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The “Polyploid Hop”: Shifting Challenges and Opportunities Over the Evolutionary Lifespan of Genome Duplications

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The duplication of an entire genome is no small affair. Whole genome duplication (WGD) is a dramatic mutation with long-lasting effects, yet it occurs repeatedly in all eukaryotic kingdoms. Plants are particularly rich in documented WGDs, with recent and ancient polyploidization events in all major extant lineages. However, challenges immediately following WGD, such as the maintenance of stable chromosome segregation or detrimental ecological interactions with diploid progenitors, commonly do not permit establishment of nascent polyploids. Despite these immediate issues some lineages nevertheless persist and thrive. In fact, ecological modeling commonly supports patterns of adaptive niche differentiation in polyploids, with young polyploids often invading new niches and leaving their diploid progenitors behind. In line with these observations of polyploid evolutionary success, recent work documents instant physiological consequences of WGD associated with increased dehydration stress tolerance in first-generation autotetraploids. Furthermore, population genetic theory predicts both short- and long-term benefits of polyploidy and new empirical data suggests that established polyploids may act as “sponges” accumulating adaptive allelic diversity. In addition to their increased genetic variability, introgression with other tetraploid lineages, diploid progenitors, or even other species, further increases the available pool of genetic variants to polyploids. Despite this, the evolutionary advantages of polyploidy are still questioned, and the debate over the idea of polyploidy as an evolutionary dead-end carries on. Here we broadly synthesize the newest empirical data moving this debate forward. Altogether, evidence suggests that if early barriers are overcome, WGD can offer instantaneous fitness advantages opening the way to a transformed fitness landscape by sampling a higher diversity of alleles, including some already preadapted to their local environment. This occurs in the context of intragenomic, population genomic, and physiological modifications that can, on occasion, offer an evolutionary edge. Yet in the long run, early advantages can turn into long-term hindrances, and without ecological drivers such as novel ecological niche availability or agricultural propagation, a restabilization of the genome via diploidization will begin the cycle anew.

Keywords: polyploidy, selection, population genetics, evolution, autopolyploidy, genome duplication

INTRODUCTION

Whole genome duplication (WGD) is a pervasive event in the evolution of eukaryotes, with an especially strong representation throughout the plant kingdom. Despite this prevalence, however, WGD is no easy victory: the presence of an extra set of chromosomes creates numerous biological challenges ranging from chromosome mis-segregation to altered gene expression, changes in cell size or in intracellular physiology (Ramsey and Schemske, 2002; Osborn et al., 2003; Adams and Wendel, 2005; Comai, 2005; Chen and Ni, 2006; Chen, 2007; Otto, 2007; Parisod et al., 2010; Brownfield and Köhler, 2011; Hollister, 2015). Numerous studies have shown evidence of dysfunction in newly formed polyploids across kingdoms: in plants, fungi and animals, including notably cancer cells (Ramsey and Schemske, 2002; Storchova and Pellman, 2004; Comai, 2005; Yant and Bomblies, 2017). Even more, polyploid establishment is substantially constrained by overall low chances of polyploid mutants persisting among their diploid progenitors (Levin, 2002; Ramsey and Schemske, 2002). This stems from both direct competition between the two cytotypes (Yamauchi et al., 2004) and frequency dependent selection (Levin, 1975), which suggests most autopolyploids are likely to go extinct before establishment (Levin, 1975; Husband, 2000).

Despite these challenges, WGD events have occurred repeatedly throughout the evolution of eukaryotes (Gregory and Mable, 2005; Wood et al., 2009; Wendel, 2015), leading to an abundance of established polyploid species in the wild. There is clear evidence of WGD in the ancestry of most plant lineages (Vision et al., 2000; Bowers et al., 2003; Paterson et al., 2004; Schlueter et al., 2004; Pfeil et al., 2005; Barker et al., 2008; Burleigh et al., 2008; Shi et al., 2010). Among angiosperms, it is estimated that 30–70% have undergone additional WGD events (Stebbins, 1938; Grant, 1963; Goldblatt, 1980; Masterson, 1994; Wood et al., 2009; Mayrose et al., 2011; Ruprecht et al., 2017). Polyploidy is also common among important crops (e.g., wheat, maize, sugar cane, coffee, cotton, potato, and tobacco), suggesting that WGD is often a key factor in successful crop domestication (Salman-Minkov et al., 2016). Obtaining precise estimates of the extent of polyploidy can be complicated, in part due to difficulties obtaining direct empirical evidence. For example, autopolyploids, resulting from within-species genome duplication, are often not considered a separate species from their diploid progenitors. As a result, their overall abundance compared to allopolyploids (where two distinct genomes are combined) have historically been underestimated (Soltis et al., 2007; Barker et al., 2016).

Polyploidy, a High-Risk, High-Gain Path

Frequency estimates of WGD increase in habitats affected by environmental disturbances (Favarger, 1984; Brochmann et al., 2004; Parisod et al., 2010). Concordant with this observation, in diploid-polyploid systems overlapping former glaciation limits, polyploids are found more frequently in the previously glaciated areas while their diploid progenitors commonly remain or retreat within former refugia (Ehrendorfer, 1980; Kadereit, 2015). For example, in *Arabidopsis*, both auto

and allopolyploidization events were estimated to coincide with glacial maxima (Novikova et al., 2018). Beyond the fact that environmental stochasticity both increases the rate of WGD and provides new space for colonization (Baack, 2005; Fawcett et al., 2009; Oswald and Nuismer, 2011), such observations implicate WGD in speciation and adaptive radiation (Wood et al., 2009) and support the long-standing hypothesis that WGD *per se* can potentiate evolutionary adaptation, although evidence for this is somewhat mixed. Clear empirical evidence from *in vitro* evolution experiments in yeast demonstrated that tetraploids adapted faster than lower ploidies (Selmecki et al., 2015) and has bolstered this hypothesis. However, complementary approaches such as ecological niche modeling do not always support niche innovation in polyploids (Glennon et al., 2014). For example in primroses, the niches occupied by the three polyploid species (tetraploid, hexaploidy and octoploid) were distinct relative to the diploid progenitor but they were also narrower (Theodoridis et al., 2013).

Here we synthesize recent advances in polyploid research from new genomic, ecological, and cytological analyses with older observations and theoretical arguments into two primary dimensions (**Figure 1**): consequences (challenges vs. gains) of WGD and their time-span (short-term vs. long-term). To address specifically the effects of WGD, we focus on autopolyploids, which arise from within-species WGD events and thus carry four or more homologous copies of each chromosome (for a clear depiction, see Bomblies and Madlung, 2014). We thus largely set aside allopolyploids (polyploid hybrids), which strongly confound the effects of WGD with hybridization. On many fronts, recent results from autopolyploid systems have confirmed earlier theoretical predictions, but some have unveiled surprising new results in the context of a wide range of biological processes. Most strikingly, the population genetic consequences of WGD have been the subject of ample theoretical arguments despite thin experimental support to date, but this is changing. Our synthesis paints an overall picture of autopolyploidy as a high-risk high-gain path, where long-term complications often outweigh initial benefits while paving the way for re-diploidization. This depiction strengthens the idea of polyploidy as a transitional state, a “hop,” which has seen growing support from the polyploid community (Escudero et al., 2014; Wendel, 2015).

THE SHORT-TERM CHALLENGES

Meiosis

Perhaps the most stringent challenge faced by a nascent autopolyploid is directly tied to the very process of reproduction. A sudden doubling of homologous chromosome number disrupts regular meiotic pairing and segregation: instead of each chromosome having only one homolog with which to pair, in autotetraploids there are suddenly three.

