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Research review

Evolutionary consequences of autopolyploidy

Author for correspondence:

Christian Parisod
Tel: +41 3271 82344
Email: christian.parisod@unine.ch

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Christian Parisod^{1,2}, Rolf Holderegger³ and Christian Brochmann¹

¹National Centre for Biosystematics, Natural History Museum, University of Oslo, 0318 Oslo, Norway; ²Laboratory of Evolutionary Botany, Institute of Biology, University of Neuchâtel,

2009 Neuchâtel, Switzerland; ³WSL Swiss Federal Research Institute, 8903 Birmensdorf, Switzerland

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Summary

Autopolyploidy is more common in plants than traditionally assumed, but has received little attention compared with allopolyploidy. Hence, the advantages and disadvantages of genome doubling *per se* compared with genome doubling coupled with hybridizations in allopolyploids remain unclear. Autopolyploids are characterized by genomic redundancy and polysomic inheritance, increasing effective population size. To shed light on the evolutionary consequences of autopolyploidy, we review a broad range of studies focusing on both synthetic and natural autopolyploids encompassing levels of biological organization from genes to evolutionary lineages. The limited evidence currently available suggests that autopolyploids neither experience strong genome restructuring nor wide reorganization of gene expression during the first generations following genome doubling, but that these processes may become more important in the longer term. Biogeographic and ecological surveys point to an association between the formation of autopolyploid lineages and environmental change. We thus hypothesize that polysomic inheritance may provide a short-term evolutionary advantage for autopolyploids compared to diploid relatives when environmental change enforces range shifts. In addition, autopolyploids should possess increased genome flexibility, allowing them to adapt and persist across heterogeneous landscapes in the long run.

Introduction

Polyploidy, the acquisition of more than two sets of chromosomes, has been an important factor in eukaryote evolution (Otto, 2007). Between 30% and 70% of angiosperm species are believed to be of polyploid ancestry (Stebbins, 1971; Masterson, 1994). While genome doubling is now recognized as important in natural populations, the genetic and ecological factors affecting the abundance of polyploid lineages are still insufficiently known (Müntzing, 1936; Clausen *et al.*, 1945; Stebbins, 1971; Grant, 1981; Levin, 2002; Comai, 2005; Soltis & Soltis, 2009). Recent studies have demonstrated that polyploid genomes can be highly

dynamic and undergo rapid structural and functional alterations (e.g. diploidization; Fig. 1). These findings have renewed interest in examining genome multiplication as an evolutionary process (Doyle *et al.*, 2008; Leitch & Leitch, 2008).

The classification of polyploids into the two major categories of autopolyploids and allopolyploids is still debated (Clausen *et al.*, 1945; Ramsey & Schemske, 1998). Autopolyploids are traditionally considered to arise within a single species by doubling of structurally similar, homologous genomes (AAAA), whereas allopolyploids arise via interspecific hybridization and subsequent doubling of nonhomologous (i.e. homoeologous) genomes (AABB). Autopolyploids may

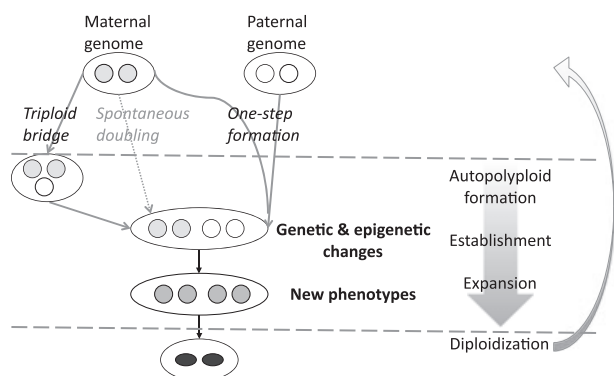


Fig. 1 Evolutionary pathway of autopolyploidy. Top panel: cross-fertilization between individuals leads to the origin of an autotetraploid individual by genome doubling, either through the direct fusion of two unreduced gametes (one-step formation) or as a two-step process of cross-fertilization between an unreduced gamete and a triploid intermediate (triploid bridge). Spontaneous doubling is rare in natural populations. Central panel: genome doubling results in genetic and epigenetic changes driving structural and functional reorganization until full diploidization in the long term. In natural populations, these genomic processes go along with the formation, establishment and expansion of autopolyploid lineages.

thus show multivalent formation during meiosis, while allopolyploids predominantly form bivalents, as nonhomologous chromosomes do not pair (Jackson, 1982; Ramsey & Schemske, 2002). Furthermore, Stebbins (1971) classified polyploid hybrid taxa mainly forming multivalents during meiosis as 'segmental allopolyploids', in order to denote the doubling of only partly differentiated genomes (AAA'A). While it is widely appreciated that polyploidy encompasses a continuum from the doubling of identical genomes to the doubling of highly differentiated genomes, it should be stressed that classification based on cytological evidence may be misleading as chromosome pairing behavior is also affected by factors other than purely structural ones (Jenczewski & Alix, 2004; Otto, 2007). Notably, autopolyploids forming only bivalents have more than two sets of homologous chromosomes to be randomly paired, and alleles at a given locus accordingly segregate at random, resulting in polysomic inheritance (Fig. 2). Polysomic inheritance has regularly been observed in natural populations (Soltis & Soltis, 1993; Jackson & Jackson, 1996; Landergott *et al.*, 2006; Stift *et al.*, 2008) and can be considered a diagnostic trait to distinguish autopolyploids from allopolyploids.

