Understanding polyploid establishment: temporary persistence or stable coexistence?

Frederik Mortier[1,2,6,✉], Quinten Bafort[1,3,6], Silvija Milosavljevic[1,2,6], Felipe Kauai[1,2,6], Lucas Prost Boxoen[1,3,6], Yves Van de Peer[1,4,5,6], Dries Bonte[1]

[1]Department of Plant Biotechnology and Bioinformatics, Ghent University Center for Plant Systems Biology, Technologiepark-Zwijnaarde 71, 9052 Gent, Belgium

[2]Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, 9000 Gent, Belgium

[3]Phycology Research Group, Ghent University, Krijgslaan 281, S8, 9000 Ghent, Belgium

[4]Center for Microbial and Ecological Genomics, Department of Biochemistry, Genetics and Microbiology, University of Pretoria, Pretoria 0028, South Africa

[5]College of Horticulture, Academy for Advanced Interdisciplinary Studies, Nanjing Agricultural University, Nanjing 210095, China

[6]VIB-UGent Center for Plant Systems Biology, Gent, Belgium

✉ Corresponding author: fremorti.mortier@ugent.be

Understanding polyploid establishment: temporary persistence or stable coexistence?

Abstract

Polyploidy, resulting from whole-genome duplication (WGD), is ubiquitous in nature and reportedly associated with extreme environments and biological invasions. However, WGD usually comes with great costs, raising questions about the establishment chance of newly formed polyploids. The surprisingly high number of polyploid and mixed-ploidy species observed in nature may be a consequence of their continuous emergence or may reflect stable polyploid persistence and even coexistence with the ancestral ploidy under certain circumstances. However, empirical studies on contemporary polyploid establishment often neglect the cost-benefit balances of polyploid characteristics, trade-offs between phenotypic characteristics, intercytotype interactions, recurrent polyploid formation, and stochastic processes. Here, we advocate for considering population-level success, combining the aforementioned factors that affect polyploid establishment and long-term coexistence with their ancestors. We approach the paradox of polyploid establishment despite high costs from a modern coexistence theory perspective and give an overview of the diversity of mechanisms and their timing that may potentially enable stable rather than transient persistence.

Keywords: whole-genome duplication, polyploid establishment, coexistence, phenotypic evolution, niche differentiation

Introduction

Whole-genome duplication (WGD) or polyploidization is a process by which organisms gain an additional copy of the entire genome. A duplication event is usually caused by the failure of chromosomes to segregate properly during cell division (Ramsey and Schemske 1998). Such errors are rare but because of the large numbers of gametes produced within individuals, within species and over many generations, WGD is a regular occurrence across the tree of life. In this forum paper, we mainly focus on flowering plants, where polyploidy is common and intensively studied (Mable 2004b). Nevertheless, many of the ideas described here should extend to other taxa where polyploidy has been frequently observed, such as in certain groups of animals (Gregory and Mable 2005, David 2022), fungi (Albertin and Marullo 2012, Campbell et al. 2016, Todd et al. 2017), ciliates (Chen 1940), algae (Nichols 1979, Albertin and Marullo 2012), and even archaea (Breuert et al. 2006, Jaakkola et al. 2014).

Some of the most influential evolutionary botanists expressed the believe that polyploids are evolutionary noise or “dead-ends” because of their low starting genetic variation and a higher genetic buffering concealing more of the left-over variation (Stebbins 1950, 1971, Wagner 1970). This “dead-ends” hypothesis was seemingly confirmed by comparative phylogenetics that indicated higher extinction rates of polyploids along the tree of life (Mayrose et al. 2011). However, the genomic signature of polyploidy in extant species demonstrates its occasional success, which seems to coincide with environmental turmoil (Van de Peer et al. 2021). For instance, many ancient WGDs in plants cluster around the Cretaceous-Paleogene boundary, suggesting that the extreme environmental conditions following the Chicxulub asteroid impact increased polyploid formation and/or facilitated polyploid survival and establishment (Fawcett et al. 2009, Vanneste et al. 2014, Lohaus and Van de Peer 2016).

The biodiversity of polyploids can only be understood by how they establish after WGD. Hypotheses on polyploid establishment have focused on reduced reproductive success due to the difficulty of finding compatible mates of the same ploidy level, i.e., same cytotype. This difficulty arises from the fact that interbreeding between different cytotypes typically produces offspring that are unfit (often called 'triploid block' Ramsey and Schemske 1998, Husband and Sabara 2004). This barrier for new polyploids leads to minority cytotype exclusion (MCE, Levin 1975), a positive density dependent mechanism on a cytotype’s population growth. However, many theoretical studies have demonstrated how a higher rate of unreduced gamete formation (Felber 1991), incomplete ‘triploid block’ (‘triploid bridge’, Felber and Bever 1997, Yamauchi et al. 2004), kinds of niche differences (Fowler and Levin 1984, Rodríguez 1996, Oswald and Nuismer 2011), asexual reproduction and selfing (Rodríguez 1996, Yamauchi et al. 2004, Rausch and Morgan 2005, Van Drunen and Friedman 2022), perenniality (Van Drunen and Friedman 2022), and spatial segregation (Li et al. 2004, Baack 2005a) all can help overcome MCE. Although there are few empirical studies on MCE, they largely confirm the barrier it presents to polyploid establishment (Husband 2000, Sutherland et al. 2020).

A vast literature of empirical studies has investigated polyploid success in many ways, focusing on specific aspects, such as the difficulties of intercytotype fertilization underlying putative MCE and additional prezygotic reproductive barriers (e.g. Husband and Sabara 2004, Baack 2005b, Castro et al. 2011, Sutherland et al. 2020). Other researchers have studied different phenotypic traits in natural or induced novel polyploids, called neopolyploids (Garbutt and Bazzaz 1983, Segraves and Thompson 1999, Richardson and Hanks 2011, Baldwin and Husband 2013, Čertner et al. 2019a, Van Drunen and Husband 2019, Wei et al. 2020, Bafort et al. 2023), and assessed the differential fitness of ancestral and polyploid phenotypes in relevant environmental conditions (Baack and Stanton 2005, Raabová et al. 2008, Ramsey 2011, Bafort et al. 2023). Ecological studies have examined the distribution of polyploids relative to their ancestral cytotype (Baack 2004, Richardson and Hanks 2011, Glennon et al. 2014, Thompson et al. 2014, Marchant et al. 2016, Čertner et al. 2019b, López-Jurado et al. 2019) or assessed polyploid occurrence in entire communities (Brochmann et al. 2004, Rice et al. 2019).

Empirical studies have shown polyploidy-related, but often species specific, phenotypic differences that possibly mitigated MCE. Some of those phenotypic differences may have been relevant for the disproportional success of polyploids in extreme habitats (Van de Peer et al. 2021, David 2022, but see Martin and Husband 2009) and in biological invasions (Pandit et al. 2011, te Beest et al. 2012, Moura et al. 2021). Although observations on extant polyploids hint at underlying reasons for polyploid success, these insights are biased to successful cases and cannot disentangle the immediate effects of genome doubling from evolution after the doubling event. Furthermore, interactions with other organisms are overlooked in empirical study systems. New polyploids are expected to interact with other species (Segraves and Thompson 1999, Münzbergová 2007, Segraves and Anneberg 2016) and with other cytotypes such as the ancestor. Important intercytotypic interactions encompass not only those associated with sexual reproduction leading to MCE but also competitive interactions between cytotypes (but see Maceira et al. 1993, Thompson et al. 2015, Anneberg et al. 2023, Guo et al. 2023, Pérez-Romero et al. 2023 that consider intercytotypic competition). Hence, understanding polyploid establishment requires understanding the population performance of a new cytotype following WGD, driven by the combination of costs/benefit balances of the phenotype, ecological interactions such as with other cytotypes, and historical contingency (as already recognized by Stebbins 1971, Ramsey and Schemske 2002).

