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Evolutionary Consequences, Constraints and Potential of Polyploidy in Plants

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Abstract

Polyploidy, the possession of more than 2 complete genomes, is a major force in plant evolution known to affect the genetic and genomic constitution and the phenotype of an organism, which will have consequences for its ecology and geography as well as for lineage diversification and speciation. In this review, we discuss phylogenetic patterns in the incidence of polyploidy including possible underlying causes, the role of polyploidy for diversification, the effects of polyploidy on geographical and ecological patterns, and putative underlying mechanisms as well as chromosome evolution and evolution of repetitive DNA following polyploidization. Spurred by technological advances, a lot has been learned about these aspects both in model and increasingly also in nonmodel species. Despite this enormous progress, long-standing questions about polyploidy still cannot be unambiguously answered, due to frequently idiosyncratic outcomes and insufficient integration of different organizational levels (from genes to ecology), but likely this will change in the near future. See also the sister article focusing on animals by Choleva and Janko in this themed issue.

Keywords

Chromosome evolution; Diversification; Ecogeography; Polyploidy; Repetitive DNA

Polyploidy, initially considered ‘a hindrance to the evolutionary success of higher plants’ [Stebbins, 1971], is now recognized as a major force in plant evolution, affecting diversification and speciation [Otto and Whitton, 2000; Adams and Wendel, 2005; Soltis et al., 2009a; Madlung, 2013]. This is also due to genomic data, which show that all angiosperms, regardless of current genome size and chromosome number, have been affected by whole genome duplications (WGD), most of them repeatedly [Wendel, 2000; Seoighe, 2003; Comai, 2005; Jiao et al., 2011; McGrath and Lynch, 2012]. Comparisons of polyploid model systems including synthetic polyploids (e.g. wheat [Feldman and Levy, 2009]; *Brassica*/Brassicaceae [Gaeta and Pires, 2010]; *Spartina*/Poaceae [Ainouche et al., 2012]; *Senecio*/Asteraceae [Hegarty et al., 2012]; tobacco [Kovarik et al., 2012]; *Tragopogon*/Asteraceae [Soltis et al., 2012]; cotton [Wendel et al., 2012]) with the older established polyploids [Xiong et al., 2011; Kovarik et al., 2012; Wendel et al., 2012] reveal that the evolutionary consequences of polyploidization are manifold. Such studies are now greatly facilitated by the use of next-generation sequencing [Egan et al., 2012] readily applicable also in nonmodel systems [Zimmer and Wen, 2012]. Extensive and partly directed genetic, epigenetic, transcriptomic, and genomic changes often occur immediately after polyploidization [Liu and Wendel, 2003; Osborn et al., 2003; Levy and Feldman, 2004;

Adams and Wendel, 2005; Cifuentes et al., 2010; Gaeta and Pires, 2010; Parisod et al., 2010a, b] and may lead to long-term genetic, physiological and morphological differentiation, eventually resulting in novel phenotypes, the raw material for evolution. Some of the consequences of polyploidy shall be discussed in this review. After briefly introducing types of polyploids, we will discuss phylogenetic patterns in the incidence of polyploidy including possible underlying causes, the role of polyploidy for diversification (speciation and extinction), the effects of polyploidy on geographical and ecological patterns, and chromosome evolution and evolution of repetitive DNA following polyploidization. For other aspects of polyploid evolution in plants, such as genic redundancy and gene evolution or the process of diploidization, and for aspects of polyploid evolution in animals, the reader is referred to other contributions to this special issue.

Two basic types of polyploidy, auto- and allopolyploidy, are usually distinguished [Kihara and Ono, 1926]. Autopolyploidy refers to multiplication of genetically (nearly) identical chromosome sets within a single (sub)species [Ramsey and Schemske, 1998, 2002], whereas allopolyploidy entails the multiplication of chromosome sets accompanying hybridization between 2 genetically different (sub)species [Stebbins, 1971; Husband et al., 2013]. Furthermore, autopolyploids are usually characterized by polysomic inheritance and multivalent formation in meiosis, whereas allopolyploids show disomic inheritance and bivalent formation [Stebbins, 1971; Ramsey and Schemske, 2002; Comai, 2005; Le Comber et al., 2010; Parisod et al., 2010b; Zielinski and Mittelsten Scheid, 2012], although exceptions to these inheritance patterns do exist (e.g. in segmental allopolyploids [Stebbins, 1971] or in autopolyploids with regular bivalent formation [Weiss and Maluszynska, 2000]). The majority of well-analyzed polyploid systems are allopolyploids [te Beest et al., 2012], but with the availability of flow cytometry, which allows the incidence of autopolyploidy in natural populations to be quantitatively analyzed [e.g. Suda et al., 2007; Sonnleitner et al., 2010; Laport et al., 2012; Suda and Herben, 2013], autopolyploids have received more attention in the last years [Soltis et al., 2007; Parisod et al., 2010b].

A different classification system for polyploids is based on their evolutionary age, recognizing (in order of increasing age) neo-, meso- and paleopolyploids [Ehrendorfer, 1980; Ramsey and Schemske, 1998, 2002; Comai, 2005]. Their precise circumscription, however, differs depending on the defining characters used (e.g. chromosome pairing [Ramsey and Schemske, 2002]; cytological differentiation [Schubert and Lysak, 2011]).