No recent review has focused on the putative evolutionary advantages of autopolyploids. For a long time, autopolyploids were believed to suffer from several evolutionary disadvantages when compared with allopolyploids, and this led Clausen *et al.* (1945) and Stebbins (1971) to propose that autopolyploids are rare and represent evolutionary dead-ends. In particular, multivalent formation after genome multiplication may cause meiotic irregularities and result in

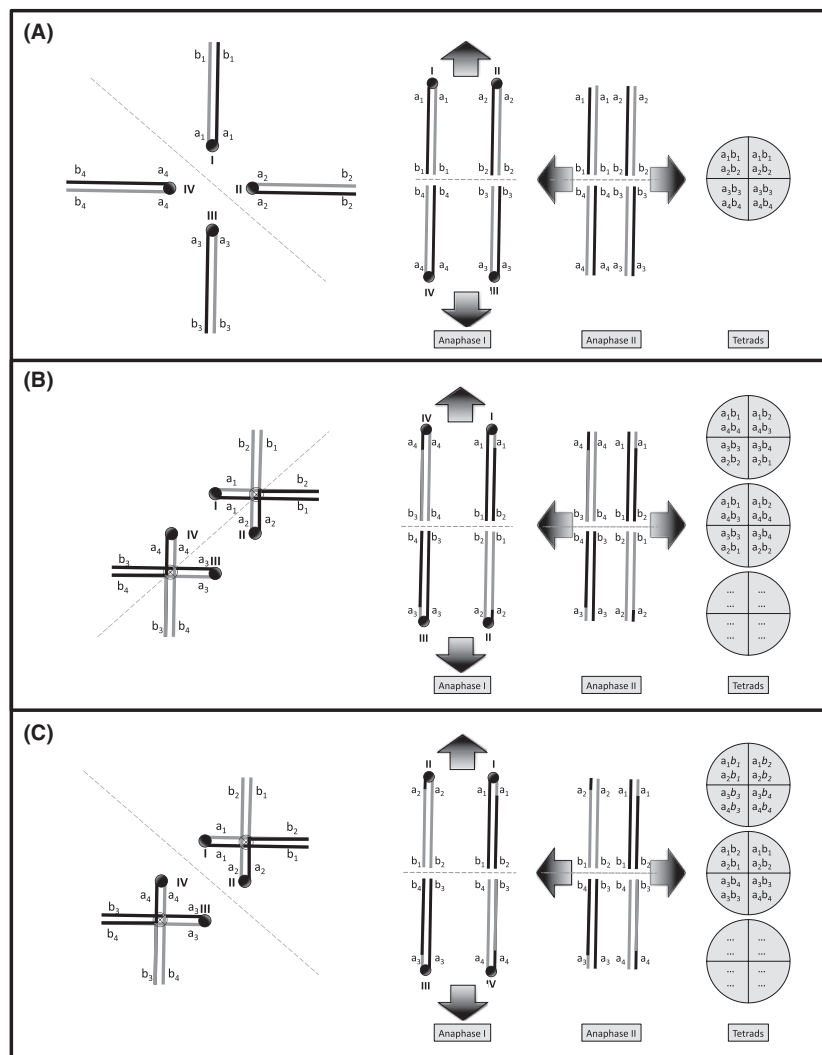
reduced fertility compared with the diploid progenitors. The importance of fertility reduction is, however, uncertain as the fertility of nascent autopolyploids is very variable and often only modestly reduced (Ramsey & Schemske, 2002). Furthermore, empirical evidence for the abundance of natural autopolyploids is notoriously difficult to obtain; many may have escaped recognition because autopolyploids typically are morphologically similar to their diploid progenitors (Soltis *et al.*, 2007). In a literature survey, Ramsey & Schemske (1998) estimated the rate of autopolyploid formation to be higher than that of allopolyploids, suggesting that autopolyploids are much more common than traditionally anticipated. The successful range expansion and radiation demonstrated in various natural autopolyploids (Manton, 1937; Soltis *et al.*, 2007) suggest that genome multiplication *per se* may represent an evolutionary advantage. Research on crops as well as on natural species indicated that genome doubling contributes to immediate acquisition of novel traits (e.g. increased cell size and gene expression, changes in physiology and ecological tolerance), but no consistent adaptive benefit is obvious (Levin, 2002; Ramsey & Schemske, 2002; Paterson, 2005). Although genetic redundancy might allow the emergence of evolutionary novelties in the longer term (Flagel & Wendel, 2009), successful establishment of autopolyploid lineages probably requires immediate advantages. Thus, the evolutionary outcome of autopolyploidy and its consequences in natural populations are still elusive. Whether genome multiplication *per se* represents an evolutionary advantage thus remains an open question.

Following Levy & Feldman (2004), polyploid evolution can be divided into two subsequent phases (Fig. 1). First, short-term 'revolutionary changes' occur immediately after polyploidization and may be important for the successful establishment of polyploids. Second, long-term 'evolutionary changes' occur during the whole lifespan of polyploids and potentially explain their long-term persistence. Here, by reviewing studies of genome reorganization in both synthetic and established autopolyploids, we assess whether genome multiplication *per se* induces structural and functional reorganization that (1) might disrupt maladaptive multivalent pairing and/or (2) might serve as a source of adaptive genetic diversity in the short and long term. Then, turning to the evolutionary consequences of genome multiplication with examples taken from natural populations, we (3) assess the circumstances favoring the formation and establishment of autopolyploid lineages and (4) evaluate to what extent genome multiplication might increase the colonization ability of autopolyploids.