Modern coexistence theory (Chesson 2000) provides a theoretical framework for understanding polyploid establishment as the outcome of interacting cytotypes. Modern coexistence theory emphasizes that the outcome of competition between two species is determined by whether each species can invade a population of its competitor at carrying capacity (i.e., mutual invasion). Modern coexistence theory also applies to different cytotypes, often considered different species because polyploidy induces immediate reproductive barriers (Levin 1983). Chesson (2000) derives that coexistence is promoted by equalizing and stabilizing mechanisms. Equalizing mechanisms reduce the difference in competitive ability between competitors. Differences in competitive ability entail differences in population growth and sensitivity to competition, irrespective of the frequency of each species (called ‘average fitness’ in Chesson, 2000). Stabilizing mechanisms are caused by niche differences that reduce the effect of interspecific compared to intraspecific interactions. Therefore, they impose negative frequency-dependency on population growth. Different niches can be available in the same location or can be spatially or temporally separated, such as with environmental niches (Chesson 1985, Snyder and Chesson 2003). In contrast, positive frequency-dependent effects have a destabilizing effect on species coexistence. An important destabilizing component in the context of polyploids comes from costs leading to MCE that reinforces the dominance of the majority cytotype at the expense of the minority cytotype. Under positive frequency-dependent growth, the outcome of competition is determined by priority effects: the earliest cytotype has a higher frequency when the other emerges and is expected to exclude that other cytotype (Grainger et al. 2019). In short, the eventual long-term survival of both cytotypes depends on the balance between competitive ability differences on the one hand and coexistence (de)stabilizing mechanisms on the other (Chesson 2000). Even if one cytotype has a superior competitive ability, it can still coexist with a competitively inferior cytotype given sufficient niche differences that overcome the competitive difference. In the absence of large competitive differences and strong (de)stabilization, neutral processes can postpone deterministic exclusion of one species or disrupt stable coexistence, which in both cases can lead to temporary coexistence (Adler et al. 2007).

Polyploid establishment represents one side of the mutual invasion criterion of modern coexistence: the low-frequency invasion of the polyploid into its ancestral population. The estimated rates of unreduced gametes range from 0.1 to 2% in vascular plants (Kreiner et al. 2017) and 0.071% in yeast (Harari et al. 2018), resulting in polyploidization rates that are estimated in the order of 10^{-5} (Ramsey and Schemske 1998). A neopolyploid can only establish if it exhibits a positive population growth, while interacting with its environment that usually includes the ancestral cytotype. However, WGD is associated with steep costs, such as those causing MCE (Levin 1975) and other fitness costs (Comai 2005), that make it less likely for a neopolyploid to achieve positive population growth. Polyploidy is not only associated with costs but often also with benefits that can stem from the wide array of phenotypic changes associated with WGD (Thompson and Lumaret 1992, te Beest et al. 2012, Porturas et al. 2019, Bomblies 2020).Polyploid establishment therefore requires sufficient niche differences to stabilize cytotype coexistence and/or other fitness benefits at or close to the time and location of WGD. Furthermore, distinguishing (de)stabilizing factors and equalizing factors will demonstrate the likelihood of establishment under a certain ancestor's population size, and whether intercytotypic competition will lead to competitive exclusion or coexistence of the ancestor and its polyploid progeny (formalized in Fowler and Levin, 1984).

Here, we review the fitness costs and benefits arising immediately after WGD that are able to alter polyploid establishment and evolutionary effects that influence long-term cytotype persistence and coexistence. We discuss how these effects lead to niche differences and/or a change in competitive difference. We also include mechanisms involving chance or priority effects that may be important to achieve establishment. Polyploidization can occur within one species (autopolyploid) but also in combination with the hybridization of two species (allopolyploidy). However, we do not explicitly distinguish between auto- and allopolyploidy but instead view them as two extremes of a continuum of hybridization with increasing genetic distance between genomes (Soltis and Soltis 2009) and increasing severity of hybrid effects. Therefore, we discuss the influence of hybridization effects polyploid establishment. We aim to stimulate an eco-evolutionary research agenda to understand the apparent paradoxical success of polyploids in time and space.

Immediate fitness effects of polyploidization: novel phenotype

The phenotype of a newly formed polyploid, or neopolyploid, can differ considerably from that of its lower ploidy ancestor. These immediate effects are crucial for polyploid establishment, influencing success from the moment of emergence. We summarize several immediate phenotypic, ecological, and fitness consequences often associated with polyploidization in a diagram that illustrates their interrelatedness (fig. 1). We present some of these relationships briefly in this section but refer to other publications for a comprehensive review on the diversity and ubiquity of immediate effects of polyploidization (for recent work see Bomblies, 2020; Clo and Kolář, 2021).

Broadly, polyploidization entails direct fitness costs (fig. 1, red) but also tends to cause other phenotypic changes that each may, but not necessarily, result in a fitness benefit (fig. 1, green). Because WGD-associated phenotypic changes are often interconnected, trait trade-offs may constrain the net fitness effect of a phenotypic change. Some of these relationships are well understood, whereas others are mostly hypothetical with little or ambiguous evidence in support. Although many trait differences between cytotypes are species-specific, several are frequently observed among both natural and induced polyploids.

Fitness costs

New polyploids often experience fitness costs that are the direct result of whole-genome duplication (fig. 1, red). A recent meta-analysis (Clo and Kolář 2021) reported consistently lower values for fitness traits of neopolyploids compared to their ancestors (on average around 70% of the ancestral value over 32 estimates). It seems that, on the one hand, the competitive ability of many polyploids is decreased due to a reduction in growth rate and/or fecundity likely stemming from a slower cell cycle, various cell-cycle problems (Comai 2005) and a higher resource demand (Guignard et al. 2016, Anneberg and Segraves 2023, Anneberg et al. 2023). On the other hand, the shift to polyploidy destabilizes coexistence with the ancestral cytotype due to costs that lead to MCE. MCE results from incompatible encounters of gametes of the low-frequency, newly emerged cytotype with gametes of the dominant ancestral cytotype (Levin 1975, Husband 2000). Together, the direct costs to WGD provide a baseline expectation for success for any emerging polyploid. In other words, they determine the immediate benefit to competitive ability and stabilizing effects of niche differences that is required for polyploid establishment.

Potential fitness benefits

Phenotypic novelty in a polyploid arises from two fundamental differences from the ancestor (fig. 1). First, all polyploid cells have more nuclear DNA. Second, a polyploid can involve the merging of two differentiated genomes, a consequence of hybridization. Hybridization effects typically impact allopolyploids containing genomes from different species but also autopolyploids from two intraspecifically differentiated parents (sometimes categorized as interracial autopolyploids or segmental allopolyploids; Soltis and Soltis 2009).

Increased cell size is a consistent phenotypic change associated with genome doubling, in both neo- and established polyploids (Bomblies 2020). This is in line with the positive genome size/cell size correlation that is found among eukaryotes, which suggests that DNA content is involved in determining an organism’s minimum cell size (Gregory 2001, Beaulieu et al. 2008). It is usually unclear and highly context specific how the multiple downstream effects of increased cell size influence fitness. An increase in cell size at the onset of polyploidy often correlates with a decrease in the number of cells (Clo and Kolář 2021). Polyploids often show larger stomatal guard cells, larger stomatal openings, a lower stomatal density, and wider xylem conduits. This in turn affects water transport but can do so in opposite directions, providing a positive (Vyas et al. 2007, Ntuli and Zobolo 2008, Zhou et al. 2015, Dudits et al. 2016, Wang et al. 2019, Yang et al. 2019, Zhang et al. 2020), negative (Niu et al. 2016), or neutral (Solhaug et al. 2016) effect on photosynthetic rates and usually increasing drought resistance (Ntuli and Zobolo 2008, Li et al. 2009, van Laere et al. 2011, Deng et al. 2012, Del Pozo and Ramirez-Parra 2014, Zhang et al. 2015, Rao et al. 2020, Jiang et al. 2022). Moreover, the increased surface area to volume ratio of larger cells slows down the cell cycle (Cavalier-Smith 1978, Comai 2005). A larger cell size often, but not always, increases body size or the size of certain structures (“gigas effect”, such as in flowers and seeds; Niu et al., 2016), which in turn influences other physiological and morphological characteristics (Lleonart et al. 2000, Price et al. 2010). An increase in size may also intensify competition through increased acquisition of certain resources. Within a community context, WGD may immediately modulate ecological interactions including those with pollinators, herbivores, mutualists and pathogens (Segraves and Anneberg 2016).

