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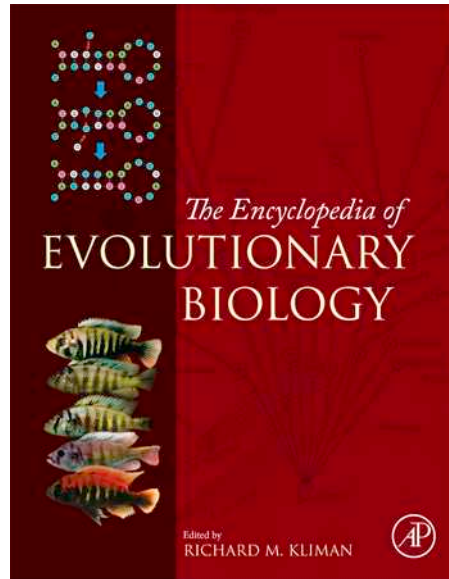
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Polyploid Speciation

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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. For example, 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.

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 [Figure 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 to either parent. Karpechenko had created a new species!

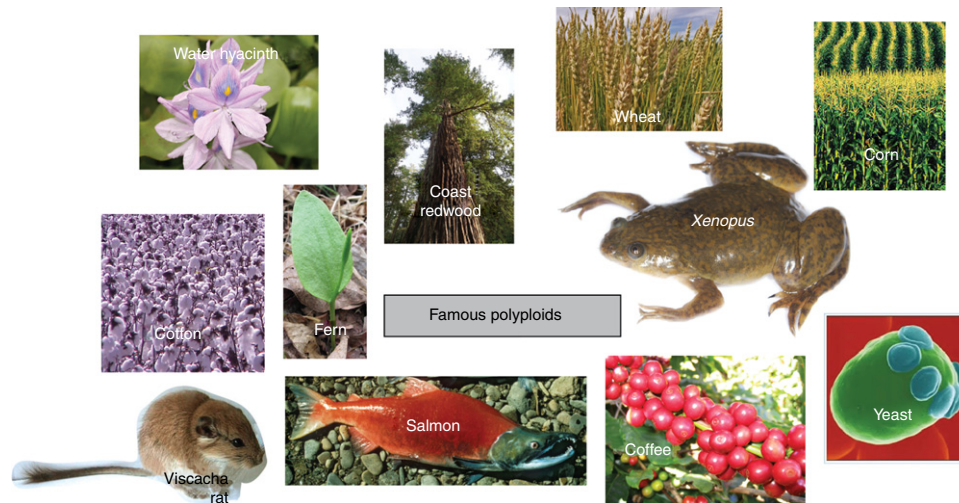


Figure 1 Illustrated are some of the most famous polyploid species, from the beautiful but highly invasive water hyacinth to the red viscacha rat, one of two known polyploid mammals. Also shown is the fern *Ophioglossum reticulatum*, the record holder for most chromosomes ($n = 720$) with about 100 copies per homologue.

This newly formed species, now called ‘radicole’ 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 absolutes, however, because polyploids formed from crosses between subspecies or distant populations may have characteristics intermediate between the two.

Polyploids are common in nature, especially in plants, and many of our most economically important plants – including both crop species and destructive weeds – are polyploids (Figure 1). For example, recent 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; 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 causes polyploids to be incompatible with their diploid parents, with crosses between them leading to low-fitness offspring (e.g., triploids). 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 toward speciation. 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 be a consequence of the polyploids combining adaptations from different parents, allowing the polyploid to outperform both parents, at least in some environments. Polyploid hybrids are particularly interesting because they can maintain both parental genomes for long periods of time (illustrated as red and blue chromosomes in Figure 2(d)), 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.

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 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 themselves)?

Polyploid Speciation I: 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’) occurs 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 (Zimmer 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,