Polyploidy Incidence and Evolutionary Potential for Diversification

Polyploidy is widespread in the plant kingdom, but its frequency and the maximum ploidies vary considerably among and within different taxonomic groups [Husband et al., 2013]. Polyploidy is absent in (or at least has played a minor role for diversification and evolution of) liverworts, hornworts and gymnosperms, while it has been very important in green algae, lycopods, ferns, and angiosperms [Barker, 2013; Husband et al., 2013; Murray, 2013; Weiss-Schneeweiss and Schneeweiss, 2013]. Even in groups, where polyploidy is rampant, it is unevenly distributed throughout different levels. For instance, within angiosperms, polyploidy is more frequent in monocots than in dicots [Otto and Whitton, 2000] and within monocots, polyploidy is more frequent in Poaceae than in Orchidaceae [Goldblatt, 1980]. Similar differences can also be observed at the interspecific level: a number of genera encompass species that participate in producing autopolyploids, allopolyploids or both, whereas related species are known from the diploid levels only [e.g. Kim et al., 2008; Brassac et al., 2012; Weiss-Schneeweiss et al., 2012].

This high variation in the frequency of polyploidy suggests different propensities for polyploidization and/or polyploid establishment in different lineages [Husband et al., 2013].

Underlying factors include rate of unreduced gamete formation [Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998, 2002; Ramsey, 2007] and features promoting polyploid formation, establishment and spreading, such as life and growth form (polyploids tend to be perennial and more often show vegetative propagation [Stebbins, 1971; Grant, 1981]), breeding system (e.g. apomixis will promote polyploid establishment and expansion [Levin, 2002]) or ecological pre-adaptations (e.g. better capabilities to invade harsher environments due to physiological changes and/or increased genetic buffering [Brochmann et al., 2004; Mable, 2004]). For allopolyploids, additional factors are the propensity for hybrid formation (e.g. wide geographic distributions or floral and inflorescence features enhancing cross-pollination such as attractiveness or longevity [Grant, 1981; Kim et al., 2008]) as well as parental divergence (i.e. higher chance of allopolyploid formation in cases of high parental divergence [Darlington, 1937; Chapman and Burke, 2007; Paun et al., 2009, 2011]), the latter probably reflecting higher rates of unreduced gamete formation in hybrids [Ramsey and Schemske, 1998], reduced number of meiotic abnormalities [Chapman and Burke, 2007], and/or increased transgressive segregation, adding to the hybrids' evolutionary potential [Stelkens and Seehausen, 2009]. The incidence of polyploidy correlates negatively with certain genomic features, such as genome size and chromosome numbers [Leitch and Leitch, 2008; Wood et al., 2009; Husband et al., 2013].

The role of polyploidy for speciation and diversification of angiosperms is still controversial. Early on, Stebbins [1950] considered polyploids as evolutionary dead ends because the additional genomes not only masked deleterious, but also beneficial mutations and because new gene combinations were rarely formed due to increased self-fertilization, both factors reducing the rate of adaptive evolution. In contrast, more recent authors emphasize the significant evolutionary potential of polyploids highlighting several advantages of polyploids, including the increased number of alleles allowing masking of deleterious recessive mutations, often stable heterosis allowing transgressive performance, and the potential of duplicated genes to acquire new or slightly varied functions [Soltis and Soltis, 1993; Wendel, 2000; Adams and Wendel, 2005; Madlung, 2013].

A favorable role of polyploidy for the diversification of angiosperms is suggested by several lines of evidence: (1) the majority of polyploid taxa are of multiple and spatially and/or temporally recurrent origin potentially increasing the polyploid's genomic diversity [Soltis and Soltis, 1999; Soltis et al., 2009b, 2012; Hegarty et al., 2012; Weiss-Schneeweiss et al., 2012]; (2) species richness and the frequency of polyploids are positively related, the greatest species richness being found in genera with 50–75% polyploid species [Petit and Thompson, 1999; Otto and Whitton, 2000; Vamosi and Dickinson, 2006]; (3) fossil evidence indicates polyploidy in the majority of angiosperms [Masterson, 1994]; and (4) *all* angiosperms show traces of at least one ancient WGD event [Jiao et al., 2011]. Accordingly, a dramatic increase in species richness in several clades of angiosperms after an ancient WGD has been interpreted as indicative for a higher diversification in polyploids [Soltis et al., 2009a], reduced risks of extinction due to functional redundancy, mutational robustness and increased rates of evolution and adaptation in polyploids [Crow and Wagner, 2006] being one possible mechanism. An increase in polyploids is also predicted by the nonadaptive null model of the polyploidy ratchet [Meyers and Levin, 2006], which is based on the assumption that polyploidy is largely irreversible [DeWet, 1968; Stebbins, 1980; Grant, 1981].