Genome doubling and hybridization can also cause ‘genomic shock’ by means of a wide variety of genetic, epigenetic, and transcriptomic effects (‘molecular changes’, fig. 1), such as a change in genome structure, transposable element activity, epigenetic and transcriptomic patterns, and homoeologous exchange (Bird et al. 2018, Qiu et al. 2020, Shimizu 2022). Genome doubling can also induce gene dosage effects, whereas hybridization increases heterozygosity, which all have downstream phenotypic consequences (te Beest et al. 2012, Moghe and Shiu 2014 for a more in-depth overview). A potential hybridization effect that is ecologically relevant, is the increased environmental responsiveness of gene expression profiles that should enable greater plastic responses to environmental conditions (Polyploidy plasticity hypothesis: Bardil et al. 2011, Dong and Adams 2011, Powell et al. 2017, Shimizu-Inatsugi et al. 2017, Shimizu 2022). The suite of polyploidy-related phenotypic changes, whether stemming from cell-size increase or genomic effects, often coincide with an increased resistance in a variety of stresses in different species (Bomblies 2020, Van de Peer et al. 2021).

Cost-reducing traits

Some fitness benefits derive from characteristics that help to avoid the cost of minority cytotype exclusion (MCE). Many polyploids feature assortative mating and asexual reproduction strategies that alleviate the cost of MCE and, thereby, stabilizing coexistence (Van Drunen and Husband 2019). Assortative mating alleviates the cost of MCE by increasing the likelihood of compatible intercytotype mating (Oswald and Nuismer 2011). It enables polyploid establishment and stabilizes coexistence by segregating gamete pools of both cytotypes. Assortative mating in flowering plants can be achieved through shifts in the behavior of pollinators as a result of ploidy-differentiated flower morphology (Segraves and Thompson 1999, Kennedy et al. 2006), floral scent (Gross and Schiestl 2015) or flowering phenology that reduces overlap in the fertilization window between polyploid and ancestor (Petit et al. 1997, Ramsey and Schemske 2002). Selfing represents an extreme form of assortative mating to assure reproductive success (Levin 1975, Schemske and Lande 1985, Rodríguez 1996, Baack 2005a, Rausch and Morgan 2005, Spoelhof et al. 2020, Van Drunen and Friedman 2022). It follows the breakdown of self-incompatibility mechanisms (Mable 2004a, Clo and Kolář 2022) and is found in many polyploids. Asexual reproduction bypasses gamete fusion altogether, allowing polyploids to avoid MCE and establish (Yamauchi et al. 2004, Spoelhof et al. 2020, Van Drunen and Friedman 2022). Shifts towards asexual strategies, such as clonal expansion or apomixis, are documented in a wide range of polyploids (Comai 2005, Kao 2007, Kolář et al. 2017). Polyploidy is also associated with perennial herbs (but not woody plants, Gustafsson 1948, Stebbins 1971, Rice et al. 2019). Perenniality can reduce MCE by providing an emerging polyploid with a longer time-window for sexual reproduction that enables other polyploids to emerge and produce compatible gametes (Gustafsson 1948, Rodríguez 1996, Van Drunen and Friedman 2022).

There is evidence that assortative mating, selfing, and asexual reproduction are caused directly by WGD, such as the shift in flowering phenology (Dixit et al. 2015, Husband et al. 2016, Corneillie et al. 2019), the breakdown of self-incompatibility (Chawla et al. 1997, Miller and Venable 2000) and certain modes of asexuality (Gustafsson 1948, Hörandl and Hojsgaard 2012, Van Drunen and Husband 2018). If such traits are caused by WGD or were present prior to WGD, as exaptation, they help to promote polyploid establishment. Perenniality, however, has generally evolved after WGD, suggesting that it helped establishment only in a limited number of polyploid species (Van Drunen and Husband 2019).

Trait trade-offs

Organisms simultaneously experience multiple WGD-associated trait changes that combine to strengthen or negate eventual fitness effects (box 1). Correlated traits and consequent trade-offs in fitness effects may arise from physical, functional, resource allocation, or genetic constrains (Roff 2001, Garland 2014, Garland et al. 2022). Such trade-offs influence polyploid success because they have the potential to equalize competitive ability differences. As an example, more robust and longer lived polyploids develop slower, hence trading-off higher survival during development with lower fecundity (Müntzing 1936, Garbutt and Bazzaz 1983). If each side of the trade-off leads to success in a different niche, a polyploidy-induced change in these correlated traits can act as a coexistence stabilizing mechanism when both niches are available. For instance, drought resistance trades-off with hydraulic conductivity in hexaploid *Atriplex canescens* (Hao et al. 2013), rendering them competitively superior compared to their diploid and tetraploid relatives in water-limited, but not water-permeable soils. This facilitates coexistence between hexaploids and di- and tetraploids in locations where both soils are available. Despite their importance, these trade-offs are seldom considered.

Box 1:

Phenotypic trade-offs

Immediate phenotypic benefits that are also associated with a cost.

- Longevity and size (of structures) - longer developmental times (Müntzing 1936, Garbutt and Bazzaz 1983).
- Larger seeds (linked with higher seed survival) - fewer seeds (Bretagnolle et al. 1995, Del Pozo and Ramirez-Parra 2014, Stevens et al. 2020).
- Increased storage to tolerate nutrient or water stress - structural integrity (Pacey et al. 2022).

- Taller or bigger plants to compete better for space - more attractive to herbivores (Solomon et al. 2014)
- Stomata and xylem drought tolerance - optimal water conductance for photosynthesis (trade-off with water conductance: van Laere et al. 2011, Hao et al. 2013; trade-off with photosynthesis: Niu et al. 2016); though photosynthesis can be higher (Senock et al. 1991, Ntuli and Zobolo 2008) or equal (Li et al. 2009) together with an increased drought resistance.

Evolutionary trade-offs

Benefits to polyploidy that trade-off with the delayed effect of mutational load

- More mutations per genome (Sharp et al. 2018) result in increased genetic diversity - more mutations that are potentially lethal (genetic load)
- Masking enables the accumulation of standing genetic variation - higher genetic load at drift-mutation equilibrium (Otto and Whitton 2000, Gerstein and Otto 2009).
- Asexual reproductive assurance - genetic load (Haag and Roze 2007, Hojsgaard and Hörandl 2015).

Many of the immediate phenotypic changes following WGD are not straightforwardly associated with a fitness cost or benefit nor are they always easily identified as equalizing or stabilizing effects. A phenotypic change can influence competitive ability, the polyploid niche, or both, depending on the frequency-independent and frequency-dependent effects. Similarly, trait covariances steer the eventual phenotype and ecological impact. The ecological success of neopolyploids can therefore only be understood and inferred by considering population performance and in the relevant environment.

Delayed fitness dynamics: evolution and changes in adaptive potential

After the immediate phenotypic effects of WGD, polyploid organisms remain subject to further trait evolution (Bomblies 2020, Clo and Kolář 2021). These emerging trait dynamics that occur with a delay after WGD can change the stabilizing or equalizing component of coexistence (Yamamichi et al. 2022) and break down existing phenotypic trade-offs (Garland et al. 2022). These delayed fitness effects therefore have the potential to change a polyploid's fate long after their formation. Insights into the phenotype of extant polyploids may therefore reveal little about their establishment, because the phenotype may have shifted substantially afterwards (acknowledged in, among others, Van Drunen and Husband 2018, Bomblies 2020, Shimizu 2022).