The situation in most diploids is relatively straightforward, with proper chromosome pairing during synapsis typically relying on programmed double-strand DNA breaks and a sequence-based homology search for the homolog using these broken fragments (Grelon et al., 2001; Page and Hawley, 2003; Stacey et al., 2006; Hartung et al., 2007). Once homologous

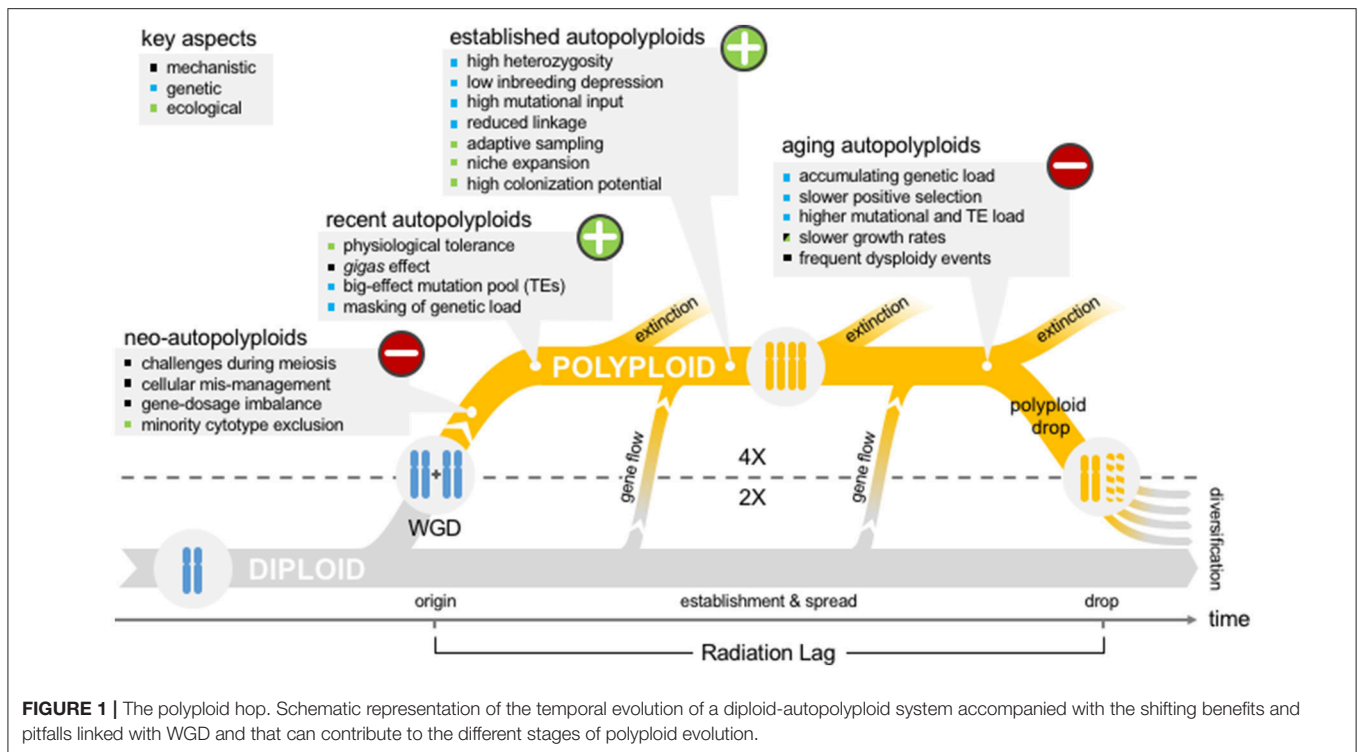


FIGURE 1 | The polyploid hop. Schematic representation of the temporal evolution of a diploid-autopolyploid system accompanied with the shifting benefits and pitfalls linked with WGD and that can contribute to the different stages of polyploid evolution.

chromosomes have aligned, a small fraction of these breaks mature into crossovers (COs) between homologues, thus creating bivalent chromosome pairs physically linked by the CO. These bivalents then align parallel to the poles at which point the COs are essential for the creation of mechanical tension between the assembling spindles via connections to each centromere. This tension transmitted through the obligate COs ensures the correct orderly segregation of chromosomes and further acts as an essential cell cycle checkpoint allowing progression to anaphase (Lampson and Cheeseman, 2011; Campbell and Desai, 2013).

In newly formed polyploids however, the presence of multiple equivalent partners for each chromosome leads to more complex arrays of CO formations. If there is more than one crossover per bivalent, a single homolog can have two separate partners, resulting in a multivalent. Most multivalent configurations are not conducive to the formation of regular tension (Bomblies et al., 2016) and some entirely fail to involve one homolog, leading to mis-segregation and aneuploidy. Compounding this, in nascent autopolyploids entanglements and interlocks can occur between non-homologs. If left unresolved these can result in catastrophic chromosome damage, losses and rearrangements. Such entanglements and interlocks do occur in diploids but are much more commonly resolved (Storlazzi et al., 2010). Thus, meiotic stability is a key hurdle that must be overcome following WGD and is one of the hallmarks of an adapted polyploid. Indeed, loci that encode genes controlling meiotic recombination and crossovers are strongly implicated in adaptation to WGD (Hollister et al., 2012; Yant et al., 2013).

Of course, one way to bypass unstable meiosis is to simply not use it. It has long been recognized that asexual reproduction (vegetative propagation and agamospermy) and

WGD are correlated, with polyploids displaying elevated rates of asexual propagation compared to diploid relatives (Manning and Dickson, 1986; Schinkel et al., 2016; Herben et al., 2017). Such a reproductive strategy may even confer short-term benefits. Asexual reproduction is considered advantageous during range expansion (Baker, 1967), and this may go some way in explaining the invasive nature of many polyploids. Likewise, vegetative propagation could be a short-term fix; buying time for stable meiosis to evolve (Vallejo-Marín and Hiscock, 2016) and reducing the frequency of mating with the diploid progenitors (see section Cytotype and Competitive Exclusion below). Despite potential short-term gains, however, asexuality may not be a viable long-term strategy, and many polyploids are sexual.

In established sexual autopolyploids meiotic instability is often resolved (Yant et al., 2013; Bomblies et al., 2015), with chromosomes forming bivalents or multivalents that segregate regularly. Indeed, there are multiple conceivable ways to modify meiosis and escape genomic instability, but there is considerable empirical work yet to do to learn how many of these exist in nature, much less the mechanistic basis of different solutions. An elegant theory suggests that simply increasing the degree of CO interference could solve this problem (Bomblies et al., 2016). Under this theory if the range of CO interference is greater than the distance to the end of the chromosome, the number of COs would be reduced to one, and if the range of CO interference is only slightly smaller than the chromosome length the COs will be terminalized. This would favor conformations that produce appropriate tension leading to orderly anaphase (Bomblies et al., 2016). Whatever the mechanism, stabilizing meiosis would seem the best solution given the advantages of sex in the long run.