In contrast, Wood et al. [2009] found no correlation of polyploidization rates with species richness. Instead, despite ubiquitous polyploidy in ferns and angiosperms only 31 and 15%, respectively, of all speciation events were associated with polyploidization. Similarly, Mayrose et al. [2011] inferred that polyploidization events were overrepresented at the tips of a phylogenetic tree and that net diversification rates of polyploids were significantly less

than the rates of diploids due to reduced or, if accounting for the reduced probability of polyploid speciation in an already polyploid lineage, unchanged speciation rates in established polyploids and due to increased extinction rates in neopolyploids. Taken together, this suggests that the observed high frequency of polyploids is a consequence of their high formation rate rather than the diversification of polyploids themselves [Arrigo and Barker, 2012]. Even if polyploidy often will be an evolutionary dead end, some of these events can result in very successful lineages, as is evident from the paleopolyploid ancestor of extant angiosperms. This may be because (1) polyploids originated at specific times favorable for polyploid diversification (due to e.g. ample availability of novel niches), as has been suggested for several clades of angiosperms at the Cretaceous-Tertiary mass extinction event [Fawcett et al., 2009], (2) WGD conferred increased plant complexity via retention of duplicated genes underlying transcriptional regulatory networks [DeBodt et al., 2005], or (3) WGD can increase the evolutionary potential over a long period of time [Fawcett et al., 2013]. Further research will be necessary to establish the precise role of polyploidy for lineage diversification over different temporal scales and its underlying mechanisms.

Ecogeographical Consequences of Polyploidy

Polyploidy is considered an important factor shaping the geographical range of a species. Initial evidence for a link between ploidy and distribution came from surveys of relative frequencies of polyploids in different floras or taxonomic groups. These revealed that the frequency of polyploids increases with increasing latitude [compilations in Löve and Löve, 1949–1951; Reese, 1958; Grant, 1981], even within the Arctic [Brochmann et al., 2004], increasing altitude [compilation in Hanelt, 1966; Löve and Löve, 1967] or other forms of increasing environmental extremeness, such as salinity [Tischler, 1937]. Of these mentioned, only the high incidence of polyploidy at high altitudes appears to hold [Husband et al., 2013]. A variety of factors have been suggested to explain such trends, including high genetic and biochemical diversity in polyploids [Otto and Whitton, 2000; Brochmann et al., 2004], better colonizing capabilities of polyploids especially into deglaciated areas [Stebbins, 1984, 1985; Brochmann et al., 2004], the age of a flora [Reese, 1958; Ehrendorfer, 1980], or conditions brought about by Milankovitch climatic oscillations. These conditions, because of lack of species specialized to the newly emerged environmental conditions, provide new expansion possibilities allowing direct competition with progenitors to be avoided, and promoting secondary contact zones [Dynesius and Jansson, 2000]. Testing these hypotheses is impeded by uncertainty concerning the general validity of a latitudinal trend because of geographically uneven sampling (subtropical and tropical regions remain understudied), high inconsistency in the geographic position of diploids and polyploids within a certain taxonomic group, and the failure to account for confounding effects of different biogeographic and phylogenetic histories [Husband et al., 2013]. These obstacles are not insurmountable: flow cytometric ploidy determination, calibrated by karyologically verified chromosome numbers, allows ploidy data to be gathered for many samples (preferably from the region under consideration [Ehrendorfer, 1980]) in a relatively short period of time [Suda et al., 2007] and phylogenetic history can be readily accommodated by using phylogenetic comparative techniques [Harvey and Pagel, 1991; Pagel, 1999]. Clearly, a broad comparison of a large number of diploid and polyploid species is needed to comprehensively test the long-standing hypothesis of a latitudinal ploidy gradient.

A corollary of the hypothesis that polyploids have greater genetic and biochemical diversity and thus greater ecological tolerance is that polyploids are expected to have larger geographic ranges and/or occur in more habitats than diploids [Levin, 2002]. Such relationships are indeed observed in specific taxonomic groups: e.g. broader ecological niches in hexaploids compared to diploids in the *Claytonia perfoliata* complex

(Portulacaceae) [McIntyre, 2012b], the wide distribution of tetraploid *Biscutella laevigata* (Brassicaceae) compared to small distribution areas of diploids associated with Pleistocene glacial refugia [Tremetsberger et al., 2002; Parisod and Besnard, 2007], or significantly larger ranges in polyploid species of *Clarkia* (Onagraceae) compared to diploid ones [Lowry and Lester, 2006]. Survey data on percentages of polyploids in widespread European genera [Stebbins and Dawe, 1987], on the range of ecological requirements of Pyrenean plants [Petit and Thompson, 1999], and on extent and mean geographic and ecological ranges in North American plants [Martin and Husband, 2009] provide, however, no support for this hypothesis. Further studies employing large surveys while taking phylogenetic relationships into account will be necessary to ascertain that polyploidy does not translate into larger ranges and/or greater diversity of occupied habitats.

An indirect association between range size and polyploidy arises via invasiveness and rarity. Comparative evidence [Pandit, 2006; Pandit et al., 2011] shows that the incidence of polyploidy is positively correlated with invasiveness (invasive species tend to be widespread in their native ranges [Pyšek et al., 2009; Hovick et al., 2012]), but negatively correlated with rarity (rare species tend to be narrowly distributed [Gaston, 1996]). In general, polyploidy is considered an important factor in species invasion success via, e.g. pre-adaptation to novel conditions or higher adaptive potential due to increased genetic diversity [te Beest et al., 2012].

