of mammals). For example, the leafy green parts of most mosses are haploid.

Homolog/homeolog - Chromosome pairs inherited from one’s mother and father are known as “homologs” (e.g., the two X chromosomes in a daughter are homologs). Chromosomes that are similar to each other because they both descend from a polyploidization event are known as “homeologs”.

Minority cytotype exclusion - The idea that when there is a mixture of ploidy levels within a population, the rarer type would tend to disappear because it more often mates with another ploidy level, producing offspring of intermediate ploidy and lower fitness (i.e., it suffers from a triploid block).

Neopolyploidy - A polyploidization event that occurred in the recent past.

Paleopolyploidy - A polyploidization event that occurred in the distant past. It is typically reserved for events that happened long enough ago that they have to be inferred from data other than chromosome counts alone.

Ploidy - The number of complete chromosome sets a cell contains. E.g., a human egg cell contains one set whereas the cells of an adult human have two sets.

Polyploid - Having more than two sets of each chromosome in the majority of cells of an organism (3 sets = triploid, 4 sets = tetraploid, 5 sets = pentaploid, 6 sets = hexaploid, etc.).

Polyploidization - The process by which an organism (or cell) has more genome copies than did its progenitors.

Triploid block - The idea that triploids prevent the establishment of polyploids because of their low viability and fertility. In particular, if newly formed tetraploids are rare they might predominantly mate with diploid relatives and produce only low fitness (or sterile) triploids.

Triploid bridge - The idea that triploids may provide an important stepping stone to the establishment of tetraploids because they can produce some haploid, diploid, or triploid gametes that can combine with the gametes from other individuals in a population to generate additional polyploid individuals. The triploid bridge also increases gene flow between ploidy levels and introduces genetic variation to the polyploids.

Unreduced gametes - The production of gametes that have not undergone the normal process of reductive division, such that the gamete has the same number of chromosomes as the parent instead of half the number.

Abstract

Genome duplication represents a dramatic, yet relatively common, genomic change, having occurred in the evolutionary history of angiosperms, vertebrates, and yeast, among many other groups. The result of such duplications (“polyploidy”, the existence of multiple complete sets of chromosomes within the genome) has long been recognized and was implicated as a rapid route to speciation starting nearly a century ago. We review recent studies that clarify how often polyploid species form from their diploid relatives, as well as studies that investigate the impact of polyploidization on the diversification of descendant species—these two distinct processes are often conflated under the umbrella of “polyploid speciation”. Although the contribution of polyploidization to evolutionary processes is becoming increasingly clear, we conclude with a discussion of what remains unknown about the contribution of polyploidization to the formation of new species.

Introduction

Particularly remarkable is it that tetraploids while crossing with each other, yield a sufficient quantity of seeds, but in crosses with [the progenitor diploids] almost no formation of seeds occurs, i.e. the tetraploid hybrids prove already singled out from the parental species

Karpechenko (1928), p. 62.

The structure and size of genomes are fluid, changing over evolutionary time via a variety of mechanisms including gene duplications, translocations, inversions, and, most strikingly, polyploidization. The “ploidy” level of an organism refers to the number of copies of each chromosome it contains: haploid for one (think of a human egg or sperm cell), diploid for two (e.g., a human adult), and polyploid for any larger number (triploid: three, tetraploid: four, pentaploid: five, etc.). Differences in ploidy are frequently observed among species, particularly in plants, with some of the most famous polyploids illustrated in [Fig. 1](#). Furthermore, individuals of different ploidy levels are often reproductively isolated from one another, leading biologists to consider “polyploid speciation” to be one of the most direct routes to the formation of new species.

Karpechenko (1928) was one of the first to describe the experimental formation of a new polyploid species, obtained by crossing cabbage (*Brassica oleracea*) and radish (*Raphanus sativus*). Both parent species are diploids with $n = 9$ (“ n ” refers to the gametic number of chromosomes—the number after meiosis and before fertilization). The vast majority of the hybrid seeds failed to produce fertile plants, but a few were fertile and produced remarkably vigorous offspring. Counting their chromosomes, Karpechenko discovered that they had double the number of chromosomes ($n = 18$) and featured a mix of traits of both parents. Furthermore, these new hybrid polyploid plants were able to mate with one another but were infertile when crossed with either parent. Karpechenko had created a new species!

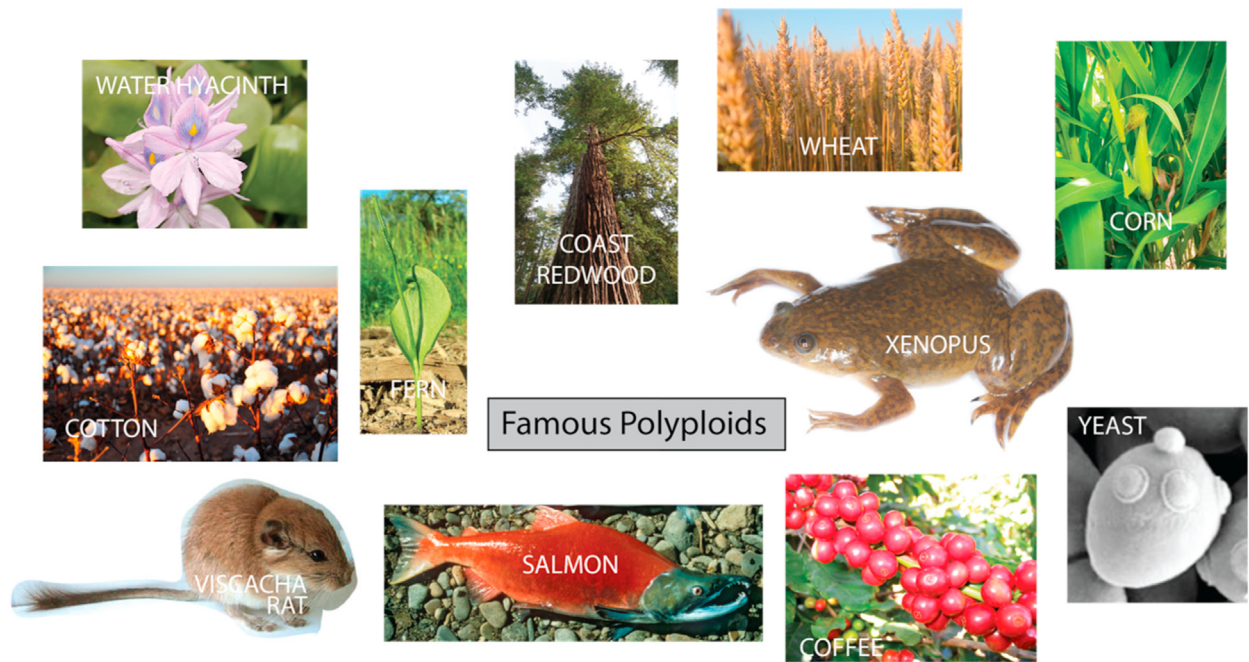


Fig. 1 Illustrated are some of the most famous polyploid species, from the beautiful but highly invasive water hyacinth to the red viscacha rat, considered to be one of the few potentially polyploid mammals. Also shown is a fern in the genus *Ophioglossum*, which varies widely in gametic chromosome number (from $n = 30$ to 720 in *O. reticulatum*, the current record holder for most chromosomes) due to multiple rounds of polyploidization (Khandelwal, 1990).

This newly formed species, now called radicle and used as a crop for animal fodder, represents an “allopolyploid,” as coined by Kihara and Ono (1926)—it is a polyploid formed by the union of genomes from different species. Not all polyploids form in this way. An alternative possibility, “autopolyploidy,” refers to the increase in ploidy level within a species. These categories are not absolute, however, because polyploids may form from crosses between subspecies or distant populations of a single species and thus be intermediate between “pure” allopolyploids and “pure” autopolyploids.

Polyploids are common in nature, especially in plants, and many of our most economically important plants—including crop species and destructive weeds—are polyploids (Fig. 1). For example, estimates suggest that 35% of vascular plants are recent polyploids (“neopolyploids”), having doubled in genome size since their genus arose (Wood et al., 2009). Moreover, if one goes back far enough, all seed plants (Jiao et al., 2011) and tetrapods (i.e., four-limbed vertebrates, including humans; Postlethwait et al., 1998) have descended from polyploid ancestors.

Polyploidy is thought to play a major role in speciation for two reasons. The first is that chromosome doubling typically causes polyploids to be reproductively incompatible with their diploid parents, with crosses between them failing or leading to low fitness offspring (e.g., triploids, which are often sterile). Consequently, polyploidy could be a rapid route to reproductive isolation, reducing gene flow between newly formed polyploids and their parental populations, and hence taking a key step towards speciation. In the extreme case, such as Karpechenko found with radicle, the new polyploid may be fully isolated from its parents. The second reason is that polyploids often differ phenotypically from their diploid parents. These differences can be the immediate consequence of a doubled genome size (see next section) or a consequence of bringing genes from different parents together into the same polyploid genome. If a polyploid combines genetic adaptations from its two parents, it may outperform both, at least in some environments. When chromosomes from each parent segregate separately (as illustrated by red and blue chromosomes in Fig. 2D), polyploid hybrids can maintain the attributes from both parental genomes together for long periods of time (“fixed heterozygosity”), perpetuating the advantages displayed by some hybrids (“hybrid vigor”). Furthermore, polyploids often avoid the sterility problems that can plague diploid hybrids by balancing the contributions of each genome and providing each chromosome with a closely related partner (a homolog) for pairing in meiosis.