Genome structural reorganization and multivalent pairing in autopolyploids

Allopolyploid genomes are subjected to extensive and reproducible genomic changes during the first generations

Fig. 2 Polysomic inheritance in an autotetraploid individual following the formation of quadrivalents (based on Bever & Felber, 1992; Ronfort *et al.*, 1998; Butruille & Boiteux, 2000). Segregation patterns depend on the frequency of crossing over between the centromere and the given loci. In the absence of crossing over (part A), gametes may originate from any combination of homologous chromosomes, and two sister chromatids never sort into the same gamete (i.e. random chromosome segregation). When a crossing over (indicated by circled cross) occurs between the centromere (a) and a locus (b), chromatids may behave independently and segregate randomly into gametes (i.e. random chromatid segregation). The anaphase I (represented by dashed line) can segregate four chromatids (part B) or two pairs of chromatids (part C). In the last case, the second division (anaphase II) may lead to double reduction (i.e. sister chromatids located in the same gamete). Only a subset of the potential tetrads formed is represented, and gametes having undergone double reduction are shown in italics. Polysomic inheritance produces homozygote as well as different types of (partially) heterozygote offspring. Note that random bivalent pairing of homologous chromosomes also results in polysomic inheritance.



after their formation (Levy & Feldman, 2004). However, hybridization rather than genome doubling *per se* seems to trigger genome changes in allopolyploid formation (Rieseberg, 2001). For example, in the *c.* 150-yr-old allopolyploid *Spartina anglica*, structural genomic changes are about five times more frequent after hybridization than genome doubling (Parisod *et al.*, 2009). It is therefore possible that the substantial ‘revolutionary changes’, which probably serve to overcome incompatibilities among divergent genomes in allopolyploids, might not be required in autopolyploid formation.

Immediate structural changes after genome doubling

Studies of structural changes in synthetic autopolyploids have reported contrasting trends (Table 1). Immediate loss of *c.* 17% of total DNA has been observed in synthetic autopolyploids of *Phlox drummondii*, with a further reduction of up to 25% upon the third generation (Raina *et al.*, 1994). This decrease in genome size was accompanied by a

substantial increase in seed set, suggesting an adaptive diploidization process. In the exclusively bivalent pairing *Elymus elongatus*, both newly synthesized autopolyploids as well as natural accessions showed a loss of 10% DNA compared with their diploid progenitors (Eilam *et al.*, 2009). Reduction in DNA content immediately follows genome doubling in this species and possibly sustains bivalent pairing. By contrast, Santos *et al.* (2003) revealed no major chromosomal rearrangements and a preponderance of multivalent pairing in a synthetic autopolyploid of *Arabidopsis thaliana*, for which Ozkan *et al.* (2006) reported no loss of DNA. In addition, genetic markers did not reveal any structural changes during the first generations following autopolyploid formation in *A. thaliana* (Ozkan *et al.*, 2006). A synthetic autotetraploid of *Paspalum notatum* exhibited 9.5% sequence elimination relative to its diploid progenitor (Martelotto *et al.*, 2007).

In conclusion, rapid elimination of DNA sequences from autopolyploid genomes seems to occur, but the limited data available so far imply that autopolyploids experience less

Table 1 Genomic structural changes after genome doubling in autopolyploids

Taxon	Immediate ¹	Long term ²	Remarks	Reference
<i>Arabidopsis thaliana</i>	–	+	Accumulation of structural changes associated with increasing bivalent pairing through generations	Santos <i>et al.</i> (2003); Ozkan <i>et al.</i> (2006); Weiss & Maluszynska (2000)
<i>Elymus elongatus</i>	+	+	Strict bivalent pairing	Eilam <i>et al.</i> (2009)
<i>Phlox drummondii</i>	+	NE	Decrease in genome size associated with increased fertility through generations	Raina <i>et al.</i> (1994)
<i>Paspalum notatum</i>	+	NE		Martelotto <i>et al.</i> (2007)
<i>Hordeum murinum</i> subsp. <i>murinum</i>	NE	+	Strict bivalent pairing	Eilam <i>et al.</i> (2009)
<i>Hordeum marinum</i> subsp. <i>gussoneanum</i>	NE	–	Strict bivalent pairing	Eilam <i>et al.</i> (2009)
<i>Hordeum bulbosum</i>	NE	–	Multivalent pairing	Eilam <i>et al.</i> (2009)
<i>Hepatica nobilis</i> var. <i>pubescens</i>	NE	+	Relocation of rDNA loci	Weiss-Schneeweiss <i>et al.</i> (2007)

+, Significant changes; –, nonsignificant changes; NE, not estimated.

¹Structural reorganization in synthetic autopolyploids.

²Structural reorganization in established autopolyploids (i.e. naturally occurring taxa or > 20 generations-old synthetic accession in *A. thaliana*).

genome restructuring than allopolyploids. To what extent differentiation of homologous chromosomes is required for the proper functioning of nascent autopolyploid genomes remains uncertain.

Long-term structural changes in autopolyploids

Genome restructuring occurring throughout the lifespan of an established polyploid lineage may promote its long-term diversification and persistence. Lim *et al.* (2007) nicely illustrated that insertion, deletion and homogenization of repetitive sequences in *Nicotiana* allopolyploids provoked a complete turnover of nongenic portions of the genome in < 5 million yr, leading to structural diploidization within a well-conserved karyotype structure. Comparable data are lacking for autopolyploids, but it is tempting to speculate that genetic redundancy leads to long-term genome instability and that similar sequence turnover may be at work after chromosome doubling to gradually restore a diploid-like behavior of autopolyploid genomes.