Even if there is no consistent trend in geographic patterns of polyploids, there is no doubt that polyploids usually are geographically and/or ecologically differentiated from their diploid ancestors. Ecogeographic isolation (i.e. the combined role of ecology and geography as a reproductive barrier) is recognized as an important factor in plant speciation in general [Sobel et al., 2010] and is amply documented in diploid-polyploid systems [e.g. Felber-Girard et al., 1996; Halverson et al., 2008; Duchoslav et al., 2010; Sonnleitner et al., 2010; Glennon et al., 2012; Kolář et al., 2012; McIntyre, 2012a, b], also on a local scale (fig. 1a) [Baack, 2004; Schönswetter et al., 2007; Hülber et al., 2009]. The pervasiveness of ecogeographic divergence is in line with modeling results [Fowler and Levin, 1984; Rodriguez, 1996; Oswald and Nuismer, 2011] showing that niche differentiation is an important way of escaping the minority cytotype exclusion [Levin, 1975], i.e. the exclusion of newly emerging and initially rare polyploids from a diploid population due to (unsuccessful) pollination (triploid block [Köhler et al., 2010]) with pollen from the much more common diploids [Suda and Herben, 2013]. Factors potentially reinforcing niche differentiation are reproductive assurance (via increased selfing) [Rodriguez, 1996; Rausch and Morgan, 2005], known for angiosperms [Mable, 2004; Barringer, 2007], or via asexuality, including apomixis [Hörandl, 2006; Kao, 2008] and vegetative propagation [Gustafsson, 1948, Otto and Whitton, 2000, but see Baldwin and Husband, 2013] or by higher assortative mating [Husband, 2000; Oswald and Nuismer, 2011], which may be achieved by local pollen and seed dispersal [Baack, 2005]. Although the minority cytotype exclusion principle has been developed for autopolyploids and segmental allopolyploids [Levin, 1975], fitness disadvantages due to e.g. stigma clogging [Lloyd and Webb, 1986; Webb and Lloyd, 1986] can also be expected for allopolyploids if in minority. Furthermore, niche differentiation is an important way of competition avoidance both for autopolyploids and allopolyploids, as it is for homoploid species.

Valuable insights into the ecological factors (habitat features) that putatively underlie cytotype divergence can be gained from correlations of cytotype distribution with ecological (habitat) features. For instance, in *Senecio carniolicus* (Asteraceae) diploids occur in more open and usually also more exposed habitats, whereas polyploids are found in more dense vegetation (fig. 1a) [Hülber et al., 2009; Sonnleitner et al., 2010]; in *Aster amellus* (Asteraceae), sites of diploid and hexaploid populations differ significantly in vegetation and

soil properties [Raabova et al., 2008]; compared to diploid *Centaurea maculosa* (Asteraceae) tetraploid cytotypes show a shift towards drier climates, which is even more pronounced in the introduced North American range [Treier et al., 2009]; the distribution of diploid and tetraploid races of *Brachypodium distachyon* (Poaceae) is geographically structured and associated with an aridity gradient [Manzaneda et al., 2012].

Establishing a causal link between ploidy and ecogeographic differentiation remains, however, challenging. First, little is known whether this divergence is due to nonadaptive processes (dispersal limitation, phylogeographic structure due to e.g. different Pleistocene refugia) or due to adaptive processes. For instance, current distribution patterns of tetra- and octoploid *Cardamine torrentis* s. l. (Brassicaceae) were suggested to be caused by historical factors, mainly Late Pleistocene climatic oscillations [Marhold et al., 2010]. Testing this or a similar hypothesis requires reciprocal transplant experiments. If nonadaptive processes were responsible, then cytotypes are expected to perform at least as well in the other cytotype's habitat as in their own. Consequently, the lack of observing any advantage in the parental habitat, as seen in *Ranunculus adoneus* (Ranunculaceae) [Baack and Stanton, 2005], is indicative of nonadaptive divergence. In other cases, it has been shown that ecogeographic differentiation is due to local adaptation [e.g. Flégrová and Krahulec, 1999; Raabova et al., 2008; Ramsey, 2011]. Clearly, considerably more data will be necessary to address the relative importance of nonadaptive versus adaptive cytotype divergence.