Given the prevalence (and apparent success) of numerous polyploid species and the ease with which changes in ploidy can contribute to reproductive isolation, it is natural to assume that polyploidy has played an important and broad role in speciation. In this article, we discuss the current evidence for polyploid speciation and its consequences. We address two distinct but related questions. What role do *ploidy changes* play in speciation (i.e., in the instantaneous formation of new species)? And what influence does polyploidy have on subsequent speciation events (i.e., do polyploid species, *once formed*, have a greater or lesser tendency to speciate)? The answer to these questions requires that we distinguish two types of polyploid species: those formed by polyploidization from lower ploidy levels (Type 1) and those formed by speciation of polyploid species without a change in ploidy (Type 2).

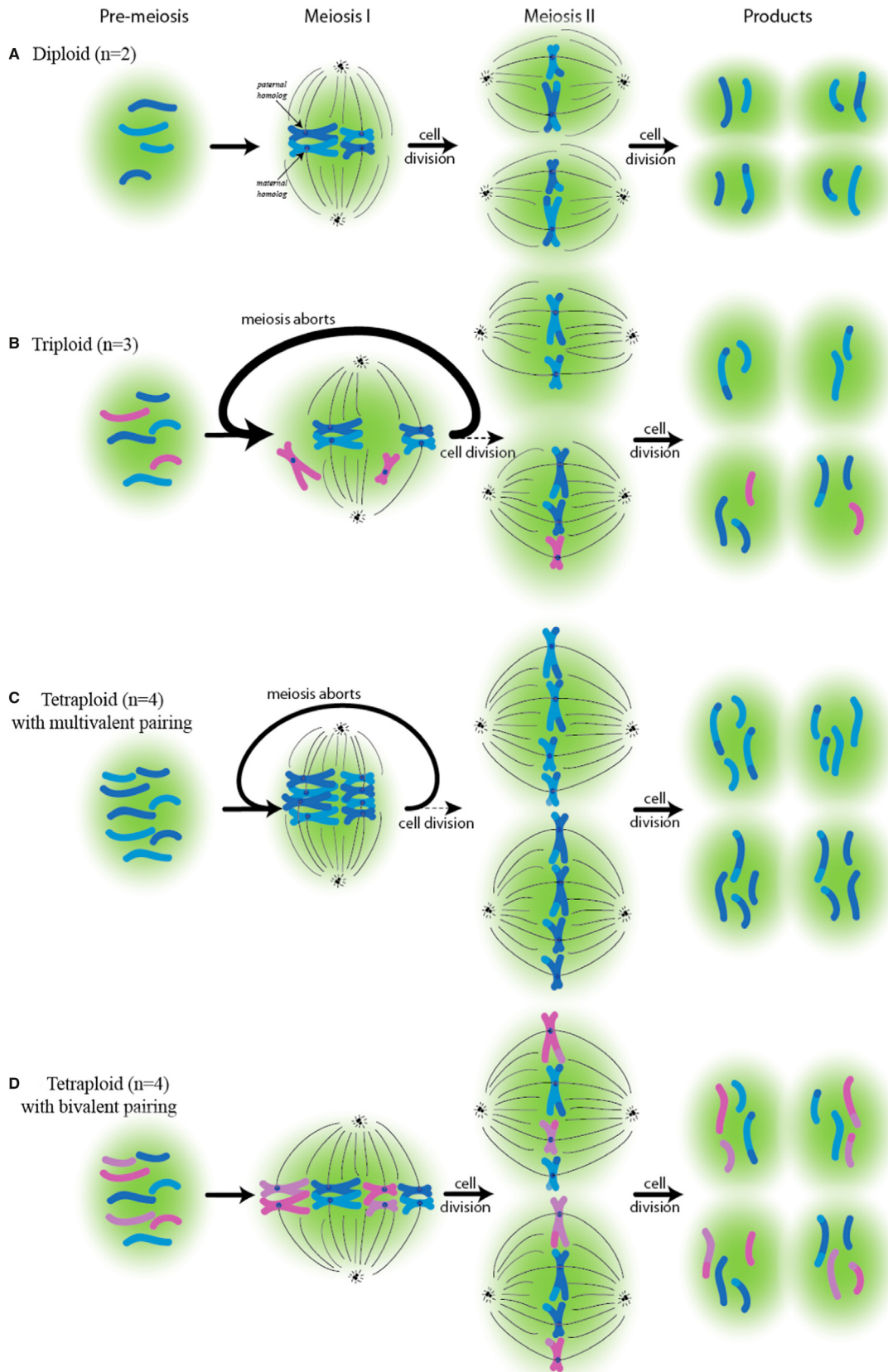


Fig. 2 The segregation of chromosomes in diploids (A), triploids (B), and tetraploids (C, D). Tetraploid segregation patterns are shown both for the case where all four sets of chromosomes come together at metaphase (“multivalent formation”, C) and where only two sets come together (“bivalent formation”, D). While meiosis is more likely to proceed normally via bivalent formation in allopolyploids, autopolyploids also frequently exhibit bivalent meiosis (Ramsey and Schemske, 2002).

Type I Polyploid Speciation: The Formation of New Species by Polyploidization

Mechanisms of Polyploidization

Before discussing the impact of polyploidy on speciation, we briefly review the mechanisms by which polyploids form. An increase in ploidy level (“polyploidization”) can occur via three primary mechanisms: somatic doubling, polyspermy, and unreduced gamete formation.

Somatic doubling occurs when DNA replication is not followed by a cell division. If this doubling occurs early in development, the entire (otherwise diploid) animal or plant can become tetraploid. If later in development, only part of the organism will be tetraploid. Although such tetraploid cells are often associated with cancer, they also arise normally during development in several tissues, including the heart, bone marrow, and liver in humans and other mammals (Zimmet and Ravid, 2000; Ganem et al., 2007). However, for the doubled genome to be inherited—for there to be a chance of a new species forming—the doubling must occur in the germline. There is evidence that some polyploids do form in this way, including one of the first described allopolyploids, *Primula kewensis* (Newton and Pellew, 1929). Somatic doubling is, however, thought to be a relatively uncommon route to polyploidy (Ramsey and Schemske, 1998).

Another route to polyploidization is *polyspermy*, the fertilization of an egg by more than one sperm. This mechanism is also thought to be rare in plants (Ramsey and Schemske, 1998), but it may be more common in animals. For example, in humans, polyspermy is a frequent cause of polyploid conceptions (60%); these polyploid conceptions generally do not come to term and account for a relatively large fraction (10%) of spontaneous abortions (Zaragoza et al., 2000).

Finally, the production of *unreduced gametes* through a failure in meiosis is the predominant route to polyploidy in plants (Ramsey and Schemske, 1998; De Storme and Mason, 2014) and the second most common route to polyploidy in humans (Zaragoza et al., 2000). Unreduced gametes can arise by a failure to divide during meiosis I or meiosis II (referred to as “first division restitution” and “second division restitution”, respectively; Hermesen, 1984); these two forms can be distinguished based on the pattern of segregation of markers near and far from the centromere (Fig. 3). Unreduced gametes can also arise when there is an endomitosis—an extra doubling of a cell’s genome—prior to meiosis I (“Döpp-Manton sporogenesis”; Döpp, 1932; Manton, 1950).

Through any of these mechanisms, a triploid offspring would be expected in the next generation (assuming that unreduced gametes are rare and are most likely to combine with reduced gametes). There are, however, circumstances under which the production of unreduced gametes is sufficiently common that two unreduced gametes might fuse, leading directly to tetraploidy. One such circumstance is cold shock (Fankhauser, 1945; Bogart et al., 1989; Ramsey and Schemske, 1998), which might account for the association between polyploidy and high altitude and high latitude populations. Interestingly, unreduced gametes are also more common among hybrids (Harlan and deWet, 1975; Kobel, 1996; Ramsey and Schemske, 1998), occurring at 50-fold higher rates in hybrid plants than in non-hybrids (Ramsey and Schemske, 1998). Unreduced gamete formation among hybrids is thought to be particularly important for allopolyploid formation, whereby, as in the radicle example, a mostly sterile diploid hybrid is able to produce some unreduced gametes, which, when crossed with each other, restore fertility.

The Nature of New Polyploids

The pathway by which polyploidization occurs can have a major impact on the genetic variation observed among the newly formed polyploids. For example, tetraploids formed from two unreduced gametes from the same parent (selfing) bear a maximum of two alleles across their four gene copies, whereas four alleles can be captured if the unreduced gametes come from different parents. In addition, more genetic variation is captured when several independent polyploids are formed within a population (“multiple origins”). While observing multiple polyploidization events may seem highly unlikely, circumstances that make it more likely for one polyploid to form (e.g., cold shock, hybridization, or genotypes predisposed to produce unreduced gametes), also make it more likely for multiple polyploids to form, as has been observed in several studies (Soltis and Soltis, 1999; Kaur et al., 2014; Sigel et al., 2014). Genetic diversity can be further augmented by matings between polyploids and diploid relatives. While such crosses often lead to partially sterile triploids, the few unreduced gametes produced by these triploids may contribute substantially to the number of tetraploids as well as their genetic diversity (the “triploid bridge” mechanism, Ramsey and Schemske, 1998; an analogous process can facilitate gene flow among higher ploidy levels, Ptáček et al., 2023). For all of these reasons, young polyploid populations may not be as genetically depauperate as one might initially expect.

Phenotypically, newly formed polyploids often differ from their diploid progenitors. The most reliable phenotypic difference is increased cell size (Cavalier-Smith, 1978). Larger cell size can lead to larger body size in multicellular organisms, an association common in invertebrates, sometimes observed in plants, but rarely found in vertebrates (Otto and Whitton, 2000). In addition, polyploidization can affect development time, with polyploids often taking longer to develop (Ramsey and Schemske, 1998; Otto and Whitton, 2000). In plants, newly formed polyploids often differ from their diploid progenitors in morphology (e.g., thicker leaves), reproductive characters (e.g., larger flowers and later flowering times), and physiology (e.g., altered water transpiration and photosynthesis; Ramsey and Schemske, 1998). Ecologically, diploids and polyploids often differ in resistance to pests and pathogens (e.g., Van de Peer et al., 2021; Mehlferber et al., 2022), sensitivity to nutrient stress, susceptibility to drought, and tolerance of extreme abiotic conditions (heat, cold, etc.; Levin, 1983; Van de Peer et al., 2021). Many of these differences are idiosyncratic (e.g., with some tetraploids being more cold tolerant and some less so), making it impossible to predict the exact phenotypic shift likely to emerge in a new polyploid.