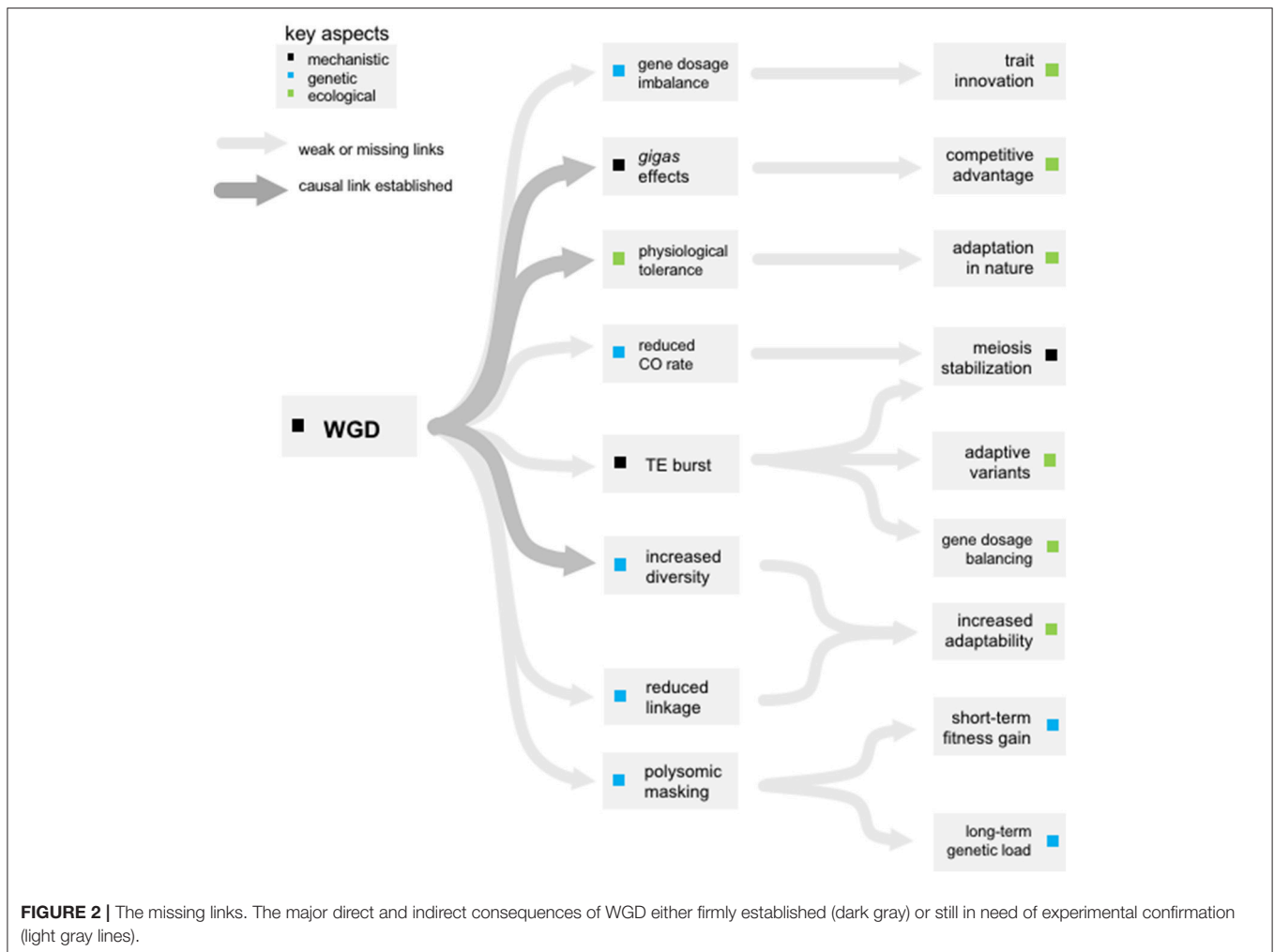
Gene Dosage

It was historically expected that an increase in gene number would result in a uniform increase in gene expression (Comai, 2005). This would correspond to a 1:1 dosage effect where 1x diploid expression per genome results in double the total gene expression per cell in an autotetraploid. However, other dosage responses are also possible (Coate and Doyle, 2010): for example, dosage compensation could reduce the per genome expression by half to match overall diploid expression levels per cell (0.5:1 in autotetraploids). This compensation could be partial (ratio between 0.5:1 and 1:1) or even negative (ratios below 0.5:1). In the other direction, dosage effects could also amplify the expression level increase resulting from polyploidy (ratios above 1:1). The impact of these effects could vary across the transcriptome with some gene categories more likely to follow a 1:1 response while others respond differently. The evidence for an overall 1:1 dosage response to WGD in autopolyploids stems primarily from one study of a synthetic polyploid series in maize (Guo et al., 1996). Among the 18 genes followed, most exhibited a 1:1 dosage response, but there were several exceptions and the dosage compensation response of some genes varied over different ploidy levels. Compared to the extensive literature on gene expression changes in allopolyploids (e.g., expression level dominance, genome-wide transcriptomic rewiring, biased fractionation) this represents a major gap in our understanding in autopolyploids. This gap should be closed, as recent empirical evidence points clearly to selective sweeps in transcription-related loci. This suggests that adaptation of the transcriptional machinery to cope with gene dosage effects may be important in neo-autopolyploids. Indeed, one of the most dramatic genome-wide selective sweeps in response to adaptation to WGD in *A. arenosa* is in the locus encoding the *Transcription initiation factor IIF (TFIIF) beta subunit*, a key member of the complex that drives RNA synthesis during the transcription (Hollister et al., 2012; Yant et al., 2013).

This gap in our understanding of the mechanistic basis behind dosage compensation is partly the result of technical difficulties. Methods commonly used to evaluate genome-wide expression patterns (microarrays and RNAseq) rely on extensive normalization of the RNA input and therefore are perfectly appropriate to detect relative changes in gene expression but not at all to measure variations in absolute transcriptome size (Lovén et al., 2012; Coate and Doyle, 2015). Only recently has a directed investigation of expression differences between diploids and autotetraploids been reported, using three normalization procedures to take into account transcriptome size, biomass, and cell density (Visger et al., 2017). This allows a clearer discrimination of expression differences than was previously possible, as concentration-based normalizations can mask up to 50% of expression differences. Indeed, in previous relative transcriptome comparisons (Stupar et al., 2007; del Pozo and Ramirez-Parra, 2014; Zhang et al., 2014) <10% of the transcriptome undergoes expression changes in response to WGD. However, when absolute differences were measured by Visger et al. approximately 1.5 times more genes showed expression differences; 80% of which had a dosage sensitive response with a ratio >0.5:1 (overexpressed in autotetraploid

cells compared to diploids) thus compensating for the lower cell density of tetraploids (similar expression per biomass). As the first global analysis of gene dosage response to WGD properly taking into account potential changes in overall transcriptome sizes, this study by Visger et al. effectively demonstrates that 1) most genes are compensating for gene dosage (83% with no differences between diploid and tetraploid cells) and 2) that the genes which do not (17%) mostly present increased expression per cell (ratio >0.5:1) somehow compensating for gene dosage per biomass. This data thus does not support a general trend for 1:1 dosage effects, and also shows other responses are possible (underexpression per cell in tetraploids). More empirical work in this area is required (Figure 2) as antagonistic dosage effects in particular may open possibilities for WGD-induced transcriptomic innovations. In particular, some functional categories were enriched for dosage-sensitivity, mostly in relation to photosynthesis or the chloroplast.

Indeed, parallel evidence from the study of patterns of gene retention following allo-polyploidization (Maere et al., 2005; Thomas et al., 2006; Coate et al., 2011) or from more manageable experimental systems like the X chromosome (Birchler, 2014) support the idea that dosage responses are selectively constrained by genetic pathways. This idea was formalized as the dosage balance hypothesis by Papp et al. (2003), who argued that greater fitness loss would result from perturbing the relative abundance of components of a signaling cascade or of a multi-subunit protein complex than from absolute but concerted concentration changes that would maintain overall stoichiometry. For genes under this selection for gene dosage balance, WGD itself may not greatly disrupt relative abundances, as all genes would see their dosage increased more or less proportionally to one another. If that is the case, however, gene dosage compensation mechanisms (from reduction of gene expression to loss of gene duplicates) would be strongly constrained following WGD, as these would need to be concerted across all interacting subunits to maintain stoichiometry. Hence, the gene duplicates of interacting proteins have been well-preserved even over long time-spans following polyploidization (Papp et al., 2003; Thomas et al., 2006; Birchler and Veitia, 2010). This could be a major hindrance for polyploids as this selection would limit an ability to rectify deleterious gene dosage effects. One way to circumvent this selection would be a uniform reduction of gene expressions across the genome, which, Freeling et al. (2015) argue, is precisely one of the effects predicted for transposition bursts (see section Transposition Burst and the Generation of a High-Effect Mutation Pool below). Supporting this potential importance of TEs in dosage response, dosage-dependent genes in *A. thaliana* × *A. arenosa* polyploid series containing from 4 to 0 copies of the *A. thaliana* genome were depleted of TEs while dosage-independent genes were enriched in TEs (Shi et al., 2015). Under the assumption that TEs are equally likely to insert near both categories of genes, this data suggests that TE insertions near dosage-independent genes are selected against. This is consistent with the gene dosage balance hypothesis, as genes within a network would be unlikely affected synchronously, except in the case of a transposition burst where the effect of TEs would be evenly scattered across the genome. This hypothesis remains to be explored further (Figure 2), as



there could also be reverse effects, where presence of TEs in the vicinity of a gene might itself influence the gene-dosage response of that gene. Such effects are yet to be tested but it could help explain the diversity of transcriptomic responses to WGD observed even between accessions of the same species. In *A. thaliana*, Yu et al. (2010) detected ~500 genes differentially expressed in the Col-0 genotype after WGD but only nine in Ler. Notably, the three genes Yu et al. identify as highly but differentially ploidy-responsive across Col-0, Ler, and a panel of seven other accessions (AT1G53480, AT4G32280, AT5G18030) are all located within 1 kb of a TE insertion (anno-j.org).