Second, despite an early interest in the underlying mechanisms of ecogeographic differentiation of polyploids from diploids [e.g. Hagerup, 1932, 1933], effects of polyploidy on physiological and morphological traits determining the ecology of plants remain poorly understood [Soltis et al., 2010]. Numerous physiological traits have been found to differ between polyploids and diploids, including growth rates [Garbutt and Bazzaz, 1983], secondary metabolism [McArthur and Sanderson, 1999], cold tolerance [Liu et al., 2011], water relations [Maherali et al., 2009], or stress tolerance [Schlaepfer et al., 2010; Coate et al., 2013]. The adaptive potential of such differences has been recently shown in *B. distachyon* (Poaceae), where the higher water-use efficiency of tetraploids likely is co-responsible for its occurrence in more arid regions compared to the diploid cytotype [Manzaneda et al., 2012], and in *Atriplex canescens* (Chenopodiaceae), where higher ploidy cytotypes have greater xylem cavitation resistance than diploids, allowing them to grow on more drought-prone soils [Hao et al., 2013]. Polyploidization has an immediate effect on plant morphology via usually enlarged cell sizes [Müntzing, 1936], which via changes in cellular architecture, regulatory functions and replication times [Bennett and Leitch, 2005; Comai, 2005] may also affect metabolism and growth rates [Cavalier-Smith, 1978]. In allopolyploids, heterosis conferred by, for example, epigenetic modifications of circadian clock genes [Ni et al., 2009] can contribute to increased morphological vigor [Chen, 2010]. Morphologically, polyploids (at least in the first phase after their origin) often are larger in habit (fig. 1b–d) and have larger seeds [Garbutt and Bazzaz, 1983; Bretagnolle and Lumaret, 1995; Bretagnolle et al., 1995], which may lead to increased competitiveness [Maceira et al., 1993; Schlaepfer et al., 2010; but see Burton and Husband, 2000; Hülber et al., 2011]. Furthermore, they usually have larger flowers (fig. 1b–d), which may increase pollinator visitation frequencies [Kennedy et al., 2006] or alter pollinator spectra [Segraves and Thompson, 1999], and they have more flowers per inflorescence [Vamosi et al., 2007], which may increase selfing rates via geitonogamy [Harder and Barrett, 1995]. Because of their hybrid origin, allopolyploids show earlier and more pronounced changes in gene expression than autopolyploids [Church and Spaulding, 2009; Hegarty et al., 2012], which may translate into more pronounced variation in physiological and morphological traits in allopolyploids [e.g. Oates et al., 2012]. Evidently, more studies, which can profit from data on trait evolution following polyploidy obtained from crop and non-crop model species [e.g.

Pires et al., 2004b; Bansal et al., 2012; Miller et al., 2012], will be necessary to fully understand the role of traits and their interaction for cytotype divergence.

Finally, the commonly used approach of comparing diploids with naturally occurring polyploids fails to distinguish between differences caused by polyploidy per se from those evolved since the polyploid formation. Although recently (i.e. in historical times) evolved allopolyploids, such as North American *Tragopogon* species (Asteraceae; Soltis et al. [2004]), *Spartina anglica* (Poaceae; Ainouche et al. [2004]) or *S. cambrensis* (Asteraceae; Abbott and Lowe [2004]), constitute valuable model systems, especially size-related differences between cytotypes appear to decrease rapidly over a few generations [Otto and Whitton, 2000], rendering their assessment even in those systems difficult. An alternative approach is to use first generation polyploids (selected polyploid offspring of diploid parents or induced polyploids [Ramsey, 2007; Wu et al., 2012]) and compare these to both the diploid ancestors and established polyploid lineages (of usually unknown age). Using this approach, Ramsey [2011] found that newly generated hexaploids of *Achillea borealis* (Asteraceae) possessed a 70% survival advantage in habitats of established hexaploids (Mediterranean type habitats, such as sand dunes or oak woodlands) compared to the parental tetraploids (found in more mesic habitats). In *Chamerion angustifolium* (Onagraceae), newly generated polyploids had physiological tolerances to water stress comparable to the diploids [Maherali et al., 2009], higher evolvability of flowering time in response to selective pressure [Martin and Husband, 2012], lower pollen siring success than both diploids and established tetraploids [Baldwin and Husband, 2011], and low intrinsic cost of selfing [Husband et al., 2008]. Data from this powerful approach are still too scarce to allow generalizations, and it remains to be tested, to what extent changes in traits potentially conferring ecogeographic divergence are due to the polyploidization event versus subsequent changes due to selection.

Repetitive DNA and Chromosomal Evolution

In contrast to genomes of higher animals [Kejnovsky et al., 2009], plant genomes contain large proportions of repetitive DNA [Schmidt and Heslop-Harrison, 1998; Leitch and Leitch, 2008; Heslop-Harrison and Schwarzacher, 2011]. This genome fraction in plants consists of tandem repeats (rDNA, satellite DNA) and of dispersed repeats, mainly transposable elements (mostly LTR retro-elements comprising Ty1-*copia* and Ty3-*gypsy* elements [Kumar and Bennetzen, 1999; Bennetzen, 2002; Bento et al., this issue]). Evolution of transposable elements in most of the polyploid genomes is specific for the type of transposable element and very dynamic [Baumel et al., 2002; Petit et al., 2007, 2010; Parisod et al., 2012], with the possible exception of cotton [Wendel et al., 2012]. In the pre-genomic era, methodological constraints have restricted analysis of repetitive DNA in polyploids mostly to the highly conserved and ubiquitous rDNA [Maluszynska et al., 1998] or to a few available or newly isolated tandemly repeated DNA types [Zhao et al., 1998; Lim et al., 2000b, 2008; Pires et al., 2004a; Chester et al., 2010; Petit et al., 2010; Kolano et al., 2011]. This has changed with the availability of next-generation sequencing techniques allowing in depth characterization of repetitive DNA [e.g. Macas et al., 2007, 2011; Wicker et al., 2009; Hribová et al., 2010] also in polyploids (allopolyploid tobacco [Renny-Byfield et al., 2011; Buggs et al., 2012; Parisod et al., 2012], cotton [Wendel et al., 2012] and *Tragopogon*/Asteraceae [Soltis et al., 2012] as well as the likely autotetraploid [Schneeweiss et al., 2004] *Orobancha gracilis* [Piednoël et al., 2012]).