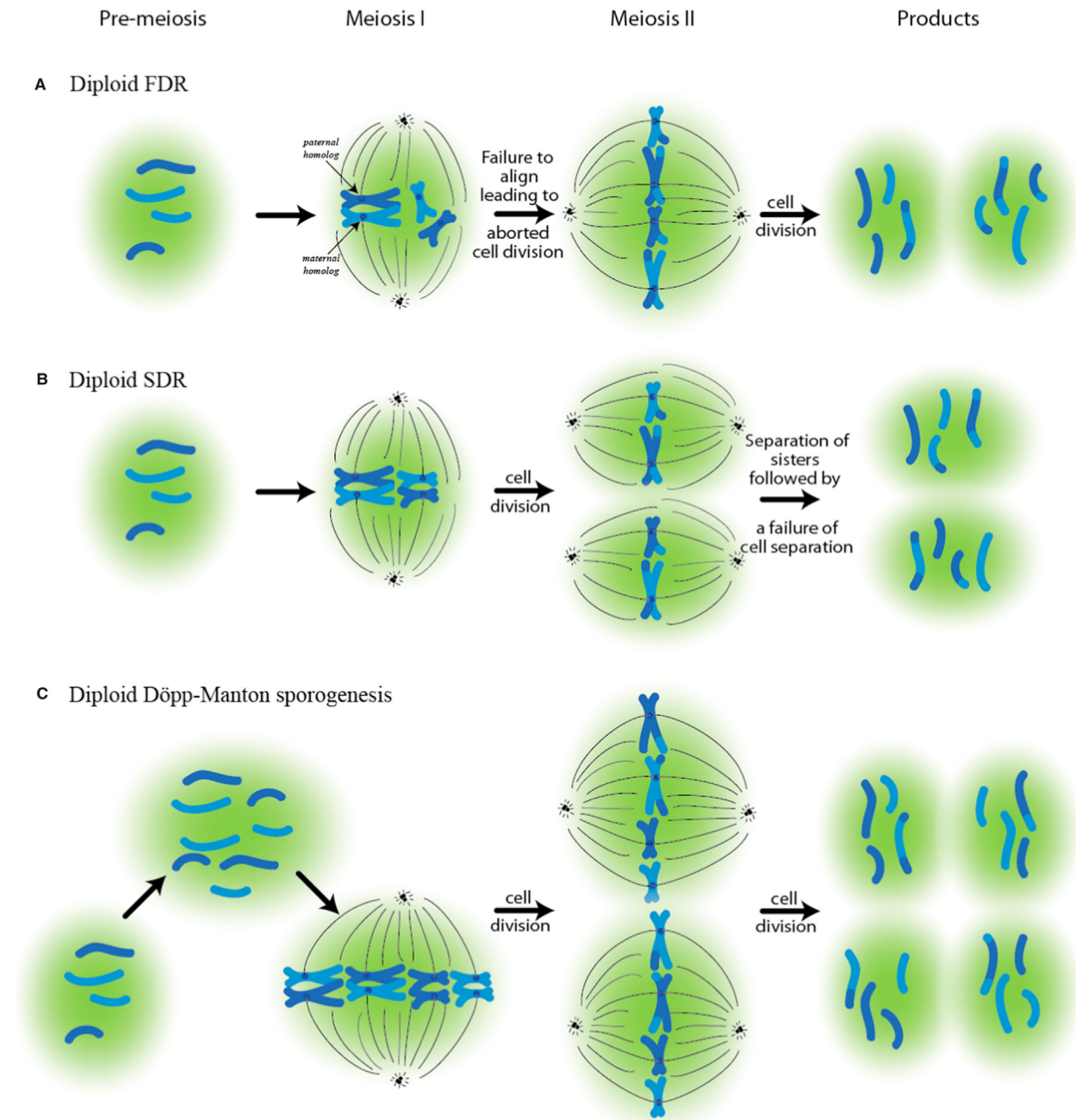


Fig. 3 Abnormal segregation patterns leading to unreduced gametes. The three panels illustrate the three main routes to unreduced gametes (Köhler et al., 2010): failure to divide the cell during meiosis I (“first division restitution”; A), failure to divide the cell during meiosis II (“second division restitution”; B), or an extra doubling of the genome prior to meiosis (“Döpp-Manton sporogenesis”; C).

What is important is that polyploids are, immediately upon their formation, phenotypically different in ways that may make them better suited to some environments and less suited to others, shifting the ecological niche or the “adaptive gestalt” of a population (Levin, 1983).

Moreover, some phenotypic shifts may additionally contribute immediately to reproductive isolation between polyploids and their diploid progenitors. For example, changes in flowering time associated with polyploidy can immediately isolate (at least partially) the new polyploids from their diploid progenitors (Husband and Schemske, 2000). Similarly, frogs in the genus *Hyla* both sing at lower frequencies (the males) and prefer lower frequency songs (the females) following increases in ploidy level, likely caused by increased cell sizes (Tucker and Gerhardt, 2012). By contributing both to ecological divergence and to reduced gene flow, polyploidization in such cases may represent a particularly easy route to speciation (a so-called “magic trait”; Coyne and Orr, 2004).

The Rate at Which New Polyploids Establish

Shifts between ploidy levels are inferred using two main signatures. The first is genomic: evidence that whole tracts of genes have been duplicated at the same point in time. This signature can last for hundreds of millions of years and is typically the information used to infer ancient polyploidization events (e.g., [Bowers et al., 2003](#); [Jiao et al., 2011](#)). The second signature is a wholesale shift in the number of chromosomes within a lineage. For example, if all species in a genus have seven chromosomes after meiosis, except one species has 14 (and roughly twice the genome size), the latter is likely polyploid. In addition, because genome doubling always yields an even number of chromosomes, excesses of even over odd gametic chromosome numbers can be used to infer rates of polyploidization. This pattern is common in plants (63.2% of ferns have even numbers, 59.4% of monocots, and 54.9% of dicots; [Otto and Whitton, 2000](#)), which, assuming a conservative estimate of how often chromosome numbers change, yields an estimate of the rate of polyploidization relative to the rate of speciation of 2%–4% in angiosperms and 7% in ferns ([Otto and Whitton, 2000](#)). A more refined approach maps chromosome number shifts along the phylogeny of a group of species. Using this approach, [Wood et al. \(2009\)](#) estimated that the rate of polyploidization was, on average, 15% that of the rate of speciation across a set of 123 angiosperm genera and 31% across 20 fern genera.

The above estimates do not account for differences in the rate of speciation and extinction between diploids and polyploids. Studies that have done so have yielded much higher estimated rates of ploidy change. For example, [Scarpino et al. \(2014\)](#) fitted a model to data from 60 genera of angiosperms. Their model estimated how much speciation and polyploidization is needed for each genus to have evolved from one species to the number of species of each ploidy level that exist today, allowing diploids and polyploids to speciate at different rates. This study inferred that, on average, diploids undergo polyploidization at a rate that is 39.9% the rate of speciation (in a model with no extinction). Performing a phylogenetic analysis that allowed for rates of both speciation and extinction to vary, [Mayrose et al. \(2011\)](#) also obtained high estimates for the rate of polyploidization: angiosperms polyploidized at a rate 29.6% that of the speciation rate, a number that rose to 41.0% for non-seed plants, averaged across 50 angiosperm and 13 non-seed plant phylogenies, mostly at the genus level.¹ These numbers were inferred using a model that assumed polyploidization occurs over time (“anagenesis”), during the evolution of a lineage. An alternative model that allowed polyploidization to occur only at speciation events (“cladogenesis”) yielded similar rate estimates (29.7% for angiosperms, and 38.7% for non-seed plants; [Mayrose et al., 2011](#)). Thus, our best available inferences suggest that plant species become polyploid at roughly $\frac{1}{3}$ the overall speciation rate. As these analyses use data from within genera, they only estimate rates from the relatively recent past and do not account for polyploidization rate variation over time. Indeed, it has been argued that times of environmental stress may increase the rate of polyploidization, with evidence of an excess of polyploidization events dating back to the Cretaceous–Paleogene boundary, a time of massive environmental upheaval and widespread extinction ([Vanneste et al., 2014](#)).

An important and still largely open question is how often these polyploidization events involve hybridization between species versus arise within a species (i.e., allo- versus autopolyploidy). Of the above studies, only [Scarpino et al. \(2014\)](#) attempted to tease apart the nature of the polyploids; they found that allopolyploidy was roughly four times more common than autopolyploidy. This inference conforms to the traditional view that autopolyploid species should form less frequently because they suffer reduced fertility due to multivalent formation during meiosis ([Fig. 2C](#); [Clausen et al., 1945](#); [Stebbins, 1971](#)). It is also consistent with phylogenetic studies of groups with lots of polyploids, which tend to find a preponderance of allo- versus autopolyploids (e.g., [Doyle et al., 2003](#); [Brysting et al., 2007](#); [Rothfels et al., 2014](#); [Patel et al., 2023](#)). On the other hand, estimates of autopolyploid speciation may be biased downwards because autopolyploids are frequently overlooked as unique species due to their morphological similarity to diploid progenitors, even if they satisfy the conditions of most species concepts ([Soltis et al., 2007](#)). Indeed, recent studies suggest that autopolyploids may form and establish at high rates ([Ramsey and Schemske, 1998, 2002](#); [Barker et al., 2016](#)) and autopolyploid speciation may be more common than previously thought ([Parisod et al., 2010b](#)). Future studies are needed to quantify more precisely the contribution of allopolyploidy and autopolyploidy to polyploid speciation.