Established autopolyploids generally experience a significant decrease in chromosome length (Rivero-Guerra, 2008). For example, the young autotetraploid *Biscutella laevigata* shows successive down-sizing of its genome along its post-glacial recolonization pathway (König & Müllner, 2005). Genome size variation in established autopolyploids in the Triticeae reveals a variety of patterns (Eilam *et al.*, 2009; Table 1). Whereas the multivalent forming *Hordeum bulbosum* showed no significant change in genome size compared with its diploid progenitor, the strictly bivalent forming *Hordeum murinum* subsp. *murinum* showed a 23% reduction in the amount of DNA. However, the bivalent forming *Hordeum marinum* subsp. *gussoneanum* unexpectedly showed the exact additive genome size of its

progenitor, indicating that at least in some cases there is no association between genome down-sizing and pairing behavior of chromosomes. Genome arrangements might also involve the relocation of chromosomal segments. Asymmetrical relocation and loss of rDNA loci has been reported for the autopolyploid *Hepatica nobilis* var. *pubescens* (Weiss-Schneeweiss *et al.*, 2007). In a synthetic autotetraploid lineage of *Arabidopsis thaliana* grown for 20–30 generations, translocation of the 45S rDNA from chromosome 4 to chromosome 3 has been identified (Weiss & Maluszynska, 2000). This accession forms > 85% bivalents, which contrasts with multivalent pairing observed in newly synthesized autopolyploids (Santos *et al.*, 2003), suggesting that diploidization proceeded through structural rearrangements within 30 generations.

In contrast to nascent autopolyploids, established autopolyploids show substantial genome reorganization compared with their diploid relatives. Structural changes thus accumulate over time (Table 1). However, additional studies addressing the timing and abundance of restructuring after genome multiplication *per se* are clearly required.

Genome functional reorganization in autopolyploids

Intense epigenetic changes modulating gene expression without changing DNA sequences have commonly been reported in allopolyploid species (Liu & Wendel, 2003; Levy & Feldman, 2004). However, methylation changes seem to be predominantly associated with hybridization in allopolyploid *Spartina anglica*, but only rarely with genome doubling (Parisod *et al.*, 2009). In both synthetic and natural allopolyploids of *Senecio cambrensis*, interspecific hybridization was shown to trigger substantial reorganization of

the gene expression network, while genome doubling reformed it to a state similar to that of its diploid progenitors (Hegarty *et al.*, 2006). In contrast to allopolyploidy, which merges regulatory hierarchies from different species and which might induce substantial epigenetic changes to promote intergenomic coordination (Rieseberg, 2001; Riddle & Birchler, 2003; Parisod *et al.*, 2010), genome doubling *per se* should not necessarily involve regulation among homologous subgenomes.

Short-term functional changes after genome doubling

In synthetic autopolyploids of *Isatis indigotica*, only 4.2% of the genes analysed by cDNA microarrays changed expression patterns compared with diploids (Lu *et al.*, 2006). Using a similar approach, Stupar *et al.* (2007) reported only few significant expression changes among 9000 genes surveyed in synthetic autopolyploids of potato (*Solanum phureja*). Martelotto *et al.* (2005) reported that 129 out of 9617 genes surveyed (1.34%) changed expression levels in synthetic autopolyploids of *P. notatum*. Investigating the proteome, Albertin *et al.* (2005) revealed no significant changes in gene expression in synthetic autopolyploids of *Brassica oleracea*, while an analogous study on synthetic allopolyploid *Brassica napus* found up to 38% of nonadditive gene expression compared with the parental species (Albertin *et al.*, 2007).

To what extent autopolyploidy induces a 'rewiring' of the regulatory network remains largely unknown, but the limited evidence available suggests that genome doubling *per se* induces only a little functional reorganization. Accordingly, since structural and functional reorganization seem to be limited after genome multiplication *per se*, only a few evolutionary novelties or transgressive traits (i.e. exceeding the range of parental values; Rieseberg & Willis, 2007) might be immediately available for nascent autopolyploids to establish via adaptive processes.

Long-term functional changes and selection in autopolyploids

Little is currently known about the functional reorganization of autopolyploid genomes in the long term. A recent analysis of naturally occurring populations of diploid, autotetraploid and autohexaploid *Helianthus decapetalus* with cDNA-AFLPs revealed only 6.6% variation among established ploidy levels (Church & Spaulding, 2009), suggesting that gene expression is not strongly affected by genome doubling in the long term.

Theoretically, genetic redundancy may, however, imply relaxed selection on the copies of duplicated genes and allow them to follow new evolutionary trajectories. Long-term drift, mutation and selection mostly lead to inactivation of duplicated genes, but a certain fraction of duplicated

alleles are expected to fix by adaptive processes, because they either acquire a new function (i.e. neofunctionalization) or evolve towards complementation functions (i.e. subfunctionalization; Lynch *et al.*, 2001). Whether such models apply to autopolyploids is speculative, and we lack compelling data supporting the diversification of redundant alleles into evolutionary innovations in autopolyploids (Flagel & Wendel, 2009).