How polyploids evolve is also affected by changes in the genomic structure after WGD. First, polyploids have in principle a double amount of DNA following a WGD and therefore twice the number of mutational sites. While the per-nucleotide mutation rate is reported to decrease, the per-genome mutation rates increase with the level of ploidy in yeast (Sharp et al. 2018). Given equal population size, polyploids are expected to generate greater genetic variation for selection to act on. Second, due to a higher number of gene copies, recessive mutations are better 'masked' because they are only expressed in homozygotes, which comprise a smaller proportion of the population (Otto and Whitton 2000). Recessive alleles, whether advantageous or deleterious, are therefore less efficiently selected in polyploids. Recessive beneficial alleles are expected to get fixed more slowly, whereas recessive deleterious mutations are expected to initially cause less inbreeding depression (Clo and Kolář 2022) and accumulate faster over time (Otto and Whitton 2000, Gerstein and Otto 2009). Selmecki et al. (2015) revealed an increase in genetic variation and a higher adaptation rate in tetraploid yeast. Third, an increased complexity from doubled and/or merged gene regulatory networks (GRN) is expected to enable more extreme phenotypes (Yao et al. 2019, Ebadi et al. 2023). This increased GRN complexity can therefore be regarded as a genome-wide effect that enables larger phenotypic changes from mutations, possibly beneficial under extreme environmental change (Yao et al. 2019). In contrast, others have argued that increased complexity in GRNs could equally contribute to higher robustness against mutations through stabilizing selection (Sevim and Rikvold 2008). Fourth, a doubled genome creates opportunities for novel gene functions or altered gene expression to evolve over macroevolutionary time scales (neo- and subfunctionalization: Blanc and Wolfe 2004, Adams and Wendel 2005). This can arise because each gene in a doubled genome has a homoeologous copy which will be released from purifying selection against mutations and therefore may accumulate mutations (Keane et al. 2014).

A neopolyploid population is expected to start with relatively low adaptive potential due to the bottleneck at WGD (Ramsey and Schemske 1998, Otto and Whitton 2000), even if repeated WGD and intercytotypic gene flow introduce some genetic variation (Soltis and Soltis 1999). Adaptive evolution in polyploids will therefore be mostly limited by genetic variation rather than the efficiency of selection. The faster accumulation of recessive deleterious genetic variation may therefore outweigh the less efficient selection of recessive mutations due to masking in doubled genomes (Otto and Whitton 2000, Gerstein and Otto 2009). Compared to immediate fitness effects (discussed in previous section), the differences in evolutionary processes are expected to have a negligible effect on success in neopolyploids. However, evolutionary effects become more relevant when they compound over generations. A polyploid may this way gradually acquire further adaptations that deal with the challenges of polyploidy and restore its competitive ability to help long-term persistence. This could explain how established polyploids are usually fitter than their neopolyploid counterparts and perform at similar levels as their ancestor (Clo and Kolář 2022). Further evolution of niche differentiation may additionally ensure long term persistence that also stabilizes coexistence with the ancestor, though, destabilization is possible as well (Yamauchi et al. 2004). Therefore, we expect the differences in evolution to have a small impact on initial polyploid establishment but a significant impact on long-term cytotype persistence and coexistence.

The importance of chance and priority

The ecological success or failure of polyploids is not only determined by deterministic processes. Polyploidization itself shows strong stochasticity, stemming from accidental cell cycle errors such as unreduced gamete formation. Considering how this and other stochastic processes affect polyploid establishment is exceedingly relevant. To date, explanations involving stochastic mechanisms and historical contingency are often put forth when deterministic processes fail to explain the establishment of a polyploid (Van Dijk and Bakx-Schotman 1997, Hanzl et al. 2014, Čertner et al. 2019b). However, deterministic and stochastic explanations deserve equal consideration as non-mutually exclusive influences on the establishment process (Lohaus and Van de Peer 2016).

Higher rates of unreduced gamete formation lead to higher polyploid emergence and make polyploid establishment more likely (Felber 1991, Felber and Bever 1997). This effect provides polyploid population growth that is not caused by higher polyploid performance. Unreduced gamete formation is observed to vary with temperature (Randolph 1932, Lewis 1943, Ramsey and Schemske 1998, Mable 2004b, Pécrix et al. 2011, de Storme et al. 2012) and nutrient stress (Grant 1953). Therefore, a higher rate of polyploid formation may partly explain the occurrence of many polyploids in extreme environments.

Also after polyploid formation, stochastic processes impact their success. Any genetic variant (or species), even those lacking net fitness benefits, can get eliminated or succeed in a population (or community) by chance through repeated sampling of individuals and genes from one generation to the next (genetic drift: Kimura 1983, Ohta and Gillespie 1996; community drift: Hubbell 2001, Alonso et al. 2006). Sampling has a bigger impact in smaller populations to a point that sufficiently strong drift may overwhelm any deterministic outcome, such as competitive exclusion but also stable coexistence (Adler et al. 2007). This means that if a novel polyploid emerges from an ancestral population with a low effective population size, drift has the potential to overcome the general fitness costs associated with WGD (Rausch and Morgan 2005). Drift is even expected to overcome the indirect fitness costs of unreduced gamete formation (Clo et al. 2022).

Strong drift effects especially play a role during the colonization of competition-free environments (Peter and Slatkin 2015), such as newly emerged islands, habitat becoming available at range margins due to climate change, or human-introductions in non-native regions. Such founder effects may enable lower-fitness genotypes to establish and persist (Kliber and Eckert 2005, Travis et al. 2007, Čertner et al. 2019b). Colonization provides a route to successful polyploid establishment away from the ancestral population, by enabling polyploids to avoid MCE or competition with the ancestor that may be too strong. Successful polyploid founders can later monopolize available resources and prevent the invasion of putatively fitter variants. Such priority effects reinforce the dominance of the earliest cytotype, independent of its fitness (Grainger et al. 2019). Hence, priority effects can preserve the persistence of lower-fitness variants that would not be able to persist with a stronger competitor if they would compete at equal density. Priority effects may have constrained the expansion of competitively superior tetraploids of the *Centaurea stoebe* complex in microhabitats where diploids occur (Mráz et al. 2012) and of competitively superior hexaploid populations of *Achillea borealis* in places where tetraploids occur (Ramsey 2011). MCE results from inherent negative priority effects that impedes polyploid establishment but whose effects also work the other way around. An ancestral cytotype that invades a polyploid-founded population will experience a similar cost to sexual reproduction from being the minority cytotype.

Dispersal limitation and subsequent spatial clumping are common in most organisms, including polyploids (Husband and Sabara 2004, Baack 2005a). Such clustering determines the spatial extent of sampling with regard to mating, competition and survival. Spatial clumping can facilitate polyploid establishment and coexistence by providing more nearby compatible mates and, thereby, locally alleviating the cost associated with MCE (Baack 2005a, Spoelhof et al. 2020). Furthermore, it promotes competition within rather than between cytotypes (De

Aguiar et al. 2009, Kauai et al. 2023) and enhances the effects of drift by the local population size.

Recurrent polyploid formation, drift, founder effects, priority effects and dispersal limitation may each contribute to creating and maintaining a mosaic distribution of cytotypes across the landscape, and to promote establishment of a new polyploid at their distribution range edge. Priority effects and eventual adaptive evolution can then reinforce the distributional difference, resulting in a parapatric or allopatric pattern. Such geographically divergent polyploid occurrences are often attributed to niche shifts (Marchant et al. 2016), even though the role of drift and priority effects may be underappreciated.

Outlook & outstanding questions

Conspicuous phenotypic changes associated with polyploidy, their remarkable presence in stressful environments as well as their putative origin and long-term establishment in times of environmental upheaval (Van De Peer et al. 2017) have fueled the view of polyploids as ecological and evolutionary favored hopeful monsters (Otto and Whitton 2000, Dietrich 2003, Vanneste et al. 2014, Yao et al. 2019). Nonetheless, genomic archives demonstrate the recurrent extinction of polyploids or their reversal to non-duplicated states (Mayrose et al. 2011, Dodsworth et al. 2016). This paradox raises the question whether contemporary distributions of polyploids are only transient or whether they persist permanently under certain conditions. By focusing on polyploid success at the population level, considering all the costs and benefits, the interaction between polyploids and their ancestral cytotype, and the environment, we provide an eco-evolutionary oriented perspective on the establishment, extinction, and distribution of polyploids in nature. We present a list of 6 outstanding questions to be answered by combining experimental, modelling, and phylogenetic tools to understand all evolutionary and ecological factors involved in polyploid establishment.