The Role of Polyploidization in the Formation of Species

In the previous subsection, we discussed estimates of the rate at which polyploid species arise. Here, we tackle the more difficult question: to what extent is the change in ploidy, itself, responsible for the formation of new species?

Because newly formed polyploids can be reproductively isolated from their diploid progenitor species, as exemplified by radicle, and because many closely related species differ in ploidy level ([Wood et al., 2009](#)), it is often assumed that polyploidization drove speciation for all species pairs that differ in ploidy. For example, in the fern genus *Pteris*, [Chao et al. \(2012\)](#) found that 40 out of 106 studied species were polyploid and concluded that these were the result of polyploid speciation. An alternative, however, is that new species form via mechanisms that are not associated with ploidy shifts (e.g., the accumulation of genetic incompatibilities in isolated populations), with the ploidy shifts occurring independently over evolutionary time (anagenesis). In the only study to examine this question across many groups of plants, [Zhan et al. \(2016\)](#) assessed whether polyploidization and speciation in plants are temporally correlated, as expected when polyploidization contributes to the speciation process (cladogenesis), or if they are uncorrelated in time (anagenesis). While there was substantial uncertainty in the rates, 10x more genera supported the inclusion

¹Calculated from the rates reported in the supplementary materials of Mayrose et al.

of cladogenetic change (instead of only anagenetic change) than vice versa, suggesting that ploidy shifts may often co-occur with speciation (Zhan et al., 2016).

Ideally, we would learn about the role of polyploidization in the generation of new species by directly observing the process of speciation. Unfortunately, we typically only have snapshots at different stages in different taxa. There have, however, been studies that explore very closely related taxa and measure the contributions of various features, including ploidy differences, to reproductive isolation. For example, one study of diploid and tetraploid subspecies of fireweed, *Chamaenerion angustifolium*, found that the reproductive isolation between them was almost entirely (98%) due to mechanisms like pollinator differences and preferences for high versus low elevation habitats: little of the observed reproductive isolation was due to the hybrid sterility typically assumed to prevent gene flow between diploids and polyploids (Husband and Sabara, 2004; Martin and Husband, 2013).

This case illustrates many of the problems facing scientists investigating polyploid speciation. For one, it is difficult to know what mechanisms acting to separate species today were important in driving or facilitating their initial divergence. Did fireweed divide into high and low elevation habitats, and subsequently there happened to be a polyploidization event whose descendants came to dominate the lower elevation population, or did polyploidization facilitate the initial divergence? A second problem is that, even if polyploidization was the first step toward speciation, it is hard to know which features of the new polyploids mattered most. It could be that the critical feature was an altered morphology or ecological tolerance of the polyploid, not its genetic incompatibility with the diploids. If polyploids form often enough (estimated at a frequency of 0.24% in fireweed; Husband and Sabara, 2004) and if they have an advantage over the diploids in certain habitats, then eventually a self-sustaining population of polyploids may colonize sites beyond the range—and niche—of the diploid. Here, for example, polyploids may have established because they can better survive at lower elevations; the sterility of crosses between polyploids and diploids may have been largely irrelevant.

The view that polyploidy provides an “instantaneous” reproductive barrier between species is based largely on the assumption that crosses between diploids and tetraploids will generate infertile triploids (the “triploid block”). Having an odd number of chromosome sets can reduce fertility, because meiosis either fails in the absence of paired chromosomes or proceeds but leads to gametes without a full set of chromosomes (“aneuploidy”; Fig. 2B). Nevertheless, this view is now considered too absolute: inter-ploidy hybrids need not be completely sterile, and even if they are, other routes can allow gene flow between populations of different ploidy levels (Soltis and Soltis, 1989).

In fact, rather than causing a block, triploids may provide an important genetic connection between different ploidy levels—a “triploid bridge”—particularly in the early phases when a new tetraploid population is first establishing (Bever and Felber, 1992; Husband, 2004; Rieseberg and Willis, 2007). Triploids can facilitate tetraploid establishment by occasionally producing unreduced (triploid) gametes that fertilize a normal haploid gamete to produce a new tetraploid individual or by producing partially reduced (e.g., diploid) gametes that can combine with a diploid gamete produced by a tetraploid—in either case, genetic material can flow to the tetraploid population, contributing to genetic diversity of the polyploid. An increasing number of empirical studies have documented gene flow between ploidy levels, including gene flow from diploids to both auto- and allopolyploids (Slotte et al., 2008; Parisod et al., 2010b; Jørgensen et al., 2011; Ptáček et al., 2023).

Of course, even if reproductive isolation is initially incomplete, selection acting on new polyploid populations will favor stronger reproductive barriers to avoid the production of sterile (or partially sterile) triploid offspring. This process—selection favoring the evolution of greater degrees of reproductive isolation to avoid wasting gametes on low-fitness hybrids—is referred to as reinforcement and is expected to be particularly relevant to the establishment of new polyploids, which might otherwise breed repeatedly with their diploid progenitors until they go extinct (“minority cytotype exclusion”; Levin, 1975; Butlin, 1987).

In addition to the issue of reproductive isolation between a polyploid and its diploid progenitors, another consideration is how polyploids affect gene flow between diploids. The triploid bridge, for example, might allow introgression (via an allopolyploid) of genes between two parental species that are otherwise genetically isolated. Similarly, if two diploid species are reproductively isolated but both generate autotetraploids that are more compatible, then alleles from one diploid species may enter the other by first introgressing through crosses among the polyploids (as modelled by Kauai et al., 2024). The opposite is also possible, however, if polyploid hybrids replace inter-fertile diploid hybrids at points of contact between two species and reduce gene flow between them (e.g., through increased meiotic breakdown in triploid progeny). Both of these outcomes are theoretically possible, but whether polyploids tend to facilitate or hinder divergence between parental diploid species is an interesting open question.

Type II Polyploid Speciation: The Speciation of Polyploids

The Influence of Ploidy on Diversification Rates

Another way that polyploidy can impact speciation, aside from the formation of new species by ploidy changes, is by altering the rate of speciation. Whether polyploid species themselves form new species (or go extinct) more or less often than their non-polyploid relatives is a question with a rich and contentious history. Early evolutionary biologists tended to believe that, while polyploids may form frequently, they rarely themselves speciated and instead tended to go extinct: they were “evolutionary dead-ends” (Stebbins, 1950; Wagner, 1970). This opinion was informed, in part, by the belief that the “extra” genomes of polyploids would mask mutations from selection (as most mutations are recessive), reducing the efficacy of selection and ultimately making polyploids less adaptable (Stebbins, 1950). However, there are also theoretical arguments in favour of polyploids speciating more frequently or going extinct more slowly. For example, by uniting multiple genomes, polyploids often exhibit greater enzymatic variability (Roose and Gottlieb, 1976) and maintain higher levels of heterozygosity, which has the potential to increase evolutionary

flexibility (Mable and Roberts, 1997; Petit and Thompson, 1999; Parisod et al., 2010a, 2010b) and promote diversification (Stebbins, 1985; Ricklefs and Renner, 1994). Polyploids may also benefit from the redundancy inherent in polyploidization in that they have “back-up” copies of each gene if ever one is damaged (and thus they may go extinct more slowly) and because these “extra” gene copies, even if initially identical, are available to be molded by selection for different uses (Ohno, 1970; Zhang, 2003; Des Marais and Rausher, 2008), potentially increasing speciation rates. For example, Hofberger et al. (2013) argue that polyploidy allowed the evolution of a key group of defensive compounds in the mustard plant family, Málaga-Trillo and Meyer (2001) similarly link the extensive body plan variation in fish to rounds of ancestral polyploidy, and Qi et al. (2021) found that duplicate genes remaining from past polyploidization events contributed disproportionately to adaptations during the domestication of various *Brassica rapa* crops.

Polyploids may also have increased diversification rates if reproductive isolation builds more rapidly between their populations. Because most mutations that affect fitness are deleterious, the probable fate of a duplicate gene pair is the silencing of one of its members. If different copies of an important gene are silenced in two populations, offspring of a cross between those populations will have reduced fitness because some of their progeny will not inherit any functional copies. Because this “reciprocal silencing” or “divergent resolution” can happen at multiple loci, isolated polyploid populations may rapidly lose the ability to produce fertile hybrids with each other (Werth and Windham, 1991; Taylor et al., 2001).

These theoretical links between polyploidy and elevated diversification rates are seemingly supported by four main empirical observations. First, clades with a higher percentage of polyploids tend to contain more species (Petit and Thompson, 1999; Otto and Whitton, 2000; Vamوسي and Dickinson, 2006), although this pattern may simply reflect the fact that small young clades have not had time to accumulate polyploids, or that clades that speciate by both polyploidization (Type I polyploid speciation) and diploid divergence are larger than those that speciate by diploid diversification alone. Second, extant polyploids can be highly ecologically successful relative to their diploid relatives (Hahn et al., 2012; Te Beest et al., 2012), while their related diploids are rare, undiscovered, or extinct (e.g., Grusz et al., 2009; Beck et al., 2010). Third, studies of both paleontological and genomic data have inferred multiple “paleopolyploidy” events in the history of most major lineages (e.g., Masterson, 1994; Sidow, 1996; Wolfe and Shields, 1997; Soltis, 2005; Leebens-Mack et al., 2019; Zhang C et al., 2020). Fourth, some of these paleopolyploidy events appear to have occurred at the base of major radiations (for example, at the base of the angiosperms and the base of teleost fishes), suggesting that polyploidization may have increased diversification in these lineages (Hoegg et al., 2004; De Bodt et al., 2005; Barker et al., 2008; Santini et al., 2009; Tank et al., 2015).