Cytotype and Competitive Exclusion

Newly formed polyploids are expected to suffer a mating disadvantage when they are relatively rare in the population (Husband, 2000). This type of frequency-dependent disadvantage is known as minority cytotype exclusion (Levin, 1975). The minority cytotype principle is based on the idea that, under random mating, rare cytotypes are expected to be involved in interploidy matings more often than common cytotypes. Assuming that interploidy matings are more likely to produce inviable or sterile offspring, rare cytotypes should have reduced

relative fitness. Such a frequency-dependent mating disadvantage was described from experimental and natural mixed-ploidy populations (Hagberg and Elleström, 1959; Maceira et al., 1993; Husband, 2000; Baack and Stanton, 2005; Mráz et al., 2012), but only a few studies further evaluated its significance for polyploid establishment. Interestingly, studies of mixed-ploidy populations of *Chamerion angustifolium* indicate a surprising asymmetry in this relationship between ploidies. In experimental arrays in field conditions, diploid fitness was frequency-dependent, while fitness in tetraploids was unaffected by their relative frequency. This was likely a result of pollinators preferentially visiting flowers of tetraploid individuals, particularly when rare, and also due to skewed pollen competition favoring tetraploids (Husband, 2000; Husband et al., 2002). Interestingly the effect was mirrored in natural mixed-ploidy populations, where tetraploid mothers produced fewer triploid hybrids than diploid mothers (Husband and Sabara, 2003; Sabara et al., 2013). These studies thus provide a demonstration of minority cytotype exclusion in action and a novel mechanism by which polyploids may avoid its consequences through assortative mating. Indeed, given that WGD can yield larger flowers through the *gigas* effect (Ramsey and Schemske, 2002; Simon-Porcar et al., 2017), and pollinators

often show a preference for visiting larger flowers, non-random mating in mixed-ploidy populations may be important for alleviating the costs of rarity. Additional mechanisms to reduce the costs of inter-cytotype mating are to shift toward self-pollination (Barringer, 2007), or bypass sex altogether either through agamospermy (Thompson and Whitton, 2006; Kao, 2007), or increased vegetative reproduction, as shown both by association studies, (Herben et al., 2017), and in synthetic polyploids (Drunen and Husband, 2018).

In addition, direct competition between the parental diploid and its derivative autopolyploid can hinder the establishment of a nascent polyploid as predicted by theory (Rodríguez, 1996; Yamauchi et al., 2004). This of course depends on niche overlap between the diploid and polyploid. Unlike allopolyploids, where hybridization is expected to create novel genetic combinations unique to the hybrids, autopolyploids may not immediately possess such dramatic genetic differentiation from their progenitors. On the other hand, ploidy-altered traits may translate to better polyploid performance in competition either with its diploid progenitor or with other species. Studies experimentally addressing competition between diploids and their naturally-occurring, recently arisen autopolyploid derivatives are, however, very rare and either support this view (Maceira et al., 1993) or show no difference (Thompson et al., 2015). Alternatively, ploidy-altered traits may also help to cope with competition with other species and may broaden niches, opening the possibility to escape from minority cytotype exclusion. This notion is supported by theoretical models (Rodríguez, 1996) and the observation that polyploids are more frequent in competitive, demanding, and human-disrupted habitats than their diploid relatives (Ehrendorfer, 1980). However, despite the frequent invocation of superior competitive ability to explain polyploid success, this has only rarely been addressed experimentally and available results speak against this trend in autopolyploids (Münzbergová, 2007; Fialová and Duchoslav, 2014), in contrast to allopolyploids (Rey et al., 2017).

THE SHORT-TERM GAINS

Masking of Deleterious Mutations

Haldane pointed out in 1933 that in the short-term polyploidy should greatly reduce the effect of genetic load by masking recessive or partially-recessive deleterious mutations behind an increased allelic multiplicity (Haldane, 1933). Indeed, at a given allele frequency q , the proportion of homozygotes in a diploid population will be q^2 but this drops exponentially to q^4 in an autotetraploid population. Thus, for deleterious recessive alleles, the frequency of autotetraploids expressing the associated phenotype will be an order of magnitude lower (or two if q is already small). This means that deleterious recessive alleles can reach much higher frequencies in autotetraploid populations before being exposed to strong selection and equilibrium frequencies are higher in autotetraploids vs. diploids. As newly formed polyploids initially inherit genetic load from a diploid genomic background where the equilibrium frequency is much lower, genetic load will be relieved in young polyploids, providing

an early benefit (Figure 1). As a result, as long as most deleterious alleles are at least partially recessive (which is the case in both *Mimulus* and yeast; Willis, 1999; Agrawal and Whitlock, 2011), WGD is predicted to lead to temporary fitness increases (Korona, 1999; Otto and Whitton, 2000; Mable and Otto, 2001), although empirical evidence for this is still missing (Figure 2).

Instantly Altered Physiological Properties

Both population genetic theory and emerging empirical evidence suggest that a broad set of factors interact to alter the genomic landscape of autopolyploids. However, understanding the effect of WGD in isolation from separate yet correlated effects has only recently made major progress. While it was suggested 35 years ago that biochemical and physiological changes resulting from WGD might underlie polyploid adaptability (Levin, 1983), the best evidence of a direct link took three decades to emerge, when Chao et al. (2013) elegantly demonstrated that *A. thaliana* first generation autotetraploids have instantaneously enhanced salt tolerance compared to isogenic diploids. Neo-autotetraploid *A. thaliana* lines were shown to experience a tradeoff, being less fit compared to diploid progenitors under non-saline conditions, but more fit in response to saline challenge (Chao et al., 2013). The authors proposed that in conditions of salinity stress the autopolyploid lineages would benefit from a fitness advantage that could contribute to their establishment and persistence, thanks to an improved ability to accumulate potassium and exclude sodium. Indeed, the following year it was shown that autotetraploid *A. thaliana* are additionally more drought tolerant (del Pozo and Ramirez-Parra, 2014). A major challenge now is to determine the molecular events that bind WGD to this enhanced stress tolerance. It appears that the key tissue to investigate is the root, where salinity and drought tolerance meet potassium homeostasis and ABA signaling (Saleh et al., 2008; Meng et al., 2011; Allario et al., 2013; Chao et al., 2013; Wang et al., 2013; del Pozo and Ramirez-Parra, 2014). Work there promises to reveal mechanistically how WGD has an immediate effect on cellular physiology that is independent of increased genetic diversity.

There is also good evidence that somatic WGD may enhance stress resilience. For example, in *Medicago* and sorghum root endopolyploidy correlates with salt tolerance (Ceccarelli et al., 2006; Elmaghrabi et al., 2013) and can be induced by salt in tolerant, but not sensitive, strains (Ceccarelli et al., 2006). Thus, the ability to induce endopolyploidy may be responsible for salinity tolerance, perhaps due to cell size changes in the roots that alter ion uptake. Higher proportions of endopolyploid cells also correlate with greater drought tolerance (Cookson et al., 2006; Saleh et al., 2008; Meng et al., 2011; Chao et al., 2013).

Equally importantly, some effects have been disentangled from polyploidy and shown to be unrelated. A recent study by Solhaug et al. (2016) demonstrated that the allopolyploid *Arabidopsis suecica* had enhanced carbon assimilation via photosynthesis and elevated respiration rates relative to its progenitors *A. arenosa* and *A. thaliana*. This enhanced photosynthetic capacity was environment specific (dependent on high light levels) suggesting a potential mechanism for range expansion by the allopolyploid into novel niches. This advantage was not the direct result of polyploidization, as shown

by comparing 12 accessions of isogenic diploid *A. thaliana* to colchicine-generated neo-polyploids. These autopolyploids showed no difference in carbon assimilation by photosynthesis compared to their diploid progenitors, suggesting that the photosynthetic vigor of *A. suecica* is a result of hybridization and not WGD.

Despite this progress, the majority of functional studies do not capture the final link: proof that the observed WGD-associated change is adaptive in the natural environment (**Figure 2**). An exception was provided by Ramsey, who used reciprocal transplants involving tetraploids, hexaploids, and neo-hexaploids (produced from the tetraploids) of *Achillea borealis* to show a link between WGD and increased fitness in the native environment (Ramsey, 2011). There, WGD itself accounted for 70% of the fitness difference, while the remaining variation (i.e., difference between neo-hexaploids and native hexaploids) could be ascribed to subsequent evolution of the native polyploid. However, the physiological mechanism and its genetic basis in this case remains unknown, which highlights the difficulty of comprehensive inter-disciplinary studies combining genetics, physiology, and ecology.