In this context, a crucial question is whether autopolyploids respond more rapidly to selection than their diploid progenitors (Ramsey & Schemske, 2002). Natural selection is theoretically more difficult to analyse in autopolyploids than in diploids, because of their complex population genetics (Luo *et al.*, 2006). Response to selection is always greater in diploids than in autotetraploids, but is less dependent on the intensity of selection for dominant than for recessive or additive alleles in autopolyploids (Bever & Felber, 1992). Although this suggests that autopolyploids adapt more slowly than diploids, adaptive processes may be more efficient after genome doubling as effective population size rises, rendering selection more efficient, and increases in fitness seem to depend more on the establishment of new mutations or alleles than on the efficiency of selection, at least in moderately sized populations (Otto & Whitton, 2000).

In conclusion, genetic redundancy could potentially facilitate adaptive divergence of duplicated genes, increasing the long-term genome flexibility of autopolyploids and favoring their retention. However, the efficiency of selection and the long-term adaptive potential of autopolyploids remain largely unexplored.

Natural autopolyploid lineages

Prevalent formation of autopolyploid lineages under environmental change?

Polyploids generally appear to be particularly common in habitats affected by climatic and edaphic fluctuations (Stebbins, 1971; Favarger, 1984; Brochmann *et al.*, 2004). For example, diploids are typically found in disjunct refugial areas, while polyploids are more frequent in previously glaciated areas (Ehrendorfer, 1980). This pattern has also been confirmed for most autopolyploid complexes investigated to date and suggests that genome doubling *per se* is tightly associated with environmental change (Table 2).

Stebbins (1984) proposed the 'secondary contact hypothesis' to explain the origin of allopolyploids: climate-enforced range shifts promote secondary contact and admixture between formerly allopatric taxa, with the resulting hybrids evolving via chromosome doubling to restore fertility. Brochmann *et al.* (2004) reviewed polyploid evolution in arctic plants and concluded that differentiation in distinct glacial refugia produced the raw material for allo-

Table 2 Examples of naturally occurring autopolyploid lineages

Taxa	Evidence for autopolyploidy	Cytotype distribution
<i>Achillea millefolium</i>	Morphology (Clausen <i>et al.</i> , 1948)	Various habitats (Ramsey <i>et al.</i> , 2008)
<i>Anthoxanthum alpinum</i>	Segregation (Zeroual-Humbert-Droz & Felber, 1999)	2× more cold-tolerant than 4× (Felber-Girard <i>et al.</i> , 1996)
<i>Biscutella laevigata</i>	Segregation (Tremetsberger <i>et al.</i> , 2002)	2× in glacial refugia; 4× in previously glaciated areas (Manton, 1937); 4× with broad ecological tolerance, being active recolonizers and locally adapted to environmental heterogeneity (Gasser, 1986; Parisod & Besnard, 2007; Parisod & Bonvin, 2008; Parisod & Christin, 2008)
<i>Cardamine digitata</i> agg.	Morphology (Jorgensen <i>et al.</i> , 2008)	2× in glacial refugia; 4× in previously glaciated areas (Jorgensen <i>et al.</i> , 2008)
<i>Centaurea jacea</i>	Segregation (Hardy <i>et al.</i> , 2000)	2× more cold-tolerant than 4× (Hardy <i>et al.</i> , 2000)
<i>Chamerion angustifolium</i>	Segregation (Husband & Schemske, 1997)	2× more cold-tolerant than 4× (Husband & Schemske, 2000)
<i>Dactylis glomerata</i>	Segregation (Lumaret <i>et al.</i> , 1987)	2× confined to shaded woodland habitats vs 4× in high light conditions; 2× in glacial refugia; 4× in previously glaciated areas (Lumaret <i>et al.</i> , 1989; Bretagnolle & Thompson, 2001)
<i>Empetrum nigrum</i>	Morphology (Elvebakk & Spjelkavik, 1995)	2× less cold-tolerant than 4× (Elvebakk & Spjelkavik, 1995)
<i>Eragrostis cambessediana</i>	Morphology (Levin, 2002)	2× occur in wet habitats; cytotypes with increasing ploidy levels occur in successively more xeric habitats (Levin, 2002)
<i>Galax urceolata</i>	Morphology (Burton & Husband, 1999)	2× restricted to more xeric habitats than polyploids (Johnson <i>et al.</i> , 2003)
<i>Galium anisophyllum</i>	Morphology (Ehrendorfer, 1965)	2× in glacial refugia; 4× in previously glaciated areas (Ehrendorfer, 1965)
<i>Hepatica nobilis</i> var. <i>pubescens</i>	Morphology (Mabuchi <i>et al.</i> , 2005)	
<i>Heuchera grossulariifolia</i>	Segregation (Segraves <i>et al.</i> , 1999)	Sympatric 2× and 4× differ in pollinator assemblages (Thompson & Merg, 2008)
<i>Heuchera micrantha</i>	Segregation (Soltis & Soltis, 1989)	2× are restricted to disjunct areas within the 4× range (Soltis & Soltis, 1989)
<i>Parnassia palustris</i>	Segregation (Borgen & Hultgard, 2003)	2× in glacial refugia; 4× in previously glaciated areas (Borgen & Hultgard, 2003)
<i>Plantago media</i>	Morphology (VanDijk & Bakx-Schotman, 1997)	2× in glacial refugia; 4× in previously glaciated areas (VanDijk & Bakx-Schotman, 1997)
<i>Santolina pectinata</i>	Morphology (Rivero-Guerra, 2008)	2× in different habitats; 4× restricted to disturbed habitats (Rivero-Guerra, 2008)
<i>Tolmiea menziesii</i>	Segregation (Soltis & Soltis, 1988)	2× in glacial refugia; 4× in previously glaciated areas (Soltis & Soltis, 1989)
<i>Helianthus decapetalus</i>	Morphology (Rogers <i>et al.</i> , 1982)	