However, additional investigations have cast doubt on the arguments that polyploids should have increased diversification rates. At a theoretical level, the model of Muir and Hahn (2015) shows that the conditions under which reciprocal silencing leads to speciation are very restrictive, requiring nearly complete geographical isolation. The empirical arguments, likewise, are not as compelling as they first appear. For example, while clades with polyploids do tend to have more species than clades composed entirely of diploids, that pattern appears to be driven by the diploids in the mixed clades speciating more (both by forming new diploids and by creating polyploids; Mayrose et al., 2011; Scarpino et al., 2014); polyploid-only clades are no richer than their diploid-only relatives (Vamوسي and Dickinson, 2006). And the few studies to systematically examine the ecological “success” of polyploids (i.e., their ecological or geographic breadth in comparison with related diploids) fail to find any advantages for the polyploids (Petit and Thompson, 1999; Martin and Husband, 2009; Mata et al., 2023).

The paleopolyploidy arguments likewise are less convincing than they first appear. While there are numerous examples of paleopolyploidy, relatively few analyses have asked whether there are more such cases than expected given the high rate at which polyploidization occurs. Because diploids can rapidly give rise to polyploids, but not vice versa, there is a ratchet-like process of increasing ploidy levels, which can explain the prevalence of extant polyploids and of paleopolyploidy events without any need for polyploids to speciate more than diploids (Meyers and Levin, 2006). Indeed, a simulation study using empirical estimates of speciation, extinction, and polyploidy rates assuming that polyploids and diploids diversify at the same rates found that there should be approximately 4.6 to 8.9 paleopolyploidy events in the history of any given angiosperm species (Mayrose et al., 2011), more than the one to four such events thought to have occurred (Jiao et al., 2011; Zhang L et al., 2020). Thus, if anything, the number of paleopolyploidization events inferred in plants suggests that polyploids diversify at slower rates than diploids.

The related argument—that polyploidy events tend to occur at the base of major clades—suffers from problems related to the effects of incomplete sampling and extinction. Jiao et al. (2011), for example, reconstruct a paleopolyploidy event at the base of the seed plants, but the dating is imprecise, with the event occurring sometime during the approximately 100 million years between the divergence of the lycophytes from the rest of vascular plants and the divergence of the ancestor of extant gymnosperms from that of the angiosperms (Smith et al., 2010). Furthermore, if a polyploidization event leads to a number of dead-end lineages that go extinct before a subsequent event leads to a species-rich clade, polyploidy will appear to be at the base of the diverse clade, even though polyploidy did not cause higher speciation rates (Donoghue and Purnell, 2005).

Recognizing this sampling problem and also the fact that the effects of polyploidy on diversification might not be immediate (Robertson et al., 2017; Schranz et al., 2012), Tank et al. (2015) and Landis et al. (2018) explored a “lag-time” model whereby a diversification rate increase could occur a certain number of divergences (nodes in their phylogenetic tree) after the polyploidization event. A challenge with this approach is that characterizing ancient polyploidization via genomic analyses requires having species with genomic information in a clade of interest, which biases where we can infer polyploidization events towards species-rich clades (species-rich clades are more likely to have a member with genomic data available). (Tank et al. (2015)), in particular, were limited to (a small number of) confidently characterized polyploidization events. Thus, the correlation they recover between polyploidization and diversification could be spurious, reflecting the existence of more genomic information in more

diverse clades. Indeed, using a much larger phylogeny and greater numbers of inferred polyploidization events, Landis et al. (2018) found no evidence for a lag-time effect. Landis et al. (2018) did find that rates of diversification increased with the number of polyploidizations inferred in the history of a lineage, but causality is difficult to establish. This relationship could indeed reflect polyploidization driving up subsequent diversification rates (Type 2 polyploid speciation), but it may instead be an artefact of having more genomic information in larger clades, accumulating more polyploidization events by chance in highly diverse clades (when counting historical shifts in ploidy), or speciation occurring more readily in groups where polyploidization also contributes to reproductive isolation (Type 1 polyploid speciation). Overall, there is no strong evidence that paleopolyploidy events directly caused increased diversification (e.g., Smith et al., 2018).

Phylogenetic analyses within genera and families reinforce the emerging picture that, on average, polyploid lineages diversify more slowly than their diploid relatives (at least in plants; Mayrose et al., 2011; Husband et al., 2013; Román-Palacios et al., 2020). This diversification trend is driven by polyploids having both reduced speciation rates and elevated rates of extinction (Mayrose et al., 2011), which results in evolutionary trees where polyploids frequently arise but commonly go extinct, such that the majority of polyploids observed at the present are relatively young species that have yet to go extinct (e.g., see Beck et al., 2011; Escudero et al., 2014). Within this broad tendency, exceptions exist—for example, the Hawaiian silversword alliance, the New World cottons, and several species-rich clades of bamboos all appear to have radiated at the polyploid level (Carr et al., 1996; Adams and Wendel 2004; Triplett et al., 2014). Furthermore, there is some evidence that polyploid fish may diversify more rapidly than their diploid relatives (Zhan et al., 2014), in keeping with an increase in diversification associated with the genome duplication event at the base of the teleost fishes (Santini et al., 2009). In addition, much of the speciation advantage experienced by diploids may, ironically, be due to their greater ability to produce polyploid daughter species; by comparison, polyploids are relatively bad at (Type I) polyploid speciation (Mayrose et al., 2011; Scarpino et al., 2014)!

These studies, however, provide an incomplete picture of polyploid diversification and suffer from data-collection and methodological limitations (Rothfels, 2021). For example, changes in ploidy level are also often linked to other transitions, such as to asexuality or self-compatibility (Otto and Whitton, 2000; Neiman et al., 2014; Zenil-Ferguson et al., 2019), that may impact speciation or extinction rates, so it is difficult to isolate the impact of polyploidization itself (Mayrose et al., 2015). Recent technical developments hold promise for improving our ability to detect polyploids, map their occurrence across the tree of life, and infer their impact on evolution, including new efficient and high-throughput flow cytometry approaches to assess ploidy level (Loureiro et al., 2021), new models of the polyploid diversification process (such as polySEE for testing the lag-time hypothesis; Hagen and Beaulieu, 2023), new macroevolutionary approaches that better reflect the reticulate evolutionary history of polyploids (Rothfels, 2021), new methods for analysing next-generation sequence data for polyploids (e.g., Schafraan et al., 2023), and new approaches for inferring the macroevolutionary history of polyploids from genomic data (e.g., Nauheimer et al., 2021; Tiley et al., 2024; Freyman et al., 2023; Mendez-Reneau et al., 2023; Patel et al., 2023).

Conclusions

Polyploidy has contributed to the rich diversity of life, with ancient polyploidization events (paleopolyploidization) inferred to have occurred early in the evolution of angiosperms, teleost fishes, vertebrates, and yeast, along with numerous recent events (neopolyploidization) in many groups of plants and in some animals. However, the prevalence of polyploid species reflects the combination of two processes: the establishment of new polyploid species (Type 1), and the diversification of these species (Type 2), corresponding to the two main sections of this article. The interaction of these processes can be thought of as a balance, whereby new polyploid individuals are constantly added to populations, due largely to errors in meiosis or fertilization. Many of these ploidy mutants are, however, unfit and fail to leave descendants. Occasionally newly formed polyploids are successful and establish new populations. Once established, many of these new polyploid populations may form their own species, but these new species are also often unfit (at least in plants); only rarely are they able to avoid extinction and themselves speciate. That the ultimate fate of most polyploid individuals and populations is extinction does not preclude the potential for rare advantageous polyploids to have important long-term evolutionary consequences, including establishing major branches of the tree of life (Arrigo and Barker, 2012; Kauai et al., 2023; Mayrose et al., 2015; Tank et al., 2015; Zhang et al., 2020).

Much remains to be learned about the impact of polyploidization on speciation. It is clear that polyploids often differ phenotypically from their parents in ecologically important ways. It is also clear that chromosome-based reproductive isolation following polyploidization can provide an easy route to speciation (Coyne and Orr, 2004). Accumulating data suggest that this speciation route, however, is often not “instantaneous.” Indeed, the prevailing view is that a period of gene flow between diploids and recently formed polyploids assists in polyploid establishment, both by increasing genetic variation in the polyploids and by increasing the number of potential mates for polyploid individuals. Even in those cases where isolation is strong and rapid, it is unclear whether chromosomal incompatibilities or phenotypic differences are responsible for isolating the newly formed polyploid populations.

While there is a strengthening consensus that polyploid plant species tend to diversify more slowly than their diploid relatives (Mayrose et al., 2011; Arrigo and Barker, 2012; Escudero et al., 2014; Scarpino et al., 2014; Mayrose et al., 2015; but see Tank et al., 2015; Landis et al., 2018), it is unclear how widely applicable these results are to other taxonomic groups; the opposite pattern, for example, is suggested for polyploid fish (Santini et al., 2009; Zhan et al., 2014). In addition, why some polyploid lineages persist and even proliferate, while others are lost, remains unknown. Are successful polyploid lineages those that are lucky in the genes that

they brought together, the phenotypic traits they happen to exhibit, or the genetic changes that are made more likely following genome duplication (Nieto et al., 2020)?