Transposition Burst and the Generation of a High-Effect Mutation Pool

The hypothesis that WGD presents a genomic shock that activates transposable elements (TEs) across the genome was first proposed by Barbara McClintock (1984) to explain the association between polyploidy and increased TE content. Resident in virtually all genomes, TEs are highly mobile, making them powerful endogenous mutagens. To repress their activity, organisms target TEs with epigenetic silencing mechanisms such as DNA methylation (Bennetzen and Wang, 2014; Ito and Kakutani, 2014). However, the efficiency of TE silencing can be influenced by a number of factors, including environmental or cellular stressors. In some cases, the reactivation of TEs can be explained by the presence of stress-associated transcription factor binding sites in TE promoters (reviewed by Horváth et al., 2017). However, a more global impact of stress on the efficiency of TE-silencing mechanisms has also been suggested (Tittel-Elmer et al., 2010). In particular, genomic stress brought on by hybridization or polyploidization has global effects on epigenetic regulation and may thereby lead to TE reactivation (Kashkush et al., 2003; Madlung et al., 2005; Lopes et al., 2013; Springer et al., 2016; Edger et al., 2017). However, genome shock in polyploids has been studied primarily in allopolyploid contexts, where hybridization is the major contributor, as observed in *Senecio cambrensis* (Hegarty et al., 2006) and *Spartina anglica* (Parisod et al., 2009). To date, very few studies addressed the effect of WGD *per se* on TE transpositions apart from Bardil et al. (2015) who demonstrated an activation of LTR-retroelements following WGD, along with a contribution of gene-flow at the origin of polyploids.

Although most of the mutations TEs generate are deleterious, there is some evidence that TE insertions can be beneficial. The best example of this adaptive potential can be found in the classic case of industrial melanism in the peppered moth, where a young

TE insertion that appeared and rapidly rose to fixation during the industrial revolution (~200 years ago) has been proposed as responsible for the dark morph providing camouflage from predators (Van't Hof et al., 2016). The variation produced by TE activity can thus become a fruitful target of natural selection, providing adaptive solutions to the very stresses that initiated their reactivation (Ito et al., 2016). Thus, a global transposition burst triggered by genomic shock could immediately provide nascent polyploids with a pool of high-effect mutations to test against new challenges. In addition, the reactivation of TEs in young polyploids may also contribute to the stabilization of the neo-polyploid genome. First, TE insertions close to genes are known to have an impact, mostly negative (Hollister and Gaut, 2009) but sometimes positive (Quadrana et al., 2016), on the expression of nearby genes. Therefore, the global array of new insertions resulting from a transposition burst might result in broad re-wiring of gene expression and thereby contribute to the rebalancing of gene-dosages (Kashkush et al., 2003; Freeling et al., 2015), as was suggested by recent observations in rice neopolyploids (Zhang et al., 2015; see section Gene Dosage above). Second, TE content in centromeric regions contributes to the bulk of centric heterochromatin that is essential for the separation of sister chromatids during meiosis. Heterochromatin resists the pull exerted by microtubules and the resultant tension silences the spindle checkpoint, allowing meiosis to proceed (Stephens et al., 2013). Increased TE content generated from a transposition burst in neo-polyploids and distributed across chromosomes may thus lead to an overall strengthening of the meiotic spindles and contribute to stabilizing chaotic meiosis following WGD (see Meiosis section above).

THE LONG-TERM GAINS

Enhanced Invasiveness and Colonization Potential

Polyploids are over-represented among invasive plants. While in many cases diploids and tetraploids co-exist in the native range, the tetraploids are more often found alone in the invaded range than the contrary (e.g., Hollingsworth and Bailey, 2000). Consistent with this, polyploidy is associated with a potential for habitat colonization and transitions to weediness (Brown and Marshall, 1981; Soltis and Soltis, 2000; Pandit et al., 2006, 2011; Prentis et al., 2008). Common physiological factors contributing to invasiveness are associated with the necessary tolerance to environmental variation including stress resilience, phenotypic plasticity, or rapid cycling (early and prolific flowering aids in coping with or escaping from unpredictable environmental conditions; Baker, 1965; Grotkopp et al., 2002; Blair and Wolfe, 2004; Burns, 2004; Hall and Willis, 2006; Sherrard and Maherali, 2006; Franks et al., 2007). Such life history adaptations can help mediate trade-offs between resource accumulation and stress-avoidance and are important for wild species as well as for crops (Jung and Müller, 2009).

Are polyploids pre-adapted or innately more capable of acquiring such traits? This is an open question, but the many cases where both cytotypes occur in their native range but only

polyploids do in the invasive ranges (Lafuma et al., 2003; Mandák et al., 2005; Kubátová et al., 2007; Schlaepfer et al., 2008; Treier et al., 2009) suggest a potential pre-adaptation of polyploids for invasiveness (te Beest et al., 2012). However, environmental stresses also increase the rate of unreduced gamete formation and thus of polyploidization events (Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998). Therefore, polyploidization has also been viewed as a post-colonization process (Mandák et al., 2003) even if through hybridization (e.g., Hahn et al., 2012). Here we focus on the genetic factors implicated in invasiveness that are likely impacted by WGD (**Figure 1**). In particular, because the invasion of novel habitats typically proceeds from a small number of founders, some genetic properties of autopolyploids can enhance their chances of successful colonization. These include larger effective population sizes, a greater tolerance for selfing (and inbreeding depression), the ability to recover from the genetic bottlenecks, potentially enhanced sampling from existing standing variation, as well as expected lower levels of linked selection (below and te Beest et al., 2012).

Increased Diversity and Tolerance for Selfing

In allopolyploids, where two distinct genomes are united, fitness advantages have often been attributed to interspecific hybridization rather than WGD (Barker et al., 2016). A conservative back-of-the-envelope calculation by Barker et al. (2016) estimated that the rate of production of autopolyploid cytotypes could be 40–80 times greater than that of allopolyploids. Given the approximate parity of allo- and auto-polyploids in nature, this suggests a large advantage to hybridization over the benefits directly attributable to WGD.

Because the two sub-genomes typically do not recombine, allopolyploids can continue to enjoy the advantage of heterosis and a stable multi-allelic state over many generations. Autopolyploids on the contrary, do not benefit from fixed heterozygosity. Nevertheless, it has been proposed that polysomic inheritance alone leads to higher genetic diversity (Haldane, 1932), and experimental comparisons between autotetraploids with tetrasomic inheritance and their diploid parents validate this theoretical expectation (Soltis and Soltis, 2000). This increased diversity has been linked to both an immediate increase in the number of mutational targets (doubled number of chromosomes in the case of autotetraploids), that in the long-run provide increased effective population sizes, and an expected reduced efficiency of purifying selection (Ronfort, 1999). This rise in genetic diversity in autopolyploids is proposed as a cause of the observed successes of tetraploids compared to their diploid sister lineages (Roose and Gottlieb, 1976; Soltis and Soltis, 1989, 2000; Soltis et al., 1993; Brochmann et al., 2004). The positive relationship between phenotypic plasticity and invasiveness introduced first by Baker (1965) is now well-documented through numerous physiological and morphological comparisons of invasive and native species (reviewed in Richards et al., 2006). Increased diversity in polyploids is often invoked to explain an increased plasticity and ability of polyploids to sustain range expansions into disturbed habitats. This is a tempting speculation, but a causal

link demonstrating that the increased diversity in tetraploids confers an adaptive advantage is lacking (**Figure 2**).

In addition, reduced homozygosity in autopolyploids is expected to reduce the potential inbreeding depression associated with genetic load (Charlesworth and Charlesworth, 1987). This is because at any locus the increase in copy number in autopolyploids increases the probability of heterozygous offspring, even during selfing (Moody et al., 1993). As a result, the fitness cost associated with selfing (inbreeding depression) may be ameliorated (Lande and Schemske, 1985; Schemske and Lande, 1985) or at worst unchanged (Ronfort, 1999) depending on the range of dominance effects impacting fitness. This prediction has been confirmed in ferns, where the self-fertilization of the gametophyte makes it possible to directly measure the impact of selfing on survival rates in the resulting sporophytes. In two different diploid-tetraploid fern pairs, selfing survival rates were nearly 100% in the tetraploid races, while it ranged from 5 to 60% in the diploids (Masuyama and Watano, 1990). Similarly, a reduction of inbreeding depression is observed in other polyploid-diploid comparisons (Husband and Schemske, 1997; Galloway et al., 2003; Husband et al., 2008), even though there are cases where the opposite is observed (Johnston and Schoen, 1996).