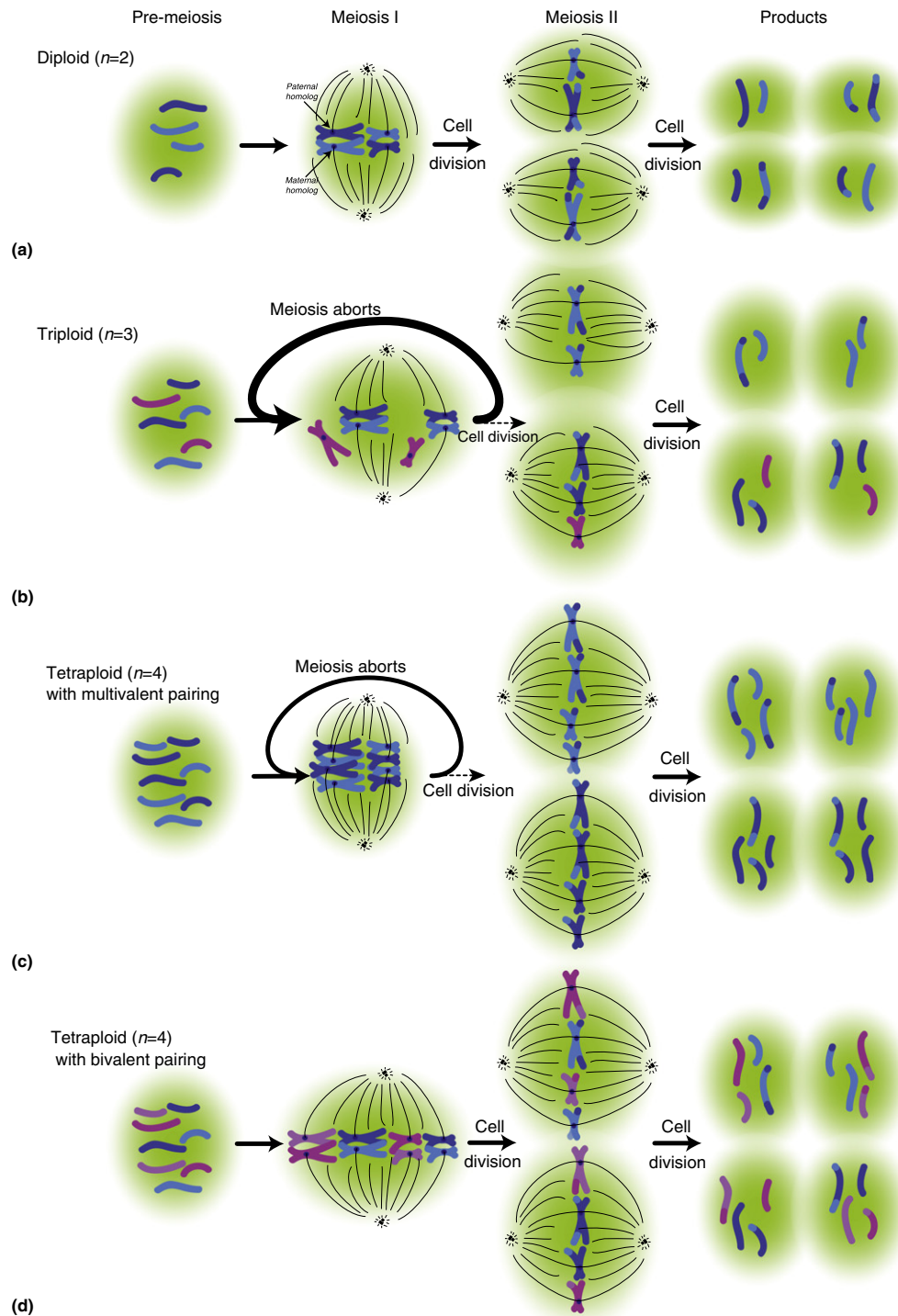


Figure 2 The segregation of chromosomes in diploids (a), triploids (b), and tetraploids (c, d). In triploids, unpaired chromosomes typically float in the cytoplasm during meiosis rather than being drawn to the metaphase plate, resulting in the abortion of meiosis or the production of highly unbalanced gametes, although occasionally balanced gametes are produced. 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).

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; Hermsen, 1984); these two forms can be distinguished based on the pattern of segregation of markers near and far from the centromere (Figure 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 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