Future research promises to clarify the role that hybridization (allopolyploidy) and environmental perturbation (Vanneste et al., 2014) play in the success or failure of polyploid lineages. Another promising area of research is to confirm the tantalizing finding that previous rounds of polyploidization inhibit subsequent rounds (Scarpino et al., 2014; Ptáček et al., 2023). Is this because rising chromosome numbers cause increasingly severe meiotic or physiological problems or because the advantages of genome doubling are stronger in small genomes, which have few genes available to take on new functions? Finally, as this review emphasizes, future research is needed to determine whether polyploid transitions are concentrated in time at speciation events, and if so, when polyploidization plays an early and/or major role in the development of reproductive isolation.

References

- Adams, K.L., Wendel, J.F., 2004. Exploring the genomic mysteries of polyploidy in cotton. *Biol. J. Linn. Soc.* 82, 573–581.
- Arrigo, N., Barker, M.S., 2012. Rarely successful polyploids and their legacy in plant genomes. *Curr. Opin. Plant Biol.* 15, 140–146. <https://doi.org/10.1016/j.pbi.2012.03.010>.
- Barker, M.S., Kane, N.C., Matvienko, M., Kozik, A., Michelmore, R.W., Knapp, S.J., Rieseberg, L.H., 2008. Multiple paleopolyploidizations during the evolution of the Compositae reveal parallel patterns of duplicate gene retention after millions of years. *Mol. Biol. Evol.* 25, 2445–2455. <https://doi.org/10.1093/molbev/msn187>.
- Barker, M.S., Arrigo, N., Baniaga, A.E., Li, Z., Levin, D.A., 2016. On the relative abundance of autopolyploids and allopolyploids. *New Phytol.* 210, 391–398. <https://doi.org/10.1111/nph.13698>.
- Beck, J.B., Windham, M.D., Pryer, K.M., 2011. Do asexual polyploid lineages lead short evolutionary lives? A case study from the fern genus *Astrolepis*. *Evolution* 65, 3217–3229.
- Beck, J.B., Windham, M.D., Yatskievych, G., Pryer, K.M., 2010. A diploids-first approach to species delimitation and interpreting polyploid evolution in the fern genus *Astrolepis* (Pteridaceae). *Syst. Bot.* 35, 223–234.
- Bever, J.D., Felber, F., 1992. The theoretical population genetics of autopolyploidy. In: *Oxford Surveys in Evolutionary Biology*, pp. 185–218.
- Bogart, J.P., Elinson, R.P., Licht, L.E., 1989. Temperature and sperm incorporation in polyploid salamanders. *Science* 246, 1032–1034.
- Bowers, J.E., Chapman, B.A., Rong, J., Paterson, A.H., 2003. Unravelling angiosperm genome evolution by phylogenetic analysis of chromosomal duplication events. *Nature* 422, 433–438.
- Brystling, A.K., Oxelman, B., Huber, K.T., Moulton, V., Brochmann, C., 2007. Untangling complex histories of genome mergings in high polyploids. *Syst. Biol.* 56, 467–476.
- Butlin, R., 1987. Speciation by reinforcement. *Trends Ecol. Evol.* 2, 8–13.
- Carr, G.D., Baldwin, B.G., Kyhos, D.W., 1996. Cytogenetic implications of artificial hybrids between the Hawaiian silversword alliance and North American tarweeds (Asteraceae: Heliantheae-Madiinae). *Am. J. Bot.* 83, 653–660.
- Cavalier-Smith, T., 1978. Nuclear volume control by nucleoskeletal DNA, selection for cell volume and cell growth rate, and the solution of the DNA C-value paradox. *J. Cell Sci.* 34, 247–278.
- Chao, Y.-S., Liu, H.-Y., Chiang, Y.-C., Chiou, W.-L., 2012. Polyploidy and speciation in *Pteris* (Pteridaceae). *J. Botany* 2012, 1–7. <https://doi.org/10.1155/2012/817920>.
- Clausen, J., Keck, D.D., Hiesey, W.M., 1945. Experimental studies on the nature of species. II. Plant evolution through amphiploidy, with examples from the Madiinae. In: *Carnegie Inst. Washington*.
- Coyne, J.A., Orr, H.A., 2004. *Speciation*. Sinauer Associates, Inc, Sunderland, MA.
- De Bodt, S., Maere, S., Van de Peer, Y., 2005. Genome duplication and the origin of angiosperms. *Trends Ecol. Evol.* 20, 591–597.
- De Storme, N., Mason, A., 2014. Plant speciation through chromosome instability and ploidy change: cellular mechanisms, molecular factors and evolutionary relevance. *Curr. Plant Biol.* <https://doi.org/10.1016/j.cpb.2014.09.002>.
- Des Marais, D.L., Rauscher, M.D., 2008. Escape from adaptive conflict after duplication in an anthocyanin pathway gene. *Nature* 454, 762–765.
- Donoghue, P.C.J., Purnell, M.A., 2005. Genome duplication, extinction and vertebrate evolution. *Trends Ecol. Evol.* 20, 312–319.
- Döpp, W., 1932. Die apogamie bei *Aspidium remotum* A. Br. *Planta* 17, 86–152.
- Doyle, J.J., Doyle, J.L., Rauscher, J.T., Brown, A.H.D., 2003. Diploid and polyploid reticulate evolution throughout the history of the perennial soybeans (*Glycine* subgenus *Glycine*). *New Phytol.* 161, 121–132.
- Escudero, M., Martín-Bravo, S., Mayrose, I., Fernández-Mazuecos, M., Fiz-Palacios, O., Hipp, A.L., Pimentel, M., Jiménez-Mejías, P., Valcárcel, V., Vargas, P., Luceño, M., 2014. Karyotypic changes through dysploidy persist longer over evolutionary time than polyploid changes. *PLoS One* 9, e85266.
- Fankhauser, G., 1945. The effects of changes in chromosome number on amphibian development. *Q. Rev. Biol.* 20, 20–78.
- Freyman, W.A., Johnson, M.G., Rothfels, C.J., 2023. homologizer: phylogenetic phasing of gene copies into polyploid subgenomes. *Methods Ecol. Evol.* 14 (5), 1230–1244.
- Ganem, N.J., Storchova, Z., Pellman, D., 2007. Tetraploidy, aneuploidy and cancer. *Curr. Opin. Genet. Dev.* 17, 157–162.
- Grusz, A.L., Windham, M.D., Pryer, K.M., 2009. Deciphering the origins of apomictic polyploids in the *Cheilanthes yavapensis* complex (Pteridaceae). *Am. J. Bot.* 96, 1636–1645. <https://doi.org/10.3732/ajb.0900019>.
- Hagen, E.R., Beaulieu, J.M., 2023. Directly testing for diversification lags post-polyploidization with polySSE. In: *Prep*.
- Hahn, M.A., Buckley, Y.M., Müller-Schärer, H., 2012. Increased population growth rate in invasive polyploid *Centaurea stoebe* in a common garden. *Ecol. Lett.* 15, 947–954. <https://doi.org/10.1111/j.1461-0248.2012.01813.x>.
- Harlan, J.R., deWet, J.M.J., 1975. On Ö. Winge and a prayer: the origins of polyploidy. *Bot. Rev.* 41, 361–390.
- Hermesen, J.G.T., 1984. Mechanisms and genetic implications of 2n-gamete formation. *Iowa State J. Res.* 58, 421–434.
- Hoegg, S., Brinkmann, H., Taylor, J.S., Meyer, A., 2004. Phylogenetic timing of the fish-specific genome duplication correlates with the diversification of teleost fish. *J. Mol. Evol.* 59, 190–203.
- Hofberger, J.A., Lyons, E., Edger, P.P., Chris Pires, J., Eric, S.M., 2013. Whole genome and tandem duplicate retention facilitated glucosinolate pathway diversification in the mustard family. *Genom. Biol. Evol.* 5, 2155–2173. <https://doi.org/10.1093/gbe/evt162>.
- Husband, B.C., 2004. The role of triploid hybrids in the evolutionary dynamics of mixed-ploidy populations. *Biol. J. Linn. Soc.* 82, 537–546.
- Husband, B.C., Baldwin, S.J., Suda, J., 2013. The incidence of polyploidy in natural plant populations: major patterns and evolutionary processes. In: *Plant Genome Diversity*. Springer Vienna, pp. 255–276.
- Husband, B.C., Sabara, H.A., 2004. Reproductive isolation between autotetraploids and their diploid progenitors in fireweed, *Chamerion angustifolium* (Onagraceae). *New Phytol.* 161, 703–713. <https://doi.org/10.1046/j.1469-8137.2003.00998.x>.
- Husband, B.C., Schemske, D.W., 2000. Ecological mechanisms of reproductive isolation between diploid and tetraploid *Chamerion angustifolium*. *Ecology* 88, 689–701.
- Jiao, Y., Wickett, N.J., Ayyampalayam, S., Chanderbali, A.S., Landherr, L., Ralph, P.E., Tomsho, L.P., Hu, Y., Liang, H., Soltis, P.S., Soltis, D.E., Clifton, S.W., Schlarbaum, S.E., Schuster, S.C., Ma, H., Leebens-Mack, J., dePamphilis, C.W., 2011. Ancestral polyploidy in seed plants and angiosperms. *Nature* 473, 97–100. <https://doi.org/10.1038/nature09916>.