Tolerance to selfing is of major importance in the ability of a population to colonize new habitats, a consideration known as “Baker’s rule” (Baker, 1967). Indeed, during the colonization process, early invaders are likely to be isolated with little opportunity for outcrossing. Selfing therefore provides reproductive assurance for the dispersed invaders (Barrett et al., 2008), and this translates to a high rate of co-occurrence between selfing or asexual propagation and low-density conditions or frequent colonization bouts (Baker, 1967; Price and Jain, 1981; Pannell and Barrett, 1998). For example, Daehler found that low inbreeding depression in hexaploid smooth cordgrass populations invading the San Francisco Bay area in California was associated with higher self-fertility and a higher fitness advantage for founding populations in the field (Daehler, 1998; Renny-Byfield et al., 2010).

Reductions in Linked Selection: An Advantage in Changing Environmental Conditions?

As a mirror image to the reduced efficiency of selection against deleterious mutations, the increase in frequencies of beneficial alleles, even when dominant, will be slower in polyploids under tetrasomic inheritance than in diploids (Hill, 1971). Therefore, the time to fixation for an allele during a selective sweep can be greatly increased in autopolyploids. This prolonged rise in allele frequency might lead to more opportunities for mutation and recombination with other haplotypes, which are even further enhanced by the increased mutation and recombination rates resulting from greater ploidy levels. Weaker linkage thus may promote adaptation through reduced interference between alleles, allowing greater opportunity for a beneficial allele to recombine onto haplotypes with fewer deleterious mutations (**Figure 1**). However, increased recombination can lead to lower fitness in constant environments by breaking

down beneficial associations (Lewontin, 1971; Feldman et al., 1980). Therefore, increased recombination may only be selected for in environments with fluctuating conditions (Charlesworth, 1976; Otto and Michalakis, 1998; Lenormand and Otto, 2000), which also happen to be environments with higher incidences of polyploids (Favarger, 1984; Brochmann et al., 2004; Parisod et al., 2010). This association between increased recombination and adaptation to environmental variation would strongly favor long-term evolution of autopolyploids, but remains to be experimentally tested (Figure 2).

Sampling of Standing Variation From Local Introgression

As an autopolyploid lineage expands its range, it may encounter populations of its diploid progenitor or other species with which hybridization is possible. Provided that such populations are locally adapted, introgression may then supply genetic variants that facilitate persistence. Although polyploidization is traditionally viewed as a means of instant speciation (Coyne and Orr, 2004), the ploidy barrier is permeable (reviewed in Ramsey and Schemske, 1998; Kolár et al., 2017). While adaptive introgression is increasingly recognized as an important force in the evolution of haploid and diploid organisms by genomic studies (reviewed by Arnold and Kunte, 2017; Schmickl et al., 2017), empirical genomic evidence for gene flow among a diploid and its autopolyploid derivative is lacking. The ability to accept genetic variation from alternative cytotype might be beneficial, as it could provide preadapted local alleles upon which selection may act and/or may alleviate inbreeding associated with founding events during range expansions (Parisod et al., 2010). We however lack well-documented examples of traits and underlying loci that may explain evolutionary significance of gene flow for establishment and further spread of a polyploid. The only case to our knowledge, although confined to allopolyploids, is across-ploidy transfer of potentially adaptive floral genes, *RAY1* and *RAY2*, from diploid *Senecio squalidus* into the allotetraploid *Senecio vulgaris* that has given rise to a novel variety of *S. vulgaris* with ray florets (Chapman and Abbott, 2010). An additional hint, coming from an autopolyploid system, is the likely uptake of a diploid-like *CONSTANS* allele during the colonization of railways by a distinct lineage of autotetraploid *A. arenosa* (Baduel et al., 2018). This allele may allow the railway ecotype to escape the repression exacted on flowering by *FLOWERING LOCUS C* and underlie the observed rapid and repeated flowering. These two examples indicate that this may be a fruitful area for future research. An alternative benefit of interploidy hybrids for polyploid establishment may result from their contribution to recurrent formation of polyploids. Triploid hybrids, if fertile, often produce unreduced ($2n = 2x$) gametes (Ramsey and Schemske, 1998; Chrtek et al., 2017) that can merge with reduced ($n = 2x$) gametes of a tetraploid leading to formation of novel tetraploids (Husband, 2004). We note, however, that much gene flow may be neutral or even maladaptive. For example, if a tetraploid has adapted to problems associated with meiotic segregation during its establishment (Yant et al., 2013), later

diluting of such co-adapted gene networks by introgression of diploid-like alleles would lead to reductions in fitness.

Even when assuming beneficial consequences, interploidy gene flow would provide relative advantages to the polyploid only in cases when (potentially adaptive) alleles flow more often into the polyploid than into progenitor diploids (Figure 1). Indeed, this seems to be the case and it was recognized as early as 1971 by Stebbins that gene flow among cytotypes is asymmetrical (Stebbins, 1971). A mechanistic explanation for this asymmetry is that while there are direct pathways for gene flow in the $2x \rightarrow 4x$ direction, the reverse is more convoluted. The unreduced $2n = 2x$ gamete of a diploid and the reduced $n = 2x$ gamete of a tetraploid can combine leading to one-step formation of a tetraploid interploidy hybrid ($2x + 2x = 4x$; Koutecký et al., 2011; Chrtek et al., 2017; Sutherland and Galloway, 2017). However, a triploid hybrid, capable of forming reduced $n = x$ gametes, is an essential stepping-stone for the creation of a diploid hybrid (Kolár et al., 2017). Thus, gene flow in the $4x \rightarrow 2x$ direction is less likely as it involves two separate crossing steps ($4x \rightarrow 3x$ and $3x \rightarrow 2x$). Moreover, the triploid hybrid is often either non-viable (triploid block) or unfit (Ramsey and Schemske, 1998; Köhler et al., 2010). Indeed, the few available empirical genetic studies document either much stronger (in autopolyploid systems: Ståhlberg, 2009; Jørgensen et al., 2011; Arnold et al., 2015) or exclusively unidirectional gene flow from the diploid into the polyploid (in allopolyploid systems: Slotte et al., 2008; Chapman and Abbott, 2010; Zohren et al., 2016). In a longer evolutionary timespan recurrent origins of autopolyploid lineages from different diploid sources followed by hybridization among these polyploids (Soltis and Soltis, 2009) would also lead to enrichment of the tetraploid gene pool by alleles from distinct diploid lineages, similar to direct unidirectional gene flow from diploid to polyploid.

If higher polyploids are formed (i.e., hexaploids, octoploid, etc.) they may hybridize with the tetraploid or among one another and further enhance variation of the polyploid lineages. The few empirical studies available show that the postzygotic barrier, both in terms of rate of hybrid formation and its fitness, is lower among the various polyploid cytotypes than it is between diploids and their polyploid derivatives (Greiner and Oberprieler, 2012; Sonnleitner et al., 2013; Hülber et al., 2015; Sutherland and Galloway, 2017). This corresponds well with the explanation of maternal: paternal genome imbalance in the endosperm as a primary cause of the postzygotic barrier (Köhler et al., 2010; Greiner and Oberprieler, 2012). Because the magnitude of endosperm imbalance in tetraploid–hexaploid hybrids is approximately one third lower than in diploid–tetraploid hybrids (Sonnleitner et al., 2013) these higher-ploidy hybrids may be more fit than diploid–tetraploid hybrids.

Aside from intraspecific gene flow, polyploidy may also break down systems of reproductive isolation present in diploid progenitors and thus increase interspecific gene flow. For example, although the reproductive isolation in diploid lineages of *Arabidopsis arenosa* and *Arabidopsis lyrata* is near complete, tetraploid *A. lyrata* can form viable hybrids with both diploid and tetraploid *A. arenosa*, likely due to the disruption of an endosperm-based barrier (Lafon-Placette et al., 2017).

Interestingly, hybridization between those species appears to have donated beneficial alleles contributing to local adaptation to harsh serpentine soils in the tetraploid *A. arenosa* (Arnold et al., 2016). In this study Arnold et al. (2016) found that several genes exhibiting signatures of selection for adaptation to serpentine soils also appeared to have been introgressed from *A. lyrata*. Finally, the tendency of polyploids to expand into novel niches may further increase chances of encountering foreign lineages with which hybridization may occur. Although the cause of this is unclear, the heightened adaptability of many polyploids fueled by introgression may provide positive feedback, allowing further spread and hybridization. Altogether, these examples illustrate a tendency for polyploids to act as evolutionary “sponges,” accumulating variation through introgression across both ploidy and species barriers. This supports the view of polyploids as diverse evolutionary amalgamates from multiple distinct ancestral lineages—a property advantageous for further expansions.