Polyploids typically show genome rearrangements involving rDNA repeat and/or locus silencing (nucleolar dominance [Preuss and Pikaard, 2007]) or loss [Vaughan et al., 1993; Lim et al., 2000a, b, 2007a, b; Weiss-Schneeweiss et al., 2007, 2012; Kotseruba et al., 2010; Kolano et al., 2011; Ksiazek et al., 2011], interlocus recombination and complete or near-

complete repeat replacement [Lim et al., 2000a; Kovarik et al., 2005; Matyasek et al., 2007; Mlinarec et al., 2012; Weiss-Schneeweiss et al., 2012], or redistribution and/or increase in loci number [Adams et al., 2000; Weiss-Schneeweiss et al., 2007]. The underlying mechanisms include physical locus loss, interchromosomal translocations [Weiss and Maluszynska, 2000], or differential and repeated amplification of minor and reduction of major loci of rDNA [Childs et al., 1981; Dubcovsky and Dvorak, 1995]. For 35S rDNA, locus loss as well as repeat type conversion and homogenization have been commonly reported especially in older allopolyploids [Clarkson et al., 2005; Weiss-Schneeweiss et al., 2012]. The evolution of 35S rDNA can be directional, loci of one parent always being lost or converted (fig. 1e) [Vaughan et al., 1993; Lim et al., 2000a; Jang et al., 2011; Renny-Byfield et al., 2011; Kovarik et al., 2012; Weiss-Schneeweiss et al., 2012]. The direction of conversion and homogenization of 35S rDNA can be biased towards the maternal [Weiss-Schneeweiss et al., 2012] or the paternal parent [Lim et al., 2000a, b; Matyasek et al., 2003; Renny-Byfield et al., 2011] and may differ in independently originated allopolyploids of identical parentage (fig. 1e) [Weiss-Schneeweiss et al., 2012]. In contrast to tobacco, in North American *Tragopogon*, containing the allopolyploids *T. mirus* (*T. dubius* × *T. porrifolius*) and *T. miscellus* (*T. dubius* × *T. pratensis*) that formed repeatedly following the introduction of 3 diploids to the United States ~80 years ago [Soltis et al., 2004], both rDNA loci number and distribution remain additive in the polyploids [Pires et al., 2004a]. Still, concerted evolution of 35S rDNA in *Tragopogon* allopolyploids is ongoing and incomplete [Kovarik et al., 2005], with transcription favoring the underrepresented *T. dubius* copies [Matyasek et al., 2007; Malinska et al., 2010]. In contrast to 35S rDNA, there is no evidence for interlocus homogenization of 5S rDNA in any of the polyploid systems analyzed (tobacco, Fulnecek et al. [2002]; cotton, Cronn et al. [1996]; *Melampodium*/Asteraceae (fig. 1e–h), Weiss-Schneeweiss et al. [2012]). 5S rDNA loci may, however, change in number, most frequently being lost [Clarkson et al., 2005; Weiss-Schneeweiss et al., 2012]. Extent and rate of rDNA loci loss roughly correlates with a polyploid's age: in younger allopolyploids and in autopolyploids, the number of loci often equals the sum of those of their progenitors [Clarkson et al., 2005; Chester et al., 2012; Rebernik et al., 2012], whereas in older allopolyploids maternal and/or paternal loci are often lost [Clarkson et al., 2005; Weiss-Schneeweiss et al., 2007, 2012; Kolano et al., 2011].

Transposable elements are important components of genome size evolution, participating not only in genome size increase, but also in genome downsizing, which seems to be a general trend in polyploids [Leitch and Bennett, 2004]. Its extent is group specific [Weiss-Schneeweiss et al., 2007], but clearly depends on the age of the polyploid, with additive genome size compared to parental genomes in young polyploids [Rebernik et al., 2012; Soltis et al., 2012] and reaching significant levels of reduction in old polyploids, where genome downsizing might also be accompanied by chromosome number reductions [Clarkson et al., 2005; Schönswetter et al., 2007; Mandakova et al., 2010; Doyle, 2012]. In *Nicotiana tabacum*, an intersectional hybrid formed within the last 200,000 years from relatives of extant diploids *N. silvestris* (genome S) and *N. tomentosiformis* (genome T [Kenton et al., 1993; Kovarik et al., 2012]), established and newly synthesized polyploids show congruent patterns of retroelement dynamics (mobility and loss) and of changes in copy number of various repetitive DNAs, suggesting that retrotransposon amplification and genome restructuring in tobacco occurs rapidly and is directional [Skalická et al., 2005; Renny-Byfield et al., 2012; Kovarik et al., 2012]. Selected families of *copia* LTR-retrotransposons diversified subsequent to allopolyploidization, with retroelement losses being more frequent from the paternal T-genome and novel insertions targeting preferentially the maternal S-genome [Petit et al., 2007, 2010]. However, spreading of genome-specific transposons to the other parental genome has also been found in cotton [Zhao et al., 1998]. Genome downsizing in tobacco [Leitch et al., 2008] can be attributed to extensive losses across most repeat types (NicCL3; A1/A2 repeats; NsEPRV, *Ty3/gypsy*