- Jørgensen, M.H., Ehrich, D., Schmickl, R., Koch, M.A., Brysting, A.K., 2011. Interspecific and interplodial gene flow in central European *Arabidopsis* (Brassicaceae). *BMC Evol. Biol.* 11, 346. <https://doi.org/10.1186/1471-2148-11-346>.
- Karpechenko, G.D., 1928. Polyploid hybrids of *Raphanus sativus* L. x *Brassica oleracea* L. *Mol. Gen. Genet.* 48, 2–85.
- Kauai, F., Bafort, Q., Mortier, F., Van Montagu, M., Bonte, D., Van de Peer, Y., 2024. Interspecific transfer of genetic information through polyploid bridges. *Proc. Natl. Acad. Sci.* 121 (21), e2400018121.
- Kauai, F., Mortier, F., Milosavljevic, S., Van de Peer, Y., Bonte, D., 2023. Neutral processes underlying the macro eco-evolutionary dynamics of mixed-ploidy systems. *Proc. R. Soc. A B.* <https://doi.org/10.1098/rspb.2022.2456>.
- Kaur, P., Banga, S., Kumar, N., Gupta, S., Akhatar, J., Banga, S.S., 2014. Polyphyletic origin of *Brassica juncea* with *B. rapa* and *B. nigra* (Brassicaceae) participating as cytoplasm donor parents in independent hybridization events. *Am. J. Bot.* 101, 1157–1166. <https://doi.org/10.3732/ajb.1400232>.
- Khandelwal, S., 1990. Chromosome evolution in the genus *Ophioglossum* L. *Bot. J. Linn. Soc.* 102, 205–217.
- Kihara, H., Ono, T., 1926. Chromosomenzahlen und systematische Gruppierung der Rumex-Arten. *Cell Tissue Res.* 4, 475–481.
- Kobel, H.R., 1996. Allopolyploid speciation. In: Tinsley, R.C., Kobel, H.R. (Eds.), *The Biology of Xenopus*. Oxford University Press, Oxford, pp. 392–401.
- Köhler, C., Mittelsten Scheid, O., Erilova, A., 2010. The impact of the triploid block on the origin and evolution of polyploid plants. *Trends Genet.* 26, 142–148.
- Landis, J.B., Soltis, D.E., Li, Z., Marx, H.E., Barker, M.S., Tank, D.C., Soltis, P.S., 2018. Impact of whole-genome duplication events on diversification rates in angiosperms. *Am. J. Bot.* 105, 348–363.
- Leebens-Mack, J.H., Barker, M.S., Carpenter, E.J., Deyholos, M.K., Gitzendanner, M.A., Graham, S.W., Grosse, I., et al., 2019. One thousand plant transcriptomes and the phylogenomics of green plants. *Nature* 574 (7780). <https://doi.org/10.1038/s41586-019-1693-2>.
- Levin, D.A., 1975. Minority cytotype exclusion in local plant populations. *Taxon* 24, 35–43.
- Levin, D.A., 1983. Polyploidy and novelty in flowering plants. *Am. Nat.* 122, 1–25.
- Loureiro, J., Kron, P., Temsch, E.M., Koutecký, P., Lopes, S., Castro, M., Castro, S., 2021. Isolation of plant nuclei for estimation of nuclear DNA content: overview and best practices. *Cytometry* 99, 318–327. <https://doi.org/10.1002/cyto.a.24331>.
- Mable, B.K., Roberts, J.D., 1997. Mitochondrial DNA evolution of tetraploids in the genus *Neobatrachus* (Anura: Myobatrachidae). *Copeia* 4, 680–689.
- Málaga-Trillo, E., Meyer, A., 2001. Genome duplications and accelerated evolution of Hox genes and cluster architecture in teleost fishes. *Am. Zool.* 41, 676–686.
- Manton, I., 1950. *Problems of Cytology and Evolution in the Pteridophyta*. Cambridge University Press, Cambridge.
- Martin, S.L., Husband, B.C., 2013. Adaptation of diploid and tetraploid *Chamerion angustifolium* to elevation but not local environment. *Evolution* 67, 1780–1791.
- Martin, S.L., Husband, B.C., 2009. Influence of phylogeny and ploidy on species ranges of North American angiosperms. *J. Ecol.* 97, 913–922. <https://doi.org/10.1111/j.1365-2745.2009.01543.x>.
- Masterson, J., 1994. Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* 264, 421–424.
- Mata, J.K., Martin, S.L., Smith, T.W., 2023. Global biodiversity data suggest allopolyploid plants do not occupy larger ranges or harsher conditions compared with their progenitors. *Ecol. Evol.* 13, e10231. <https://doi.org/10.1002/ece3.10231>.
- Mayrose, I., Zhan, S.H., Rothfels, C.J., Arrigo, N., Barker, M.S., Rieseberg, L.H., Otto, S.P., 2015. Methods for studying polyploid diversification and the dead end hypothesis: A reply to Soltis et al. (2014). *New Phytol.* 1–9.
- Mayrose, I., Zhan, S.H., Rothfels, C.J., Magnuson-Ford, K., Barker, M.S., Rieseberg, L.H., Otto, S.P., 2011. Recently formed polyploid plants diversify at lower rates. *Science* 333, 1257.
- Mehlförber, E.C., Song, M.J., Pelaez, J.N., Jaenisch, J., Coate, J.E., Koskella, B., Rothfels, C.J., 2022. Polyploidy and microbiome associations mediate similar responses to pathogens in *Arabidopsis*. *Curr. Biol.* 32, 2719–2729. <https://doi.org/10.1016/j.cub.2022.05.015>.
- Mendez-Reneau, J., Burleigh, J.G., Sigel, E.M., 2023. Target capture methods offer insight into the evolution of rapidly diverged taxa and resolve allopolyploid homeologs in the fern genus *Polypodium* ss. *Syst. Botany* 48 (1), 96–109.
- Meyers, L.A., Levin, D.A., 2006. On the abundance of polyploids in flowering plants. *Evolution* 60, 1198–1206.
- Muir, C.D., Hahn, M.W., 2015. The limited contribution of reciprocal gene loss to increased speciation rates following whole genome duplication. *Am. Nat.* 185, 70–86.
- Nauheimer, L., Weigner, N., Joyce, E., Crayn, D., Clarke, C., Nargar, K., 2021. HybPhaser: a workflow for the detection and phasing of hybrids in target capture data sets. *Appl. Plant Sci.* 9 (7).
- Neiman, M., Sharbel, T.F., Schwander, T., 2014. Genetic causes of transitions from sexual reproduction to asexuality in plants and animals. *J. Evol. Biol.* 27, 1346–1359. <https://doi.org/10.1111/jeb.12357>.
- Newton, W.C.F., Pellew, C., 1929. *Primula kewensis* and its derivatives. *J. Genet.* 20, 405–467.
- Nieto, F.G., Casacuberta, J., Wendel, J.F., 2020. Genomics of evolutionary novelty in hybrids and polyploids. *Front. Genet.* 11. <https://doi.org/10.3389/fgene.2020.00792>.
- Ohno, S., 1970. *Evolution by Gene Duplication*. Springer-Verlag, New York.
- Otto, S.P., Whitton, J., 2000. Polyploid incidence and evolution. *Annu. Rev. Genet.* 34, 401–437.
- Parisod, C., Alix, K., Just, J., Petit, M., Sarilar, V., Mhirir, C., Ainouche, M., Chalhoub, B., Grandbastien, M.-A., 2010a. Impact of transposable elements on the organization and function of allopolyploid genomes. *New Phytol.* 186, 37–45. <https://doi.org/10.1111/j.1469-8137.2009.03096.x>.
- Parisod, C., Holderegger, R., Brochmann, C., 2010b. Evolutionary consequences of autopolyploidy. *New Phytol.* 186, 5–17. <https://doi.org/10.1111/j.1469-8137.2009.03142.x>.
- Patel, N., Medina, R., Williams, L., Lemieux, O., Goffinet, B., Johnson, M., 2023. Frequent allopolyploidy with distant progenitors in the moss genera *Physcomitrium* and *Entosthodon* (Funariaceae) identified via subgenome phasing of targeted nuclear genes. *Evolution* 77, 2561–2575.
- Petit, C., Thompson, J.D., 1999. Species diversity and ecological range in relation to ploidy level in the flora of the Pyrenees. *Evol. Ecol.* 13, 45–66.
- Postlethwait, J.H., Yan, Y.L., Gates, M.A., Horne, S., Amores, A., Brownlie, A., Donovan, A., Egan, E.S., Force, A., Gong, Z., Goutel, C., Fritz, A., Kelsh, R., Knapik, E., Liao, E., Paw, B., Ransom, D., Singer, A., Thomson, M., Abduljabbar, T.S., Yelick, P., Beier, D., Joly, J.S., Larhammar, D., Rosa, F., Westerfield, M., Zon, L.I., Johnson, S.L., Talbot, W.S., 1998. Vertebrate genome evolution and the zebrafish gene map. *Nat. Genet.* 18, 345–349. <https://doi.org/10.1038/ng0498-345>.
- Ptáček, J., Ekrť, L., Homych, O., Urfus, T., 2023. Interploidy gene flow via a “pentaploid bridge” and ploidy reduction in *Cystopteris fragilis* fern complex (Cystopteridaceae: Polydiales). *Plant Reprod.* 36, 321–331. <https://doi.org/10.1007/s00497-023-00476-5>.
- Qi, X., An, H., Hall, T.E., Di, C., Blischak, P.D., McKibben, M.T.W., Hao, Y., Conant, G.C., Pires, J.C., Barker, M.S., 2021. Genes derived from ancient polyploidy have higher genetic diversity and are associated with domestication in *Brassica rapa*. *New Phytol.* 230, 372–386. <https://doi.org/10.1111/nph.17194>.
- Ramsey, J., Schemske, D.W., 2002. Neopolyploidy in flowering plants. *Annu. Rev. Ecol. Systemat.* 33, 589–639. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150437>.
- Ramsey, J., Schemske, D.W., 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annu. Rev. Ecol. Systemat.* 29, 467–501.
- Ricklefs, R.E., Renner, S.S., 1994. Species richness within families of flowering plants. *Evolution* 48, 1619–1636.
- Rieseberg, L.H., Willis, J.H., 2007. Plant speciation. *Science* 317, 910–914.
- Robertson, F.M., Gundappa, M.K., Grammes, F., Hvidsten, T.R., Redmond, A.K., Lien, S., Martin, S.A.M., Holland, P.W.H., Sandve, S.R., Macqueen, D.J., 2017. Lineage-specific rediploidization is a mechanism to explain time-lags between genome duplication and evolutionary diversification. *Genome Biol.* 1–14.
- Román-Palacios, C., Molina-Henao, Y.F., Barker, M.S., 2020. Polyploids increase overall diversity despite higher turnover than diploids in the Brassicaceae. *Proc. Royal Soc. B* 287 (1934), 20200962.
- Roose, M.L., Gottlieb, L.D., 1976. Genetic and biochemical consequences of polyploidy in *Tragopogon*. *Evolution* 30, 818–830.
- Rothfels, C.J., 2021. Polyploid phylogenetics. *New Phytol.* 230 (1), 66–72.
- Rothfels, C.J., Johnson, A.K., Windham, M.D., Pryer, K.M., 2014. Low-copy nuclear data confirm rampant allopolyploidy in the Cystopteridaceae (Polydiales). *Taxon* 63, 1026–1036.