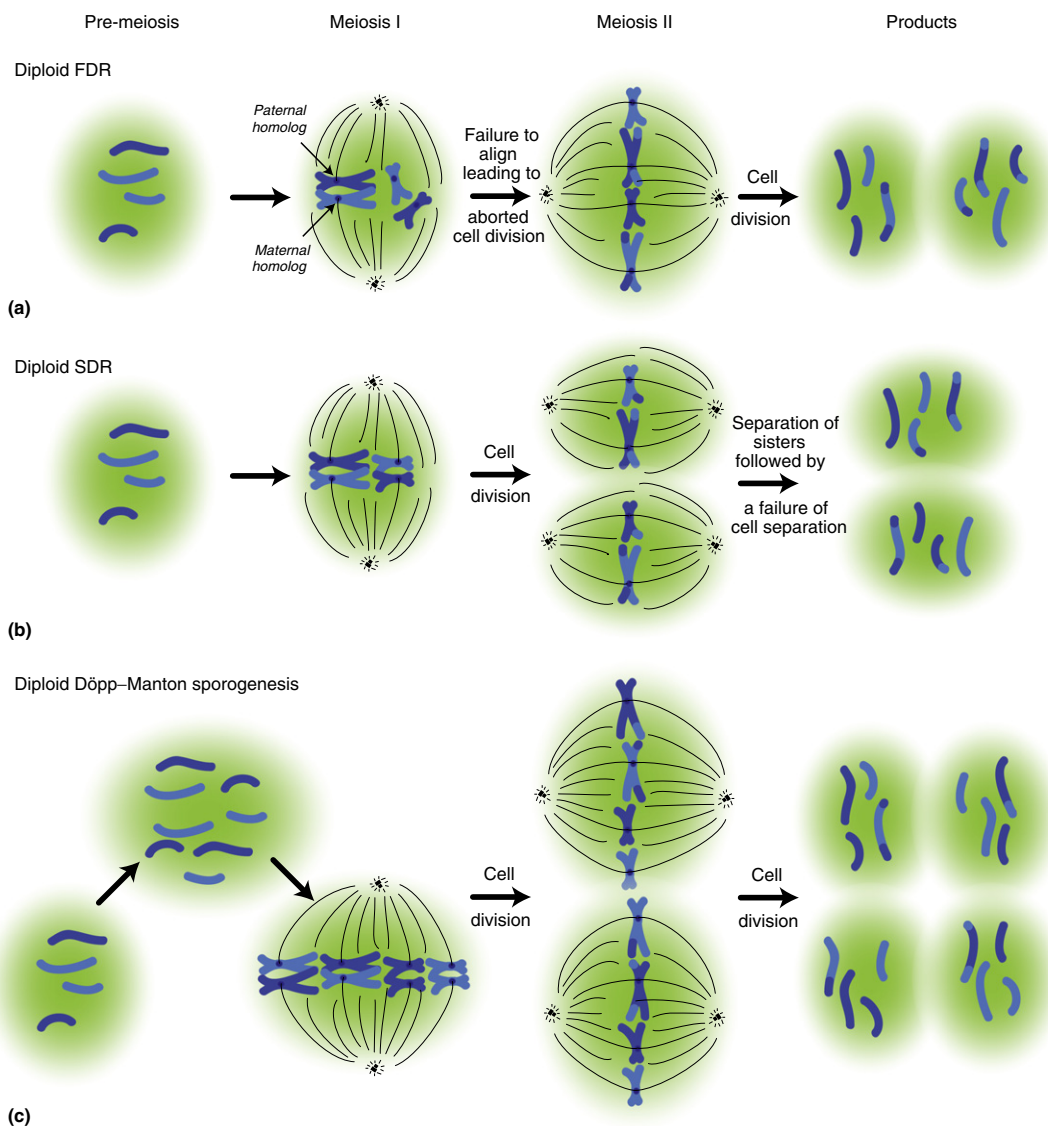


Figure 3 Abnormal segregation patterns leading to unreduced gametes. The three panels illustrate the three main routes to unreduced gametes (Köhler *et al.*, 2010): failure to divide the cell during meiosis I ('first division restitution' (a)), failure to divide the cell during meiosis II ('second division restitution' (b)), or an extra doubling of the genome prior to meiosis ('Döpp–Manton sporogenesis' (c)).

(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 polyploids are formed independently within a population ('multiple origins'). Although 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 recent 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). 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, sensitivity to nutrient stress, susceptibility to drought, and tolerance of extreme abiotic conditions (heat, cold, etc.; Levin, 1983). 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.

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 by 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 most species in a genus have seven chromosomes after meiosis, but one recently derived species has 14, 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 far have yielded much higher estimated rates of ploidy change. In one recent study, 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 known number of species of each ploidy level that exist today, allowing diploids and polyploids to speciate at different rates (but ignoring extinction). This study inferred that, on average, diploids undergo polyploidization at a rate that is 39.9% the rate of speciation. Performing a phylogenetic analysis that allowed for differences in speciation and extinction; Mayrose *et al.* (2011) also obtained high estimates for the rate of polyploidization. Angiosperms polyploidized at a rate that was 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 (Mayrose *et al.*, 2011). These numbers were inferred using a model that assumed polyploidization occurs over time, during the evolution of a lineage. An alternative model that allowed polyploidization to occur only at speciation events yielded similar estimates (29.7% for angiosperms, and 38.7% for non-seed plants). Thus, our best inferences at the moment suggest that plant species become polyploid at roughly one-third the overall speciation rate.

Importantly, these analyses only provide estimates of the relative rates at which polyploidization and speciation occur; they do not address how often they occur together. As a consequence, the extent of synchronization between changes in ploidy and the formation of species remains unclear. Furthermore, these analyses use data from within genera, and thus 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 greatly 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).