LTR elements, 35S rDNA) preferentially from the paternal T-genome [Renny-Byfield et al., 2011, 2012]. The directed preferential loss of repeats from one paternal genome may provide support for the nuclear-cytoplasmic interaction hypothesis whereby the paternal genome may be in disadvantage due to incompatibility in interactions with maternally inherited cytoplasm [Leitch et al., 2006].

Chromosomal rearrangements are often associated with rearrangements of the repetitive DNA fraction or result from extensive homeologous chromosome recombination [Gaeta et al., 2007] and may lead to considerable chromosome number reductions [Lysak et al., 2006; Mandakova et al., 2010; Weiss-Schneeweiss and Schneeweiss, 2013]. Changes in gross genome structure encompass numerous balanced (conversions, inversions, translocations, fusions, or fissions) and unbalanced (duplications, deletions or aneuploidy) chromosomal rearrangements [Lysak and Schubert, 2013] and have been addressed only in a few polyploid systems [Lim et al., 2000a, b, 2007a, b, 2008; Weiss-Schneeweiss et al., 2007, 2012; Mandakova et al., 2010; Książczyk et al., 2011; Renny-Byfield et al., 2011; Chester et al., 2012]. In tobacco, early cytogenetic analyses revealed several intergenomic translocations [Kenton et al., 1993; Moscone et al., 1996; Lim et al., 2004], some of which were fixed and some of which were also detected in synthetic tobacco [Skalická et al., 2005]. Intergenomic translocations are also known from the allopolyploid *Avena/Poaceae* [Jellen et al., 1994]. An extensive survey in *T. miscellus* revealed common intergenomic translocations, likely the result of homoeologous recombination, with some of the translocations being close to fixation [Chester et al., 2012]. Although most of the individuals analyzed were $2n = 24$ and despite earlier observations of preferential bivalent pairing in meiosis [Ownbey, 1950], very few individuals had additive karyotypes (i.e. all parental chromosomes present in 2 copies [Lim et al., 2008; Chester et al., 2012]). This compensatory (reciprocal) aneuploidy, which may result from high homology between the 2 parental genomes and subsequent (bivalent) homeologous chromosome pairing, will influence disomic versus polysomic inheritance of some genes [Chester et al., 2012]. This deviation from gene balance may also have consequences, for example, in gene expression or phenotypic traits [Birchler and Veitia, 2012]. Compensatory aneuploidy is known from other synthetic or spontaneous neo-allopolyploids (e.g. synthetic *B. napus* [Xiong et al., 2011] or wheat [Mestiri et al., 2010]). A similar system occurs also in inter-cytotype polyploids of *Prospero autumnale* (Hyacinthaceae). Allopolyploids of the diploid cytotypes with $2n = 12$ and $2n = 14$, where $2n = 12$ arose after a fusion of 2 chromosomes of the $2n = 14$ cytotype [Vaughan et al., 1997], produce – due to preferential bivalent formation between homologous or homeologous chromosomes alike – F1 progeny with balanced chromosome numbers varying from $2n = 24$ to $2n = 28$, but most common $2n = 26$ [Jang et al., 2011; Weiss-Schneeweiss et al., unpubl. data].

Chromosomal evolution of polyploids is usually driven by amplification and removal of repetitive DNA and by inflicted gross chromosomal changes, most commonly translocations, inversions, aneuploidy, or dysploidy [Ma and Gustafson, 2005]. Such changes not only affect chromosome numbers, karyotype structure or genome size, but are very important for restoring full fertility via proper chromosome pairing [Feldman and Levy, 2009]. This diploidization has 2 components: while genetic diploidization restores disomic inheritance, cytological diploidization manifests itself in regular bivalent pairing, despite homeology or redundant homology [Feldman and Levy, 2009]. As the time required for achievement of full bivalent pairing depends greatly on the degree of chromosome homeology, autopolyploids are expected to be much more prone to multivalent formation than allopolyploids. This might have consequences for establishment probabilities of newly formed polyploids, which may be higher in allopolyploids than in autopolyploids.

Conclusions

Although a lot has been learned about polyploidy both in model and, spurred by technological advances, also in nonmodel species, many long-standing questions about polyploidy concerning, for instance, its role in lineage diversification or its ecological consequences can still not be unambiguously answered. This is due to both still insufficient knowledge on many aspects of polyploidy (especially concerning ecology, physiology and evolution [Soltis et al., 2010]) and insufficient integration of different organizational levels (e.g. whether transcriptomic and genomic changes lead to greater adaptation [Madlung, 2013]). Although many of the evolutionary consequences of polyploidy reviewed herein apply to both autopolyploids and allopolyploids, their precise evolutionary trajectories are expected to differ, given that allopolyploids combine effects of genome doubling (polyploidy) with those of genome merger (hybridization). Integrative approaches combining phylogenetic, molecular and ecophysiological tools across autopolyploid and allopolyploid model systems have great potential to help us better understand the evolutionary and ecological role of polyploidy.