- Santini, F., Harmon, L.J., Carnevale, G., Alfaro, M.E., 2009. Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evol. Biol.* 9, 194. <https://doi.org/10.1186/1471-2148-9-194>.
- Scarpino, S.V., Levin, D.A., Meyers, L.A., 2014. Polyploid formation shapes flowering plant diversity. *Am. Nat.* 184, 456–465. <https://doi.org/10.1086/677752>.
- Schafraan, P., Li, F.W., Rothfels, C.J., 2023. PURC provides improved sequence inference for polyploid phylogenetics and other manifestations of the multiple-copy problem. In: *Polyploidy: Methods and Protocols*. Springer US, New York, NY, pp. 189–206.
- Schranz, M.E., Mohammadin, S., Edger, P.P., 2012. Ancient whole genome duplications, novelty and diversification: the WGD Radiation Lag-Time Model. *Curr. Opin. Plant Biol.* 15 (2), 147–153. <https://doi.org/10.1016/j.pbi.2012.03.011>.
- Sidow, A.A., 1996. Gen(om)e duplications in the evolution of early vertebrates. *Curr. Opin. Genet. Dev.* 6, 22.
- Sigel, E.M., Windham, M.D., Pryer, K.M., 2014. Evidence for reciprocal origins in *Polypodium hesperium* (Polypodiaceae): a fern model system for investigating how multiple origins shape allopolyploid genomes. *Am. J. Bot.* 101, 1476–1485. <https://doi.org/10.3732/ajb.1400190>.
- Slotte, T., Huang, H., Lascoux, M., Cepitits, A., 2008. Polyploid speciation did not confer instant reproductive isolation in *Capsella* (Brassicaceae). *Mol. Biol. Evol.* 25, 1472.
- Smith, S.A., Beaulieu, J.M., Donoghue, M.J., 2010. An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. *Proc. Natl. Acad. Sci. U.S.A.* 107, 5897–5902.
- Smith, S.A., Brown, J.W., Yang, Y., Bruenn, R., Drummond, C.P., Brockington, S.F., Walker, J.F., Last, N., Douglas, N.A., Moore, M.J., 2018. Disparity, diversity, and duplications in the Caryophyllales. *New Phytol.* 217 (2), 836–854.
- Soltis, D.E., Soltis, P.S., Schemske, D.W., Hancock, J.F., Thompson, J.N., Husband, B.C., Judd, W.S., 2007. Autopolyploidy in angiosperms: have we grossly underestimated the number of species? *Taxon* 56, 13–30.
- Soltis, D.E., Soltis, P.S., 1989. Genetic consequences of autopolyploidy in *Tolmiea* (Saxifragaceae). *Evolution* 43, 586–594.
- Soltis, D.E., Soltis, P.S., 1999. Polyploidy: recurrent formation and genome evolution. *Trends Ecol. Evol.* 14, 348–352.
- Soltis, P.S., 2005. Ancient and recent polyploidy in angiosperms. *New Phytol.* 166, 5–8.
- Stebbins, G.L., 1950. *Variation and Evolution in Plants*. Columbia University Press, New York.
- Stebbins, G.L., 1971. *Chromosomal Evolution in Higher Plants*. Addison-Wesley Publishing Company, Reading, MA.
- Stebbins, G.L., 1985. Polyploidy, hybridization, and the invasion of new habitats. *Ann. Mo. Bot. Gard.* 72, 824–832.
- Tank, D.C., Eastman, J.M., Pennell, M.W., Soltis, P.S., Soltis, D.E., Hinchliff, C.E., Brown, J.W., Sessa, E.B., Harmon, L.J., 2015. Nested radiations and the pulse of angiosperm diversification: Increased diversification rates often follow whole genome duplications. *New Phytol.* 207 (2), 454–467.
- Taylor, J.S., Van de Peer, Y.Y., Meyer, A.A., 2001. Genome duplication, divergent resolution and speciation. *Trends Genet.* 17, 299–301.
- Te Beest, M., Le Roux, J.J., Richardson, D.M., Brysting, A.K., Suda, J., Kubsova, M., Pysek, P., 2012. The more the better? The role of polyploidy in facilitating plant invasions. *Ann. Bot.* 109, 19–45. <https://doi.org/10.1093/aob/mcr277>.
- Tiley, G.P., Crowl, A.A., Manos, P.S., Sessa, E.B., Solís-Lemus, C., Yoder, A.D., Burleigh, J.G., 2024. Benefits and limits of phasing alleles for network inference of allopolyploid complexes. *Syst. Biol.* 73 (4), 666–682.
- Triplett, J.K., Clark, L.G., Fisher, A.E., Wen, J., 2014. Independent allopolyploidization events preceded speciation in the temperate and tropical woody bamboos. *New Phytol.* <https://doi.org/10.1111/nph.12988>.
- Tucker, M.A., Gerhardt, H.C., 2012. Parallel changes in mate-attracting calls and female preferences in autotriploid tree frogs. *P Roy. Soc. B-Biol. Sci.* 279, 1583–1587. <https://doi.org/10.1111/j.1460-9568.2009.06797.x>.
- Vamosi, J.C., Dickinson, T.A., 2006. Polyploidy and diversification: a phylogenetic investigation in Rosaceae. *Int. J. Plant Sci.* 167, 346–355.
- Van de Peer, Y., Ashman, T.-L., Soltis, P.S., Soltis, D.E., 2021. Polyploidy: an evolutionary and ecological force in stressful times. *Plant Cell* 33 (1), 11–26. <https://doi.org/10.1093/plcell/koaa015>.
- Vanneste, K., Baele, G., Maere, S., Van de Peer, Y., 2014. Analysis of 41 plant genomes supports a wave of successful genome duplications in association with the Cretaceous–Paleogene boundary. *Genome Res.* <https://doi.org/10.1101/gr.168997.113>.
- Wagner Jr., W.H., 1970. Biosystematics and evolutionary noise. *Taxon* 19, 146–151.
- Werth, C.R., Windham, M.D., 1991. A model for divergent, allopatric speciation of polyploid pteridophytes resulting from silencing of duplicate-gene expression. *Am. Nat.* 137, 515–526.
- Wolfe, K.H., Shields, D.C., 1997. Molecular evidence for an ancient duplication of the entire yeast genome. *Nature* 387, 703–713.
- Wood, T.E., Takebayashi, N., Barker, M.S., Mayrose, I., Greenspoon, P., Rieseberg, L.H., 2009. The frequency of polyploid speciation in vascular plants. *Proc. Natl. Acad. Sci. U.S.A.* 106, 13875.
- Zaragoza, M.V., Surti, U., Redline, R.W., Millie, E., Chakravarti, A., Hassold, T.J., 2000. Parental origin and phenotype of triploidy in spontaneous abortions: predominance of diandry and association with the partial hydatidiform mole. *Am. J. Hum. Genet.* 66, 1807–1820. <https://doi.org/10.1086/302951>.
- Zenil-Ferguson, R., Burleigh, J.G., Freyman, W.A., Igić, B., Mayrose, I., Goldberg, E.E., 2019. Interaction among ploidy, breeding system and lineage diversification. *New Phytol.* 224 (3), 1252–1265.
- Zhan, S.H., Drori, M., Goldberg, E.E., Otto, S.P., Mayrose, I., 2016. Phylogenetic evidence for cladogenetic polyploidization in land plants. *Am. J. Bot.* 103, 1252–1258.
- Zhan, S.H., Glick, L., Tsigonopoulos, C.S., Otto, S.P., Mayrose, I., 2014. Comparative analysis reveals that polyploidy does not decelerate diversification in fish. *J. Evol. Biol.* 27, 391–403. <https://doi.org/10.1111/jeb.12308>.
- Zhang, C., Zhang, T., Luebert, F., Xiang, Y., Huang, C.H., Hu, Y., Rees, M., Frohlich, M.W., Qi, J., Weigend, M., Ma, H., 2020. Asterid phylogenomics/phylotranscriptomics uncover morphological evolutionary histories and support phylogenetic placement for numerous whole-genome duplications. *Mol. Biol. Evol.* 37 (11), 3188–3210.
- Zhang, J., 2003. Evolution by gene duplication: an update. *Trends Ecol. Evol.* 18, 292–298.
- Zhang, L., Wu, S., Chang, X., Wang, X., Zhao, Y., Xia, Y., Trigiano, R.N., Jiao, Y., Chen, F., 2020. The ancient wave of polyploidization events in flowering plants and their facilitated adaptation to environmental stress. *Plant Cell Environ.* 43, 2847–2856. <https://doi.org/10.1111/pce.13898>.
- Zimmer, J., Ravid, K., 2000. Polyploidy: occurrence in nature, mechanisms, and significance for the megakaryocyte-platelet system. *Exp. Hematol.* 28, 3–16.