Another 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 (by assuming that some ploidy levels, e.g., hexaploids, would only be formed by hybridization between species); 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 (Figure 2(c); 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). 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; Ramsey and Schemske, 2002), 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* (Pteridaceae), a recent study found that 40 out of 106 studied species were polyploid and concluded that these were the result of polyploid speciation (Chao *et al.*, 2012). 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.

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. One study of diploid and tetraploid subspecies of fireweed, *Chamerion 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 example 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 (e.g., at low elevations in the fireweed example), 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 three sets of chromosomes reduces fertility, because meiosis either fails in the absence of paired chromosomes or proceeds but leads to gametes without a full set of chromosomes (‘aneuploidy’; Figure 2(b)). 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, reducing its reproductive isolation. 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).

Of course, even if reproductive isolation is initially incomplete, selection 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 progenitor until they go extinct (‘minority cytotype exclusion’; Levin, 1975; Butlin, 1987).

While the above discussion considers reproductive isolation between a polyploid and its diploid progenitors, another consideration is how polyploids – specifically allopolyploids – affect gene flow between the two parental diploid species. The triploid bridge, for example, might allow introgression (via the polyploid) of genes between two parental species that are otherwise genetically isolated. 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 break down in triploid progeny). Both of these outcomes are theoretically possible, but whether allopolyploids tend to facilitate or hinder divergence between parental diploid species is an interesting open question.

Polyploid Speciation II: 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 (and extinction). In other words, do polyploid species themselves form new species more or less often than their non-polyploid relatives? This 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 (because most mutations are recessive), reducing the efficacy of selection and ultimately making polyploids less adaptable (Stebbins, 1950). However, there are also theoretical arguments in favor 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,b) 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, and Málaga-Trillo and Meyer (2001) similarly link the extensive body plan variation in fish to rounds of ancestral polyploidy.

Polyploidy may also increase diversification rates directly by increasing the rate that reproductive isolation arises between 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 different populations, offspring of a cross between 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 (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; Vamosi and Dickinson, 2006), although this may simply reflect the fact that small young clades have not had time to accumulate polyploids or that diploids may produce polyploid daughter species at high rates in some clades (without these polyploids diversifying at high rates). 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). 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 elevated speciation rates 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, mostly in the past decade, 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](#)); polyploid-only clades are no richer than their diploid-only relatives ([Vamosi 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](#)).

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 give rise to polyploids, but not vice versa, there is a ratchet-like process to increase ploidy levels, which can explain the prevalence of polyploidy and of paleopolyploidy events, without any need for polyploids to speciate more than diploids ([Meyers and Levin, 2006](#)). Indeed, a recent 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](#)), instead of the 1 to 4 such events thought to have occurred ([Jiao et al., 2011](#)). Thus, if anything, the number of paleopolyploidization events in plants suggests that polyploids have diversified less 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 species 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](#)). Overall, there is no strong evidence that paleopolyploidy events directly caused increased diversification.

Recent analyses, typically using phylogenetic approaches, 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](#)). 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 in 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 polyploid speciation ([Mayrose et al., 2011](#); [Scarpino et al., 2014](#))!

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 polyploids reflects the combination of two processes: the establishment of new polyploid populations and the diversification of these populations, 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 form their own species, but these new species are also generally 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 ([Mayrose et al., 2014](#); [Arrigo and Barker, 2012](#)).

Much remains to be learned about the impact of polyploidization on speciation, at both these levels. At the first level, it is clear that polyploids often differ phenotypically from their parent species in ecologically important ways as well as having a degree of chromosome-based reproductive isolation, potentially providing them with an easy route to speciation ([Coyne and Orr, 2004](#)). Accumulating data suggest that this 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 the polyploid individuals. Even in those cases where isolation is strong and rapid, it is unclear whether it is the typically invoked chromosomal incompatibilities or other phenotypic differences that are most responsible for the isolation between the new polyploid and its progenitors.

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; Mayrose *et al.*, 2014; Scarpino *et al.*, 2014; but see Tank *et al.*, 2015), 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 can persist and even proliferate, while others are lost, remains unknown.

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 (Mayrose *et al.*, 2011; Scarpino *et al.*, 2014). Is this because rising chromosome numbers cause increasingly severe meiotic problems or because the advantages of genome doubling are stronger in small genomes, which may be more constrained with fewer genes 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, whether polyploidization plays an early and/or major role in the development of reproductive isolation.

See also: Hybrid Speciation. Seedless Land Plants, Evolution and Diversification of

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