1. **To what degree and under which conditions are trait trade-offs relevant for polyploid establishment?** Trade-offs between phenotypic traits are expected to be relevant to persistence under stressful conditions, affecting the extremes of their distribution (Holzman et al. 2011, Willi and Buskirk 2022). We need a systematic study of typical WGD-related trade-offs, their stabilizing or equalizing function on intercytotypic interaction under gradients of stress, and potential attenuation of trade-offs via evolution.
2. **Are cost-reducing mechanisms a result of WGD or do they typically precede or evolve after WGD?** It is often unclear when a shift in pollination, selfing, or asexual reproduction appeared in polyploids. The timing of evolving such traits determines whether it had a role in polyploid establishment or not. Comparative phylogenetics on assortative mating mechanisms (such as in Van Drunen and Husband, 2018) and a search for the origin of the mechanisms in mixed-ploidy species will enable us to assess the presence of cost-reducing mechanisms during establishment.
3. **To what extent are the mechanisms of polyploid establishment and coexistence that are identified in plants applicable to other organisms? Do other taxonomic clades have distinct mechanisms?** Many studies have addressed the question of why there is an overwhelmingly higher occurrence of polyploidy in plants than in other organisms, yet, satisfying explanations are still lacking (Mable 2004b, Fox et al. 2020). Plants may be inherently more prone to certain stabilizing or equalizing mechanisms compared to other organisms. We need to address this bias by studying how non-plant polyploid systems can be successful in overcoming the costs of WGD.
4. **Does WGD increase or decrease the rate of adaptation? Does it facilitate maladaptation?** Polyploids should start with a low standing genetic variation right after WGD but are expected to accumulate deleterious mutations faster (Otto and Whitton 2000, Clo 2022) that would increase a polyploid’s adaptive potential (Selmecki et al. 2015). The accompanying higher mutation load, however, is considered a long-term maladaptive cost for polyploids (Gerstein and Otto 2009). Furthermore, it is expected

that WGD transforms the genome in various ways. Whether the net effect of these genomic changes improve the rate adaptation remains empirically challenging to ascertain. Long-term evolutionary experiments on mutation accumulation and adaptation in the right model systems may shed light on how polyploidy influences microevolutionary processes.

5. **Does community complexity affect polyploid establishment?** New polyploids interact with their ancestral cytotype, but also with a whole community of species. Different types of interactions, antagonistic and mutualistic, and the complexity of the community may provide stabilizing or equalizing forces that affect polyploid establishment. Experimental invasion experiments can be developed to quantify putative consistent invasibility in species-poor and species-diverse communities, with respect to trophic relations and its potential condition dependence to changing environmental conditions.
6. **What is the relative impact of chance, priority, and deterministic processes on cytotype persistence and coexistence?** Researchers are starting to recognize the effects of stochasticity and historical contingency as impactful forces in evolution and population success. A mechanistic understanding of how these affect the establishment process can show or eliminate alternative explanations of polyploid establishment. A promising avenue may be to quantify fitness equality (i.e., neutrality) and estimate effective population sizes at WGD in mixed-ploidy systems. Confronting mechanistic models with data on cytotype distribution and niches through inverse modelling can help estimate relative importance of processes.

References

Adams, K. L. and Wendel, J. F. 2005. Polyploidy and genome evolution in plants. - Curr. Opin. Plant Biol. 8: 135–141.

Adler, P. B. et al. 2007. A niche for neutrality. - Ecol. Lett. 10: 95–104.

Albertin, W. and Marullo, P. 2012. Polyploidy in fungi: Evolution after whole-genome duplication. - Proc. R. Soc. B Biol. Sci. 279: 2497–2509.

Alonso, D. et al. 2006. The merits of neutral theory. - Trends Ecol. Evol. 21: 451–457.

Anneberg, T. J. and Segraves, K. A. 2023. Neopolyploidy causes increased nutrient requirements and a shift in plant growth strategy in Heuchera cylindrica. - Ecology: 1–13.

Anneberg, T. J. et al. 2023. Polyploidy impacts population growth and competition with diploids: multigenerational experiments reveal key life-history trade-offs. - New Phytol.: 1294–1304.

Baack, E. J. 2004. Cytotype segregation on regional and microgeographic scales in snow buttercups (Ranunculus adoneus: Ranunculaceae). - Am. J. Bot. 91: 1783–1788.

Baack, E. J. 2005a. To succeed globally, disperse locally: Effects of local pollen and seed dispersal on tetraploid establishment. - Heredity (Edinb). 94: 538–546.

Baack, E. J. 2005b. Ecological factors influencing tetraploid establishment in snow buttercups (Ranunculus adoneus, Ranunculaceae): Minority cytotype exclusion and barriers to triploid formation. - Am. J. Bot. 92: 1827–1835.

Baack, E. J. and Stanton, M. L. 2005. Ecological Factors Influencing Tetraploid Speciation in Snow Buttercups (Ranunculus Adoneus): Niche Differentiation and Tetraploid Establishment. - Evolution (N. Y). 59: 1936.

Bafort, Q. et al. 2023. The immediate effects of polyploidization of Spirodela polyrhiza change in a strain-specific way along environmental gradients. - Evol. Lett. 7: 37–47.

Baldwin, S. J. and Husband, B. C. 2013. The association between polyploidy and clonal reproduction in diploid and tetraploid Chamerion angustifolium. - Mol. Ecol. 22: 1806–1819.

Bardil, A. et al. 2011. Genomic expression dominance in the natural allopolyploid Coffea arabica is massively affected by growth temperature. - New Phytol. 192: 760–774.

Beaulieu, J. M. et al. 2008. Genome size is a strong predictor of cell size and stomatal density in angiosperms. - New Phytol. 179: 975–986.

Bird, K. A. et al. 2018. The causes and consequences of subgenome dominance in hybrids and recent polyploids. - New Phytol. 220: 87–93.

Blanc, G. and Wolfe, K. H. 2004. Functional divergence of duplicated genes formed by polyploidy during arabidopsis evolution. - Plant Cell 16: 1679–1691.

Bomblies, K. 2020. When everything changes at once: Finding a new normal after genome duplication: Evolutionary response to polyploidy. - Proc. R. Soc. B Biol. Sci. in press.

Bretagnolle, F. et al. 1995. The influence of seed size variation on seed germination and seedling vigour in diploid and tetraploid Dactylis Glomerata L. - Ann. Bot. 76: 607–615.

Breuert, S. et al. 2006. Regulated polyploidy in halophilic archaea. - PLoS One in press.

Brochmann, C. et al. 2004. Polyploidy in arctic plants. - Biol. J. Linn. Soc. 82: 521–536.

Campbell, M. A. et al. 2016. The case of the missing ancient fungal polyploids. - Am. Nat. 188: 602–614.

Castro, S. et al. 2011. Breeding barriers at a diploid-hexaploid contact zone in Aster amellus. - Evol. Ecol. 25: 795–814.

Cavalier-Smith, T. 1978. Nuclear volume control by nucleoskeletal DNA, selection for cell volume and cell growth rate, and the solution of the DNA C-value paradox. - J. Cell Sci. 34: 247–278.

Čertner, M. et al. 2019a. Ploidy-altered phenotype interacts with local environment and may enhance polyploid establishment in Knautia serpentinicola (Caprifoliaceae). - New Phytol. 221: 1117–1127.

Čertner, M. et al. 2019b. Climatic conditions and human activities shape diploid–tetraploid coexistence at different spatial scales in the common weed Tripleurospermum inodorum (Asteraceae). - J. Biogeogr. 46: 1355–1366.

Chawla, B. et al. 1997. Breakdown of self-incompatibility in tetraploid Lycopersicon peruvianum: Inheritance and expression of S-related proteins. - Theor. Appl. Genet. 95: 992–996.

Chen, T.-T. 1940. Polyploidy in Paramecium Bursaria. - Proc. Natl. Acad. Sci. 26: 239–240.

Chesson, P. L. 1985. Coexistence of Competitors in Spatially and Temporally Varying Environments : A Look at the Combined Effects of Different Sorts of Variability. - Theor.

Popul. Biol. 28: 263–287.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. - Annu. Rev. Ecol. Syst. 31: 343–366.

Clo, J. 2022. Polyploidization: Consequences of genome doubling on the evolutionary potential of populations. - Am. J. Bot. 109: 1213–1220.

Clo, J. and Kolář, F. 2021. Short- and long-term consequences of genome doubling: a meta-analysis. - Am. J. Bot. 108: 2315–2322.

Clo, J. and Kolář, F. 2022. Inbreeding depression in polyploid species: a meta-analysis Josselin. - bioRXiv: 1–19.