Additional cases are reported in Soltis & Soltis (1993), Levin (2002) and Soltis *et al.* (2007).

polyploid formation during postglacial expansion. Stebbins' secondary contact hypothesis can also explain the origin of autopolyploids in cases where diploid populations of the same species accumulated genome differences in isolated glacial refugia. Once brought into contact by climate-induced range shifts and after having undergone genetic admixture, intraspecific hybrids could be genetically stabilized by chromosome doubling (although still showing polysomic inheritance). Evidence supporting such an origin of autopolyploids is scarce. For example, the intermingled distribution of differentiated lineages of *B. laevigata* across the Western Alps suggests secondary contact between differentiated populations (Fig. 3; Parisod & Besnard, 2007). The circumpolar genus *Draba* encompasses 18% of diploid taxa and 82% phylogenetically young polyploid taxa

(Jordon-Thaden & Koch, 2008). Based on experimental crosses between populations lacking obvious morphological or ecological differentiation, a multitude of cryptic biological species has been identified within diploid taxa of *Draba* (Grundt *et al.*, 2006). Chromosomal rearrangements are involved in the reduction of fertility in these intraspecific hybrids (Skrede *et al.*, 2008), opening up the possibility that arctic *Draba* may have evolved autopolyploid lineages from hybridization between cryptic diploid species in secondary contact zones.

In conclusion, secondary contact might favor the origin of autopolyploid lineages by restoring the fertility of admixed individuals between divergent populations. Such a mechanism could explain why polyploid lineages originate as discrete bursts during periods of intense environmental

change (Fawcett *et al.*, 2009). However, whether secondary contact could support the successful establishment of autopolyploid populations through adaptive or neutral processes, probably depends on additional processes, as outlined in the following text.

Autopolyploid origin and genetic diversity

The origin of autopolyploids (Fig. 1) is mostly from the union of unreduced gametes, either through fusion of two unreduced gametes (bilateral polyploidization) or the fusion of reduced and unreduced gametes producing (fertile) triploids that can in turn generate tetraploid progeny through selfing or backcrossing (unilateral polyploidization; Bretagnolle & Thompson, 1995; Ramsey & Schemske, 1998). The production of unreduced gametes is heritable, governed by a few genes, and increases with increasing environmental stress (e.g. frost, wounding, herbivory, water deficit and lack of nutrients), which might further enhance the rate of autopolyploid formation during environmental change. Noticeably, autopolyploid formation allows a large part of the genetic diversity present in diploid progenitors to be incorporated into the autopolyploid gene pool (Husband, 2004). Furthermore, multiple origins of autopolyploid taxa are common (*Heuchera micrantha*, Soltis & Soltis, 1989; *Heuchera grossulariifolia*, Segraves *et al.*, 1999; *B. laevigata*, Parisod & Besnard, 2007) and increase the genetic diversity of autopolyploids, also by adding different maternal lineages (Soltis & Soltis, 1999).

In contrast to synthetic genome doubling experiments, natural autopolyploid lineages potentially include differentially adapted genotypes. To what extent the merging of slightly divergent genomes supports the establishment of autopolyploid populations through adaptive processes is, however, still unknown.

Autopolyploid establishment and ecological divergence

Natural autotetraploids arise within diploid populations and thus face a considerable minority disadvantage (Levin, 1975; Felber, 1991). While restricted seed dispersal, vegetative propagation or self-fertilization might mitigate this minority disadvantage by increasing mating within cytotypes (Baack, 2005), the successful establishment of autopolyploids is thought to require (1) a substantial competitive advantage, (2) ecological divergence and/or (3) stochasticity favoring of autopolyploids in small populations (Petit *et al.*, 1999; Rausch & Morgan, 2005), while the probability of establishment may be enhanced by (4) recurrent polyploidy (Soltis & Soltis, 1999).

Ecological divergence between cytotypes is rather common (Table 2), but autopolyploids do not consistently tolerate harsher environmental conditions and do not always

show a broader ecological niche than their diploid progenitors (Levin, 2002). For example, autotetraploids of *Santolina pectinata* are restricted to disturbed habitats while diploids are not (Rivero-Guerra, 2008). Recent studies have demonstrated that, among other mechanisms, differential interspecific interactions can contribute to ecological divergence among cytotypes and support the establishment of autopolyploid populations (Thompson *et al.*, 2004). For example, established cytotypes of the autopolyploids *Chamerion angustifolium* (Husband & Sabara, 2004) and *H. grossulariifolia* (Thompson & Merg, 2008) differ in respective pollinator assemblages, leading to partial reproductive isolation and facilitation of the coexistence of multiple ploidy levels. Cytotypes of *H. grossulariifolia* also differ with respect to herbivore assemblages (Nuismer & Thompson, 2001). Mathematical models suggest that nascent autopolyploids are more resistant to pathogens under dominance models of resistance alleles, but whether this also is a general advantage for natural and established autopolyploids is unknown (Oswald & Nuismer, 2007).

Only strict sympatric speciation requires immediate niche differentiation among cytotypes or competitive superiority of autopolyploids over diploid progenitors. Autopolyploid lineages may also spread from the periphery of a diploid taxon's distribution, establishing at sites where progenitors are absent and forming sources for further range expansion (Levin, 2002).