THE LONG-TERM CHALLENGES

This begs the question: if WGD events are common, and polyploids display advantageous traits, why are established autopolyploids relatively uncommon and paleo-polyploids so frequent? Transitions to polyploidy tend to be observed at the tips of phylogenies (Escudero et al., 2014), suggesting that polyploid lineages typically do not survive as such over longer evolutionary timescales. Consequently, the growing consensus is that polyploidy is an ephemeral but repeatedly appearing state (Wendel, 2015). This could be the result of both pervasive polyploid extinction, as there is some suggestion that recently arisen polyploids experience lower diversification rates and higher extinction rates relative to congeneric diploids (Mayrose et al., 2011, 2015; Arrigo and Barker, 2012), as well as repeated returns to diploidy and disomic inheritance after transitional polyploid phases (e.g., Haufler, 1987; Wendel, 2015; Soltis et al., 2016). To date, such a transition has only been mathematically modeled in autopolyploids (Le Comber et al., 2010); empirical evidence is lacking. Thus, in addition to the short term biological challenges faced by newly-arisen polyploids, longer-term challenges may help explain the transience of the polyploid state, even reviving the idea of polyploidy as an evolutionary “dead-end” (Wagner, 1970; Stebbins, 1971; Mayrose et al., 2011, 2015). Ironically, many of these postulated longer-term negative effects result from the continuation of earlier beneficial population genetic mechanisms.

Increased Genetic Load

If in the short-term polysomic masking results in a fitness increase, a reduced strength of purifying selection (Ronfort, 1999) would eventually lead to the slow rise of recessive deleterious mutations until mutational load reaches a new, higher equilibrium (Otto and Whitton, 2000). This new polyploid equilibrium may take hundreds of thousands of generations to establish (Otto and Whitton, 2000), but would ultimately produce a genetic load proportional to ploidy level and the

mutation rate μ per haploid genome (Haldane, 1937). A particularly strong effect of this would be on TEs, as their distribution of fitness effects is much more heavily skewed toward highly-deleterious mutations compared to single-nucleotide polymorphisms and thus are strongly affected by purifying selection. This has been demonstrated recently in *A. thaliana* (Quadrana et al., 2016), where it was shown that TEs insert throughout the genome, but are rapidly purged from genic rich regions and chromosome arms, most likely due to the deleterious consequences of insertions near or within genes (Quadrana et al., 2016). Even if evidence of this mostly comes from allopolyploid systems (wheat, *Brassica*, etc.), these long-term effects are likely to be similar in autopolyploids and in the long run we can expect the initial differences in transposition burst triggered by the two modes of polyploidization to be less important compared to the relaxation of purifying selection shared by both systems. Indeed, in the allotetraploid *Capsella bursa-pastoris*, an increase in TE content was observed around genes compared to its two parental diploid species, *C. grandiflora* and *C. orientalis*, which was attributed primarily to a relaxation of purifying selection and not to any change in TE activity (Ågren et al., 2016), and there is accumulating evidence of TE proliferation over long timespans following polyploidization (Sarilar et al., 2011; Yaakov and Kashkush, 2012; Piednoël et al., 2015). However, this doesn't seem to apply to all TE families equally. For example some gypsy-like retro-elements proliferated in *Aegilops* tetraploids while others remained quiescent (Senerchia et al., 2014). This could be due to differences in insertion preferences between TE families or more simply to the fact that many TEs are actually defective. Indeed, most of the TEs carried by a genome have lost their transpositional capacities and are fossilized: in the human genome <0.05% of TEs remain active (Mills et al., 2007). Between two active families, differences in their regulation, copy number, chromosome localization, etc. may also explain different responses to relaxed purifying selection. For example, a family inserting more commonly into genes will be more strongly purified and therefore more strongly affected by a relaxation of purifying selection than in TE families that inherently avoid inserting into gene-coding loci. Such differences in insertion preferences have been observed in one LTR retrotransposon family between *A. thaliana* where genic insertions are strongly selected against, and *A. lyrata*, where gene-poor centromeric regions are preferentially targeted, reaching much higher copy numbers (Tsukahara et al., 2012).

Eventually, it is thought that the reduced strength of purifying selection from polysomic masking may overshadow the early advantages of low mutational load, which begins at the lower diploid equilibrium levels immediately following WGD (Otto, 2007; Gerstein and Otto, 2009). At equilibrium (Figure 1), polyploids are predicted to suffer from the increased frequency of deleterious mutations, which are introduced in higher numbers (doubled in the case of autotetraploids). However, given the difficulties of finding an ancient enough system where autopolyploids have reached such an equilibrium but are still ecologically comparable to their diploid progenitors, empirical support for this remains sparse (Figure 2).

Slower Selection on Recessive Beneficial Mutations

In addition to hampering selection against deleterious mutations, polysomic masking can also prevent recessive beneficial mutations from reaching fixation. This may even effectively counter the increased input of beneficial mutations arising from the increased number of haploid genomes (Haldane, 1932; Gerstein and Otto, 2009). Whereas in haploids the rate of fitness increase only depends on the rate of appearance of beneficial mutations and their fitness effect (Haldane et al., 1927), in diploids it also depends on the dominance level of mutations. This is further intensified in polyploids (Gerstein and Otto, 2009). For example, in autotetraploids with tetrasomic inheritance, the rate of fitness increase (w) can be written as a function of the rate of appearance, the fixation probability, and the fitness effect (s) as follows:

$$\Delta w_{4x} = 4N\nu.2h_1s.s$$

Where N is the population size, ν is the beneficial mutation rate, and h_1 is the dominance of the new allele in simplex (for example Aaaa for tetraploids). Therefore, polyploids would adapt faster only when mutations are at least partially dominant ($h_1 > 0.5$) and thus not hindered by polysomic masking. In an attempt to test this prediction experimentally, Schoustra et al. (2007) observed the fastest rates of loss of a costly resistance allele in diploid strains of the fungus *Aspergillus nidulans* that periodically reverted to haploidy. These strains accumulated multiple recessive beneficial mutations in the diploid state that were exposed to positive selection in the haploid state. This pattern is reminiscent of the transitional polyploid phases postulated to have occurred throughout the evolution of plants (Haufler, 1987; Wendel, 2015; Soltis et al., 2016).

Further amplifying this effect of reduced positive selection, lower linkage in autopolyploids (see Reductions in Linked Selection: An Advantage in Changing Environmental Conditions?) increases the likelihood of recombination breaking down favorable haplotypes as they slowly rise in frequency. As a consequence, beneficial mutations in close vicinity and positively selected in autotetraploids are unlikely to remain linked to each other for long. This may be beneficial in the early stages of invasion (directional selection) or under fluctuating environments, but in the long run it is predicted to be unfavorable. Indeed, once established in their new range and closer to a new fitness optimum, selection is predicted to favor increased linkage and reduced recombination (Feldman et al., 1980, 1996).

Bigger Genomes, Slower Growth Rates

With their doubled genomes, autopolyploids are likely to face the general rule in animals and plants dictating that increased genomic content results in decreased growth and division rates (Gregory and Mable, 2005; Otto, 2007). If the impact of genome size is clear at the cellular level it is less evident at the organism level (Knight and Beaulieu, 2008) and exceptions to this rule can easily be found: first in the growth form (e.g., trees have small genomes, Beaulieu et al., 2008) and in the environment