Clo, J. et al. 2022. Polyploidization as an opportunistic mutation: The role of unreduced gametes formation and genetic drift in polyploid establishment. - J. Evol. Biol. 35: 1099–1109.

Comai, L. 2005. The advantages and disadvantages of being polyploid. - Nat. Rev. Genet. 6: 836–846.

Corneillie, S. et al. 2019. Polyploidy affects plant growth and alters cell wall composition. - Plant Physiol. 179: 74–87.

David, K. T. 2022. Global gradients in the distribution of animal polyploids. - Proc. Natl. Acad. Sci. 119: 2017.

De Aguiar, M. A. M. et al. 2009. Global patterns of speciation and diversity. - Nature 460: 384–387.

de Storme, N. et al. 2012. Production of diploid male gametes in Arabidopsis by cold-induced Destabilization of postmeiotic radial microtubule arrays. - Plant Physiol. 160: 1808–1826.

Del Pozo, J. C. and Ramirez-Parra, E. 2014. Deciphering the molecular bases for drought tolerance in Arabidopsis autotetraploids. - Plant, Cell Environ. 37: 2722–2737.

Deng, B. et al. 2012. Antioxidant response to drought, cold and nutrient stress in two ploidy levels of tobacco plants: Low resource requirement confers polytolerance in polyploids? - Plant Growth Regul. 66: 37–47.

Dietrich, M. R. 2003. Richard Goldschmidt: hopeful monsters and other “heresies.” - Nat. Rev. Genet. 4: 68–74.

Dixit, V. et al. 2015. Changes in ploidy and its effect on thymoquinone concentrations in nigella sativa l. Seeds. - J. Hortic. Sci. Biotechnol. 90: 537–542.

Dodsworth, S. et al. 2016. Is post-polyploidization diploidization the key to the evolutionary success of angiosperms? - Bot. J. Linn. Soc. 180: 1–5.

Dong, S. and Adams, K. L. 2011. Differential contributions to the transcriptome of duplicated genes in response to abiotic stresses in natural and synthetic polyploids. - New Phytol. 190: 1045–1057.

Dudits, D. et al. 2016. Response of organ structure and physiology to autotetraploidization in early development of energy willow Salix viminalis. - Plant Physiol. 170: 1504–1523.

Ebadi, M. et al. 2023. The duplication of genomes and gene regulatory networks and its potential for evolutionary adaptation and survival. - bioRXiv in press.

Fawcett, J. A. et al. 2009. Plants with double genomes might have had a better chance to survive the Cretaceous-Tertiary extinction event. - Proc. Natl. Acad. Sci. U. S. A. 106: 5737–5742.

Felber, F. 1991. Establishment of a tetraploid cytotype in a diploid population: Effect of relative fitness of the cytotypes. - J. Evol. Biol. 4: 195–207.

Felber, F. and Bever, J. D. 1997. Effect of triploid fitness on the coexistence of diploids and tetraploids. - Biol. J. Linn. Soc. 60: 95–106.

Fowler, N. L. and Levin, D. A. 1984. Ecological constraints on the establishment of a novel polyploid in competition with its diploid progenitor. - Am. Nat. 124: 703–711.

Fox, D. T. et al. 2020. Polyploidy: A Biological Force From Cells to Ecosystems. - Trends Cell Biol. 30: 688–694.

Garbutt, K. and Bazzaz, F. A. 1983. Leaf demography, flower production and biomass of diploid and tetraploid populations of Phlox drummondii hook. on a soil moisture gradient. - New Phytol. 93: 129–141.

Garland, T. 2014. Trade-offs. - Curr. Biol. 24: R60–R61.

Garland, T. et al. 2022. Trade-offs (And constraints) in organismal biology. - Physiol. Biochem. Zool. 95: 82–112.

Gerstein, A. C. and Otto, S. P. 2009. Ploidy and the causes of genomic evolution. - J. Hered. 100: 571–581.

Glennon, K. L. et al. 2014. Evidence for shared broad-scale climatic niches of diploid and polyploid plants. - Ecol. Lett. 17: 574–582.

Grainger, T. N. et al. 2019. Applying modern coexistence theory to priority effects. - Proc. Natl. Acad. Sci. 116: 6205–6210.

Grant, V. 1953. Cytogenetics of the hybrid Gilia millefoliata X achilleaefolia. - Chromosoma 5: 372–390.

Gregory, T. R. 2001. Coincidence, coevolution, or causation? DNA content, cellsize, and the C-value enigma. - Biol. Rev. 76: 65–101.

Gregory, T. R. and Mable, B. K. 2005. Polyploidy in Animals. - In: The Evolution of the Genome. Elsevier, pp. 427–517.

Gross, K. and Schiestl, F. P. 2015. Are tetraploids more successful? Floral signals, reproductive success and floral isolation in mixed-ploidy populations of a terrestrial orchid. - Ann. Bot. 115: 263–273.

Guignard, S. et al. 2016. Genome size and ploidy influence angiosperm species ’ biomass under nitrogen and phosphorus limitation. - New Phytol. 210: 1195–1206.

Guo, W. et al. 2023. Does competitive asymmetry confer polyploid advantage under changing environments? - J. Ecol.: 1–13.

Gustafsson, Å. 1948. POLYPLOIDY, LIFE-FORM AND VEGETATIVE REPRODUCTION. - Hereditas 34: 1–22.

Haag, C. R. and Roze, D. 2007. Genetic load in sexual and asexual diploids: Segregation, dominance and genetic drift. - Genetics 176: 1663–1678.

Hanzl, M. et al. 2014. Nonadaptive processes governing early stages of polyploid evolution: Insights from a primary contact zone of relict serpentine Knautia arvensis (Caprifoliaceae). - Am. J. Bot. 101: 935–945.

Hao, G. Y. et al. 2013. Polyploidy enhances the occupation of heterogeneous environments through hydraulic related trade-offs in Atriplex canescens (Chenopodiaceae). - New Phytol. 197: 970–978.

Harari, Y. et al. 2018. Spontaneous Changes in Ploidy Are Common in Yeast. - Curr. Biol. 28: 825-835.e4.

Hojsgaard, D. and Hörandl, E. 2015. A little bit of sex matters for genome evolution in asexual plants. - Front. Plant Sci. 6: 1–6.

Holzman, R. et al. 2011. Functional complexity can mitigate performance trade-offs. - Am. Nat. in press.

Hörandl, E. and Hojsgaard, D. 2012. The evolution of apomixis in angiosperms: A reappraisal. - Plant Biosyst. 146: 681–693.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. - Princeton university Press.

Husband, B. C. 2000. Constraints on polyploid evolution: A test of the minority cytotype exclusion principle. - Proc. R. Soc. B Biol. Sci. 267: 217–223.

Husband, B. C. and Sabara, H. A. 2004. Reproductive isolation between autotetraploids and their diploid progenitors in fireweed, Chamerion angustifolium (Onagraceae). - New Phytol. 161: 703–713.

Husband, B. C. et al. 2016. Direct vs. Indirect effects of whole-genome duplication on prezygotic isolation in chamerion angustifolium: Implications for rapid speciation. - Am. J. Bot. 103: 1259–1271.

Jaakkola, S. T. et al. 2014. Halophilic archaea cultivated from surface sterilized middle-late Eocene rock salt are polyploid. - PLoS One 9: 24–26.

Jiang, J. et al. 2022. Tetraploidy in Citrus wilsonii Enhances Drought Tolerance via Synergistic Regulation of Photosynthesis, Phosphorylation, and Hormonal Changes. - Front. Plant Sci. 13: 1–16.

Kao, R. H. 2007. Asexuality and the coexistence of cytotypes. - New Phytol. 175: 764–772.

Kauai, F. et al. 2023. Neutral processes underlying the macro eco-evolutionary dynamics of mixed-ploidy systems. - Proc. R. Soc. B in press.

Keane, O. M. et al. 2014. Preservation of genetic and regulatory robustness in ancient gene duplicates of Saccharomyces cerevisiae. - Genome Res. 24: 1830–1841.

Kennedy, B. F. et al. 2006. Pollinator-mediated assortative mating in mixed ploidy populations of Chamerion angustifolium (Onagraceae). - Oecologia 150: 398–408.

Kimura, M. 1983. The Neutral Theory of Molecular Evolution. - Cambridge University Press.