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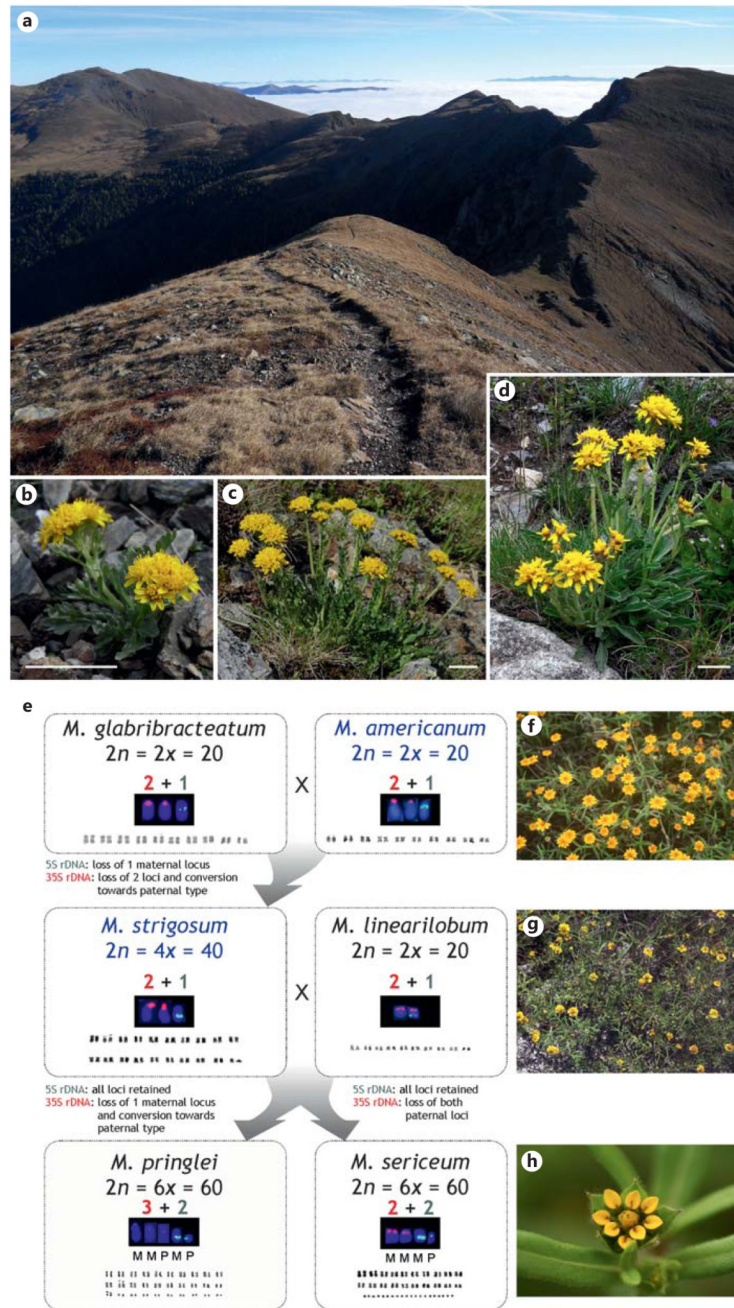


Fig. 1.
a In the easternmost Alps, the 3 main cytotypes of *Senecio carnolicus* (Asteraceae) occur in mixed populations, where they separate into different microhabitats: diploids (**b**) grow in open, rocky patches (foreground), tetraploids (**c**) are found on mostly north-exposed slopes with longer snow-cover (left side of the ridge), and hexaploids (**d**) occur in dense grass swards (right side of the ridge). The 3 cytotypes also differ morphologically with respect to overall size (scale bars in **b–d** approximately 5 cm), dimensions of the synflorescence and the flowering head, indumentum and leaf shape. **e** In *Melampodium* sect. *Melampodium* (Asteraceae), sequential allopolyploidization involved (maternal parent indicated in blue)

diploid *M. glabribracteatum* and likely *M. americanum* (**f**), giving rise to allotetraploid *M. strigosum*, which in turn together with diploid *M. linearilobum* (**g**) resulted in the allohexaploids *M. pringlei* and *M. sericeum* (**h**). Whereas no gross karyotypic change is evident during allopolyploid evolution (karyotypes are given for each species), evolution of rDNA loci is characterized by loci loss and conversion (chromosomes carrying rDNA loci are shown for each species, 5S and 35S rDNA indicated by green and red fluorescence signals, respectively), which differ in the independently originated allohexaploids despite their identical parentage. (Photo credits: **a** M. Winkler, **b– d** M. Sonnleitner, **f– h** T.F. Stuessy and E. Ortiz.)