(Zörgö et al., 2013). This led some to suggest the overall negative relationship between genome size and metabolic rate across gymnosperms and angiosperms may be the result of a rather indirect effect through other traits such as growth form (Beaulieu et al., 2007a). It should be noted, however, that these rules are based on the observation of established polyploids and therefore the impact of genome size itself remains to be directly assessed independently of the potentially confounding effects of subsequent evolution. On the cellular level, it seems clear that increased nuclear content leads to increased cell volume (Beaulieu et al., 2008; Knight and Beaulieu, 2008) and slower growth rates (Cavalier-Smith, 1978; Gregory, 2001), which have long been observed in polyploids as well (Müntzing, 1936; Stebbins, 1971; Garbutt and Bazzaz, 1983). At the organismal level, older observations have illustrated that polyploids often flower later (Smith, 1946) and are more frequently perennial (Hagerup, 1932; Müntzing, 1936; Sano et al., 1980), but the role of WGD itself has been rarely experimentally evaluated since then. For example, in synthetic *A. thaliana* tetraploids, there was no consistent trend in flowering time over 12 ecotypes investigated in two common gardens (Solhaug et al., 2016) and similarly no differences in this trait were found between diploid and synthetic polyploids of *Chamerion angustifolium* (Husband et al., 2016). On the other hand, a recent study leveraged parallel altitudinal clines and intraspecific genome size variation in maize landraces to show repeated reductions in genome size in high-altitude populations most likely via selection on flowering time (Bilinski et al., 2018). Furthermore, in growth chamber experiments Bilinski et al. were able to confirm an association, even if modest, between genome size, cell production, and cell sizes. Therefore, such constraints may turn out to be particularly costly for polyploids that successfully switched to invasiveness thanks to early advantages (see section Enhanced Invasiveness and Colonization Potential above). Indeed, invasive species commonly exhibit early flowering (Pyšek et al., 2009), lower seed sizes with higher dispersal abilities and annual life cycles which are also the prerogative of small-genome species (Grotkopp et al., 2002; Knight et al., 2005; Beaulieu et al., 2007b). Even if more research is needed to clarify the direct impact of polyploidy, evidence so far suggests that the potential slowing of growth rates may impact negatively long-term fitness. Thus, selection would likely push for a reduction of genome size, especially in transitions to invasiveness. This process may be very long and stochastic, however, as evidence in the *Nicotiana* genus shows genome downsizing is minimal in young polyploids (~200,000 years old) only appearing in polyploids approximately 4.5 million years old, at which point genome size increases are also observed (Leitch et al., 2008).

Post-polyploidy Diploidization, a Cradle for Diversification

It is now clear that nearly all plant lineages are paleo-polyploids, with their evolutionary histories including at least one round of WGD (Wendel, 2015). However, numbers of past WGD events do not correlate with chromosome numbers nor genome sizes.

For example, given the three rounds of genomic multiplications that have occurred in *Brassica* genomes (α , β , and γ , Franzke et al., 2011; Jiao et al., 2011), and assuming ancestral angiosperms had between 5 and 7 chromosomes (Stebbins, 1971; Raven, 1975), we would expect, without reductions in chromosome numbers along the way, resultant species to carry between 40 and 56 chromosomes, when some carry as few as six (Anderson and Warwick, 1999). A similar reasoning holds with genome sizes (Wendel, 2015): thus it is apparent that past polyploidization events were followed by massive genome downsizing, both in chromosome numbers and in absolute size (Leitch and Bennett, 2004; Leitch and Leitch, 2008). This genome downsizing ultimately leads to the diploidization of descendants (Soltis et al., 2015). These paleo-polyploids then commonly undergo further rounds of polyploidization, generating a cyclical process described as the “wondrous cycles of polyploidy” and occurring repeatedly over long evolutionary timescales (Wendel, 2015).

Several mechanisms have been proposed to underlie the diploidization process, all of them relying on non-homologous translocations (Mandáková and Lysak, 2018). One contributor to these illegitimate recombination events are TEs, since homology between TE copies can lead to spurious recombination events between non-homologous chromosomes (Vicent and Casacuberta, 2017). Some of the rearrangements resulting from these non-homologous recombinations (inversions, reciprocal translocations, deletions, and duplications) do not affect chromosome numbers, but others (end-to-end translocations, EETs, nested chromosome insertions, NCIs, and Robertsonian translocations) are seen as the mechanistic basis of “polyploid drop” (Mandáková and Lysak, 2018). Indeed, all three processes result in the merger of two chromosomes into one via non-homologous recombinations between two distal regions (EETs), two distal regions with a pericentromeric region (NCIs), or between a distal and a pericentromeric region (Robertsonian translocations). Distal and pericentromeric regions are particularly prone to ectopic homologies due to their enrichment in repetitive elements, in particular TEs (Quadrona et al., 2016; Vicent and Casacuberta, 2017). Therefore, even though most recombination events between TEs will lead to small indels, the possibility of large-scale chromosomal rearrangements may represent a major driver of genome restructuring during diploidization (Vicent et al., 1999). In fact, evidence supporting a role for TEs during diploidization has been observed in *Nicotiana* (Lim et al., 2007) and maize (Bruggmann et al., 2006). However, these dysploidy events have an immediate fitness cost, as the merging of two chromosomes leads to obvious chromosome segregation issues. In outcrossers in particular, the probability of forming non-aneuploid offspring is very low, and newly formed dysploids are likely to suffer from woes similar to newly-formed autopolyploids (Mandáková and Lysak, 2018). This is why it was theorized that the establishment of dysploids would be relatively favored in selfers (Charlesworth, 1992). By increasing homozygosity of the offspring, selfing indeed reduces the fitness cost of dysploidy by increasing the probability of producing offspring homozygous for the merged chromosome. Extending this reasoning, we can expect higher rates of dysploidy among weedy invasives, due to both

their propensity for selfing and their often faster cycling (e.g., Grant, 1981), which increases the probability of spurious recombinations (Mandáková and Lysak, 2018). This relationship between life-history and dysploidy rate has been confirmed (e.g., Luo et al., 2015) even though some examples show this is not always straightforward (slow polyploid drop rate in rice despite being annual, Murat et al., 2010). Furthermore, the advantage of a reduced number of chromosomes may be particularly valuable for colonizers (see section Bigger Genomes, Slower Growth Rates above).

These considerations become particularly relevant for aging polyploids, which both carry an increased TE content (see sections Transposition Burst and the Generation of a High-Effect Mutation Pool and Increased Genetic Load above) and are more likely to tolerate selfing (section Increased Diversity and Tolerance for Selfing above). Thus, factors that initially represented an advantage for the establishment of recent autopolyploids may transform into the very drivers of polyploid drop and return to diploidy (Figure 1).

Compared to WGD, which leads to an exact doubling of chromosome numbers, polyploid drop is more erratic and can produce broad variation in chromosome number. In *Brassica* for example, the variation in base chromosome numbers is the result of multiple and independent diploidizations from the mesohexaploid ancestor (Lysak et al., 2007; Mandáková et al., 2017). Indeed, the stochasticity of polyploid drop, not WGD, is thought to be a major contributor to speciations and radiations (Figure 1). However, polyploidy drop is of course not possible without an earlier WGD. Accordingly, recently revised phylogenetic evidence convincingly supports the occurrence of WGDs significantly before large angiosperm radiations, sometimes by millions of years (Tank et al., 2015; Clark and Donoghue, 2017). These reports strengthen the WGD Radiation Lag-Time Model formalized by Schranz et al. (2012), who found that in six examples of angiosperm radiations a species-poor sister-group shared a WGD event with the species-rich crown group, directly contradicting the notion that WGD was the sole immediate cause of these radiations. The lag between WGD and subsequent radiations thus has been proposed as evidence that the long and stochastic process of polyploid drop is the proximal engine of speciation and cladogenesis (Dodsworth et al., 2016; Clark and Donoghue, 2017; Mandáková and Lysak, 2018).

CONCLUSION

As best expressed by Johnathan Wendel, the “wondrous cycles” of polyploidy have gained increasing attention and support, both theoretical and empirical, over the earlier ideas that polyploids were evolutionary dead-ends. Excellent recent reviews have discussed the complex mixture of advantages and disadvantages of polyploidy (see especially Spoelhof et al., 2017), and here we aimed to extend this with the most recent evidence considered explicitly in the scope of the dynamic temporal nature of shifting costs and benefits. In doing so, we hope to bring to light the importance of the timescales at which evolutionary dynamics are at play over the lifespan,

from dawn till dusk, of any given genome duplication, thus creating the conditions for these wondrous cycles to emerge. We see a picture of each cycle of WGD-diploidization as a temporary but powerful engine of evolutionary diversification. Eventually, without specific selective pressures maintaining a strong advantage for polyploids, each hop to polyploidy is restabilized in a drop to diploid form, but there are plenty of evolutionary opportunities for speciation and radiation along the way.

AUTHOR CONTRIBUTIONS

PB drafted the manuscript and realized the figures with help from all other authors. SB drafted the manuscript with help from all

other authors. MV-M drafted the manuscript with help from all other authors. FK drafted the manuscript with help from all other authors. LY drafted the manuscript with help from all other authors.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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