Kliber, A. and Eckert, C. G. 2005. Interaction between founder effect and selection during biological invasion in an aquatic plant. - Evolution (N. Y). 59: 1900–1913.

Kolář, F. et al. 2017. Mixed-Ploidy Species: Progress and Opportunities in Polyploid Research. - Trends Plant Sci. 22: 1041–1055.

Kreiner, J. M. et al. 2017. Evolutionary Dynamics of Unreduced Gametes. - Trends Genet. 33: 583–593.

Levin, D. A. 1975. MINORITY CYTOTYPE EXCLUSION IN LOCAL PLANT POPULATIONS. - Taxon 24: 35–43.

Levin, D. A. 1983. Polyploidy and Novelty in Flowering Plants Author (s): Donald A . Levin Source : The American Naturalist , Jul ., 1983 , Vol . 122 , No . 1 (Jul ., 1983), pp . 1-25 Published by : The University of Chicago Press for The American Society of Naturalists. - Am. Nat. 122: 1–25.

Lewis, D. 1943. The incompatibility sieve for producing polyploids. - J. Genet. 45: 261–264.

Li, B. H. et al. 2004. Modelling the establishment and spread of autotetraploid plants in a spatially heterogeneous environment. - J. Evol. Biol. 17: 562–573.

Li, W. D. et al. 2009. Photosynthetic responses to chromosome doubling in relation to leaf anatomy in Lonicera japonica subjected to water stress. - Funct. Plant Biol. 36: 783–792.

Lleonart, J. et al. 2000. Removing allometric effects of body size in morphological analysis. - J. Theor. Biol. 205: 85–93.

Lohaus, R. and Van de Peer, Y. 2016. Of dups and dinos: Evolution at the K/Pg boundary. - Curr. Opin. Plant Biol. 30: 62–69.

López-Jurado, J. et al. 2019. Niche divergence and limits to expansion in the high polyploid Dianthus broteri complex. - New Phytol. 222: 1076–1087.

Mable, B. K. 2004a. Polyploidy and self-compatibility: Is there an association? - New Phytol. 162: 803–811.

Mable, B. K. 2004b. ‘Why polyploidy is rarer in animals than in plants’: myths and mechanisms. - Biol. J. Linn. Soc. 82: 453–466.

Maceira, N. O. et al. 1993. Competition between diploid and derivative autotetraploid Dactylis glomerata L. from Galicia. Implications for the establishment of novel polyploid populations. - New Phytol. 124: 321–328.

Marchant, D. B. et al. 2016. Patterns of abiotic niche shifts in allopolyploids relative to their progenitors. - New Phytol. 212: 708–718.

Martin, S. L. and Husband, B. C. 2009. Influence of phylogeny and ploidy on species ranges of North American angiosperms. - J. Ecol. 97: 913–922.

Mayrose, I. et al. 2011. Recently formed polyploid plants diversify at lower rates. - Science (80-.). 333: 1257.

Miller, J. S. and Venable, D. L. 2000. Polyploidy and the evolution of gender dimorphism in plants. - Science (80-.). 289: 2335–2338.

Moghe, G. D. and Shiu, S. H. 2014. The causes and molecular consequences of polyploidy in flowering plants. - Ann. N. Y. Acad. Sci. 1320: 16–34.

Moura, R. F. et al. 2021. Polyploidy and high environmental tolerance increase the invasive success of plants. - J. Plant Res. 134: 105–114.

Mráz, P. et al. 2012. Anthropogenic disturbance as a driver of microspatial and microhabitat segregation of cytotypes of Centaurea stoebe and cytotype interactions in secondary contact zones. - Ann. Bot. 110: 615–627.

Müntzing, A. 1936. The Evolutionary Significance of Autopolyploidy. - Hereditas 21: 363–378.

Münzbergová, Z. 2007. No effect of ploidy level in plant response to competition in a common garden experiment. - Biol. J. Linn. Soc. 92: 211–219.

Nichols, H. W. 1979. Polyploidy in algae. - Basic Life Sci. 13: 151–161.

Niu, L. et al. 2016. Identification and characterization of tetraploid and octoploid Jatropha curcas induced by colchicine. - Caryologia 69: 58–66.

Ntuli, N. R. and Zobolo, A. M. 2008. Effect of water stress on growth of colchicine induced polyploid Coccinia palmata and Lagenaria sphaerica plants. - African J. Biotechnol. 7: 3645–3649.

Ohta, T. and Gillespie, J. H. 1996. Development of neutral nearly neutral theories. - Theor. Popul. Biol. 49: 128–142.

Oswald, B. P. and Nuismer, S. L. 2011. A Unified Model of Autopolyploid Establishment and Evolution. - Am. Nat. 178: 687–700.

Otto, S. P. and Whitton, J. 2000. Polyploid Incidence and Evolution. - Annu. Rev. Genet. 34: 401–437.

Pacey, E. K. et al. 2022. Polyploidy increases storage but decreases structural stability in Arabidopsis thaliana. - Curr. Biol. 32: 4057-4063.e3.

Pandit, M. K. et al. 2011. Ploidy influences rarity and invasiveness in plants. - J. Ecol. 99: 1108–1115.

Pécrix, Y. et al. 2011. Polyploidization mechanisms: Temperature environment can induce diploid gamete formation in Rosa sp. - J. Exp. Bot. 62: 3587–3597.

Pérez-Romero, J. A. et al. 2023. Effects of ploidy and genetic diversity on competitive outcomes. - bioRXiv in press.

Peter, B. M. and Slatkin, M. 2015. The effective founder effect in a spatially expanding population. - Evolution (N. Y). 69: 721–734.

Petit, C. et al. 1997. Variation in flowering phenology and selfing rate across a contact zone between diploid and tetraploid Arrhenatherum elatius (Poaceae). - Heredity (Edinb). 79: 31–40.

Porturas, L. D. et al. 2019. A meta-analysis of whole genome duplication and the effects on flowering traits in plants. - Am. J. Bot. 106: 469–476.

Powell, J. J. et al. 2017. The defence-associated transcriptome of hexaploid wheat displays homoeolog expression and induction bias. - Plant Biotechnol. J. 15: 533–543.

Price, C. A. et al. 2010. The metabolic theory of ecology: Prospects and challenges for plant biology. - New Phytol. 188: 696–710.

Qiu, T. et al. 2020. The effects of hybridization and genome doubling in plant evolution via allopolyploidy. - Mol. Biol. Rep. 47: 5549–5558.

Raabová, J. et al. 2008. Niche differentiation between diploid and hexaploid Aster amellus. - Oecologia 158: 463–472.

Ramsey, J. 2011. Polyploidy and ecological adaptation in wild yarrow. - Proc. Natl. Acad. Sci. U. S. A. 108: 7096–7101.

Ramsey, J. and Schemske, D. W. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. - Annu. Rev. Ecol. Syst. 29: 467–501.

Ramsey, J. and Schemske, D. W. 2002. Neopolyploidy in flowering plants. - Annu. Rev. Ecol. Syst. 33: 589–639.

Randolph, L. F. 1932. Some Effects of High Temperature on Polyploidy and Other Variations in Maize. - Proc. Natl. Acad. Sci. 18: 222–229.

Rao, S. et al. 2020. Chromosome doubling mediates superior drought tolerance in Lycium ruthenicum via abscisic acid signaling. - Hortic. Res. 7: 1–18.

Rausch, J. H. and Morgan, M. T. 2005. The effect of self-fertilization, inbreeding depression, and population size on autopolyploid establishment. - Evolution (N. Y). 59: 1867–1875.

Rice, A. et al. 2019. The global biogeography of polyploid plants. - Nat. Ecol. Evol. 3: 265–273.

Richardson, M. L. and Hanks, L. M. 2011. Differences in spatial distribution, morphology, and communities of herbivorous insects among three cytotypes of Solidago altissima (Asteraceae). - Am. J. Bot. 98: 1595–1601.

Rodríguez, D. J. 1996. A model for the establishment of polyploidy in plants. - Am. Nat. 147: 33–46.

Roff, D. 2001. Life History Evolution. - In: Encyclopedia of Biodiversity. Elsevier, pp. 631–641.