In conclusion, diploids and autopolyploids commonly show ecological differentiation, but neither the mechanisms nor the timing of ecological divergence among cytotypes are easy to identify. In contrast to allopolyploidy, autopolyploidy does not necessarily produce transgressive traits to fuel adaptive ecological divergence. Autopolyploids can maintain more than two alleles per locus, allowing them to produce a variety of allozymes (i.e. enzyme multiplicity owing to heterozygosity), which, in principle, would allow them to achieve high fitness in a variety of environments. However, marked overdominance would be required for allelic diversity to explain ecological divergence and, more generally, the success of autopolyploids.

Polysomic inheritance and inbreeding depression in autopolyploids

Because of tetrasomic inheritance (Fig. 2), autotetraploid populations are characterized by high heterozygosity (i.e. partial and complete heterozygotes) and by nearly doubled effective population size compared with populations showing disomic inheritance (Ronfort *et al.*, 1998; Ronfort, 1999). Polysomic inheritance also implies that autopolyploid populations reach Hardy–Weinberg equilibrium gradually, as opposed to diploid populations, where one generation of random mating is sufficient (Bever & Felber, 1992). In response to inbreeding, heterozygosity accord-

ingly declines at a slower rate in autopolyploid than in diploid populations (Moody *et al.*, 1993). Polysomic inheritance thus has important consequences for microevolutionary processes such as the distribution of genetic variation and the amount of inbreeding depression.

If fitness solely depends on overdominance, autopolyploids should present a higher fitness loss caused by inbreeding depression than their diploid progenitors because genotypic combinations of more than two alleles will rapidly decrease (Husband *et al.*, 2008). This model has, however, received only limited and indirect support from empirical studies (Bingham, 1980; Bever & Felber, 1992; Ramsey & Schemske, 2002). By contrast, under the classical model of recessive deleterious mutations negatively affecting fitness when in a homozygous state, inbreeding depression should be half as high in autopolyploid taxa than in progenitor diploids because of a higher level of heterozygosity (Lande & Schemske, 1985). Taking partial heterozygotes and a range of dominance effects into account, Ronfort (1999) concluded that inbreeding depression might only be slightly lower or even equivalent in autopolyploids compared with diploids. If the degree of dominance was related to the dosage of alleles, inbreeding depression should increase in subsequent generations of selfed offspring. However, most empirical studies indicate an immediate reduction of inbreeding depression by almost 50% in autotetraploid populations compared with populations of related diploid species (Husband & Schemske, 1997; Galloway *et al.*, 2003; Galloway & Etterson, 2007; Husband *et al.*, 2008).

Genome doubling *per se* can lighten autopolyploids from inbreeding depression compared with diploids and might thus represent an immediate advantage favoring the establishment of autopolyploid populations. Nevertheless, further studies assessing the relationship among allelic diversity, allelic dosage and fitness are necessary to better appreciate inbreeding depression and adaptation in autopolyploids.

Expansion of natural autopolyploid lineages under environmental changes

Range expansion of autopolyploid lineages subjects them to stochasticity and environmental heterogeneity. An understanding of patterns under range expansion is thus crucial to appraise the success of autopolyploids and to understand their putative evolutionary advantages. While Levin (2002) and Soltis *et al.* (2007) have reviewed the evolutionary ecology of various natural autopolyploid taxa, we will detail selected additional recent studies that focused on the spatio-temporal dynamics of autopolyploid lineages under environmental change.

Studies on the autopolyploid complex *Achillea millefolium* provided exciting evidence for dramatic adaptive radiation in < 1 million yr (Clausen *et al.*, 1948; Ramsey *et al.*,

2008). The expansion of this autopolyploid lineage across the New World offered many opportunities for populations to colonize new and divergent habitats, forming ecological races with morphological, physiological and life-history adaptations. Interestingly, the proliferation of these distinct races was not linked with strong genetic differentiation at neutral markers, stressing the need to better understand the mechanisms of adaptive genetic differentiation in autopolyploids.

In the *B. laevigata* complex, diploid populations are genetically depauperate and relictual to glacial refugia, while autotetraploid populations have colonized a large distribution range across the European Alps after the last glacial maximum and exhibit substantial genetic diversity (Manton, 1937; Tremetsberger *et al.*, 2002; C. Parisod, unpublished). Multiple origins of autotetraploid lineages from distinct diploid populations are a likely explanation for the high genetic variation in the recently colonized main distribution area of the complex (Parisod & Besnard, 2007; Fig. 3). Moreover, genetic diversity has probably been further increased during range expansion in places where independently originated autopolyploids came into contact and produced new genotypes through recombination (Soltis & Soltis, 1999; Parisod & Besnard, 2007). In such situations, tetrasomic inheritance in *B. laevigata* might have maintained especially high levels of heterozygosity in recombinant populations (Soltis & Rieseberg, 1986; Bever & Felber, 1992), thus fostering genomic variation upon which selection could act to produce advantageous genotypes (Soltis & Soltis, 2000). Although not tested yet, admixture between distinct maternal lineages as seen in *B. laevigata* might also induce new and variable cytoplasmic–nuclear interactions, adding to the diversity of potentially adaptive traits.