Schemske, D. W. and Lande, R. 1985. The evolution of self-fertilization and inbreeding depression in plants. II. Empirical observations. - Evolution (N. Y). 39: 41–52.

Segraves, K. A. and Thompson, J. N. 1999. Plant polyploidy and pollination: Floral traits and insect visits to diploid and tetraploid Heuchera grossulariifolia. - Evolution (N. Y). 53: 1114–1127.

Segraves, K. A. and Anneberg, T. J. 2016. Species interactions and plant polyploidy. - Am. J. Bot. 103: 1326–1335.

Selmecki, A. M. et al. 2015. Polyploidy can drive rapid adaptation in yeast. - Nature 519: 349–351.

Senock, R. S. et al. 1991. Ecophysiology of the polyploid shrub Atriplex canescens (Chenopodiaceae) growing in situ in the northern Chihuahuan Desert. - J. Arid Environ. 21: 45–57.

Sevim, V. and Rikvold, P. A. 2008. Chaotic gene regulatory networks can be robust against mutations and noise. - J. Theor. Biol. 253: 323–332.

Sharp, N. P. et al. 2018. The genome-wide rate and spectrum of spontaneous mutations differ between haploid and diploid yeast. - Proc. Natl. Acad. Sci. U. S. A. 115: E5046–E5055.

Shimizu-Inatsugi, R. et al. 2017. Plant adaptive radiation mediated by polyploid plasticity in transcriptomes. - Mol. Ecol. 26: 193–207.

Shimizu, K. K. 2022. Robustness and the generalist niche of polyploid species: Genome shock or gradual evolution? - Curr. Opin. Plant Biol. 69: 102292.

Snyder, R. E. and Chesson, P. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. - Ecol. Lett. 6: 301–309.

Solhaug, E. M. et al. 2016. Environmental regulation of heterosis in the allopolyploid Arabidopsis suecica. - Plant Physiol. 170: 2251–2263.

Solomon, J. K. Q. et al. 2014. Cattle grazing preference among tetraploid and diploid annual ryegrass cultivars. - Crop Sci. 54: 430–438.

Soltis, D. E. and Soltis, P. S. 1999. Polyploidy: Recurrent formation and genome evolution. -

Trends Ecol. Evol. 14: 348–352.

Soltis, P. S. and Soltis, D. E. 2009. The role of hybridization in plant speciation. - Annu. Rev. Plant Biol. 60: 561–588.

Spoelhof, J. P. et al. 2020. Habitat Shape Affects Polyploid Establishment in a Spatial, Stochastic Model. - Front. Plant Sci. 11: 1–11.

Stebbins, G. L. 1950. Variation and Evolution in Plants. - Columbia University Press.

Stebbins, G. L. 1971. Chromosomal evolution in higher plants. - Edward Arnold Ltd.

Stevens, A. V. et al. 2020. Polyploidy affects the seed, dormancy and seedling characteristics of a perennial grass, conferring an advantage in stressful climates. - Plant Biol. 22: 500–513.

Sutherland, B. L. et al. 2020. Strength in numbers? Cytotype frequency mediates effect of reproductive barriers in mixed-ploidy arrays. - Evolution (N. Y). 74: 2281–2292.

te Beest, M. et al. 2012. The more the better? The role of polyploidy in facilitating plant invasions. - Ann. Bot. 109: 19–45.

Thompson, J. D. and Lumaret, R. 1992. The evolutionary dynamics of polyploid plants: origins, establishment and persistence. - Trends Ecol. Evol. 7: 302–307.

Thompson, K. A. et al. 2014. Climatic niche differences between diploid and tetraploid cytotypes of Chamerion angustifolium (Onagraceae). - Am. J. Bot. 101: 1868–1875.

Thompson, K. A. et al. 2015. No influence of water limitation on the outcome of competition between diploid and tetraploid Chamerion angustifolium (Onagraceae) (S Bonser, Ed.). - J. Ecol. 103: 733–741.

Todd, R. T. et al. 2017. Ploidy variation in fungi: Polyploidy, aneuploidy, and genome evolution. - The Fungal Kingdom: 599–618.

Travis, J. M. J. et al. 2007. Deleterious mutations can surf to high densities on the wave front of an expanding population. - Mol. Biol. Evol. 24: 2334–2343.

Van de Peer, Y. et al. 2021. Polyploidy: an evolutionary and ecological force in stressful times. - Plant Cell 33: 11–26.

Van De Peer, Y. et al. 2017. The evolutionary significance of polyploidy. - Nat. Rev. Genet.

18: 411–424.

Van Dijk, P. and Bakx-Schotman, T. 1997. Chloroplast DNA phylogeography and cytotype geography in autopolyploid Plantago media. - Mol. Ecol. 6: 345–352.

Van Drunen, W. E. and Husband, B. C. 2018. Immediate vs. evolutionary consequences of polyploidy on clonal reproduction in an autopolyploid plant. - Ann. Bot. 122: 195–205.

Van Drunen, W. E. and Husband, B. C. 2019. Evolutionary associations between polyploidy, clonal reproduction, and perenniality in the angiosperms. - New Phytol. 224: 1266–1277.

Van Drunen, W. E. and Friedman, J. 2022. Autopolyploid establishment depends on life-history strategy and the mating outcomes of clonal architecture. - Evolution (N. Y). 76: 1953–1970.

van Laere, K. et al. 2011. Influence of ploidy level on morphology, growth and drought susceptibility in Spathiphyllum wallisii. - Acta Physiol. Plant. 33: 1149–1156.

Vanneste, K. et al. 2014. Tangled up in two: A burst of genome duplications at the end of the Cretaceous and the consequences for plant evolution. - Philos. Trans. R. Soc. B Biol. Sci. in press.

Vyas, P. et al. 2007. Effects of polyploidy on photosynthetic properties and anatomy in leaves of Phlox drummondii. - Funct. Plant Biol. 34: 673–682.

Wagner, W. H. 1970. BIOSYSTEMATICS AND EVOLUTIONARY NOISE. - Taxon 19: 146–151.

Wang, L. et al. 2019. Morphological, cytological and nutritional changes of autotetraploid compared to its diploid counterpart in Chinese jujube (Ziziphus jujuba Mill.). - Sci. Hortic. (Amsterdam). 249: 263–270.

Wei, N. et al. 2020. Genome duplication effects on functional traits and fitness are genetic context and species dependent: studies of synthetic polyploid Fragaria. - Am. J. Bot. 107: 262–272.

Willi, Y. and Buskirk, J. Van 2022. A review on trade-offs at the warm and cold ends of geographical distributions. - Philos. Trans. R. Soc. B Biol. Sci. in press.

Yamamichi, M. et al. 2022. Integrating eco-evolutionary dynamics and modern coexistence theory. - Ecol. Lett.: 1–16.

Yamauchi, A. et al. 2004. Triploid bridge and role of parthenogenesis in the evolution of autopolyploidy. - Am. Nat. 164: 101–112.

Yang, P. M. et al. 2019. The mechanism of starch content increase in grain of autotetraploid rice (Oryza sativa L.). - Photosynthetica 57: 680–687.

Yao, Y. et al. 2019. Using digital organisms to study the evolutionary consequences of whole genome duplication and polyploidy. - PLoS One 14: 1–21.

Zhang, F. et al. 2015. Autotetraploidization enhances drought stress tolerance in two apple cultivars. - Trees - Struct. Funct. 29: 1773–1780.

Zhang, C. et al. 2020. Enhanced relative electron transport rate contributes to increased photosynthetic capacity in autotetraploid pak choi. - Plant Cell Physiol. 61: 761–774.

Zhou, Y. et al. 2015. Transcriptomic analysis reveals differential gene expressions for cell growth and functional secondary metabolites in induced autotetraploid of chinese woad (Isatis indigotica fort.). - PLoS One 10: 1–19.

Figure caption

Fig. 1. Consequences of polyploidy. We distinguish direct costs (red), phenotypic effects (green), or ecological consequences (orange) that can operate as an equalizing mechanism affecting competitive ability, a stabilizing mechanism affecting niche, or both. Molecular changes refer to (epi)genetic and transcriptomic changes. Despite the indicated interrelations, this diagram is unavoidably a simplification of the complex, multivariate, species-specific consequence of whole-genome duplication (WGD).