Studies on populations of *B. laevigata* from a single maternal lineage offered additional evidence on the putative advantages of autopolyploidy under climate change. An expanding population at the altitudinal limit of the species' distribution range demonstrated the ability of autopolyploids to maintain genetic diversity during colonization (Parisod & Bonvin, 2008). This finding fits with the theoretical expectation that autotetraploids may be less susceptible to founder effects than diploids, because tetrasomic inheritance increases effective population sizes and heterozygosity, and thereby reduces genetic drift and inbreeding depression. Polysomic inheritance is thus immediately advantageous under environmental change. Autotetraploid *B. laevigata* also exhibits large phenotypic variation and wide ecological tolerance, being locally adapted to its environment (Gasser, 1986). Parisod & Besnard (2007) showed that independent autotetraploid lineages are spread along the whole altitudinal gradient in a pattern that is not habitat-specific (Fig. 3), questioning the assumption that a wide ecological niche of autopolyploids results from the spatial juxtaposition of

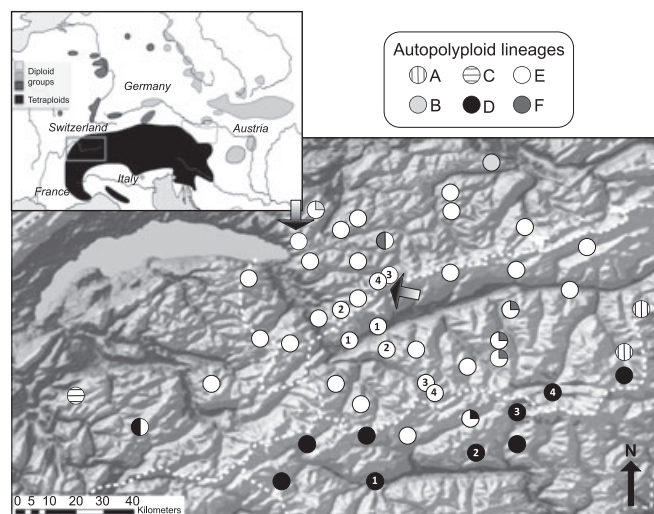


Fig. 3 Genetic structure in *Biscutella laevigata*. Inset map: distribution of diploid and polyploid taxa in the *B. laevigata* autopolyploid complex across Central Europe (after Tremetsberger *et al.*, 2002). The area delimited by the rectangle is enlarged on the main map. Main map: pie charts represent the frequency of different autopolyploid lineages (A–F) in populations across the Western European Alps (simplified from Parisod & Besnard, 2007). Most lineages are restricted to local glacial refugia, but two autopolyploid lineages (D and E, shown in black and white, respectively) experienced a widespread range expansion from the peripheral to the central Alps. Within each of these lineages, populations occur along the whole altitudinal gradients (shown with numbers: 1, c. 500 m; 2, c. 1500 m; 3, c. 2000 m; 4, c. 2500 m). Populations within the lineage E that have been investigated at the local scale (i.e. either persisting in the peripheral Alps or recolonizing the central Alps; see text) are indicated by arrows.

lineages with distinct habitat requirements (Bayer *et al.*, 1996; Soltis & Soltis, 2000). Furthermore, a fine-scale genetic survey within a large continuous population of *B. laevigata* revealed that different multilocus genotypes were consistently associated with particular ecological conditions, indicating local adaptation at a fine spatial scale (Parisod & Christin, 2008). Therefore, autopolyploidy also allows for intralines diversification and adaptation to local environmental heterogeneity.

The putative evolutionary advantages of autopolyploidy

Although some genetic, ecological and biogeographic evidence has accumulated during recent years, it is still not clear whether autopolyploids possess general evolutionary advantages compared with their diploid progenitors. Unlike allopolyploids resulting from interspecific hybridization, autopolyploid lineages may not immediately benefit from a strong advantage of heterosis. To what extent genome multiplication *per se* is an adaptation thus remains to be assessed.

Autopolyploidy as a nearly neutral process

Autopolyploidy may represent a neutral, ratcheting process, as suggested by Meyers & Levin (2006). As is apparent from the literature, the lack of attributes consistently associated with genome doubling *per se* supports this hypothesis to a certain extent. We suggest that this model should to be taken as a null model in future studies.

Genome multiplication might initiate speciation by promoting post-zygotic reproductive isolation, thereby decreasing maladaptive gene flow from related diploids and facilitating adaptive differentiation via other evolutionary processes (Grant, 1981; Rieseberg & Willis, 2007). Some studies have revealed nearly complete reproductive isolation between established cytotypes, mainly owing to geographical separation and assortative mating (Husband & Sabara, 2004). However, it should be noted that studies in diverse polyploid complexes, including allopolyploids, have reported significant gene flow across ploidy levels through fertile triploids (or pentaploids and heptaploids) and/or unreduced gametes (Brochmann *et al.*, 1992a; Bretagnolle & Thompson, 1995; Ramsey & Schemske, 1998; Petit *et al.*, 1999; Husband, 2004; Slotte *et al.*, 2008). In addition, the recurrent production of interbreeding polyploid lineages contributes to gene exchange between diploid and established polyploids (Brochmann *et al.*, 1992b; Soltis & Soltis, 1993, 1999). Accordingly, genome multiplication *per se* can be seen as an incomplete speciation mechanism that needs to be complemented by other processes, either adaptive or neutral (Otto & Whitton, 2000).

Autopolyploidy as a mechanism enhancing colonization ability

Recently disturbed landscapes may offer habitats with relaxed competition, where polyploids find opportunities for establishment. 'Faster and more efficient mobilization' of polyploid genetic variability in common early-succes-

sional communities was invoked early to explain the correlation between polyploid distribution and glaciation (Favarger, 1967; Ehrendorfer, 1980). In extreme or repeatedly glaciated environments, polyploidy may serve as an escape from genetic and ecological niche depauperation caused by drift and selfing at the diploid level (Brochmann, 1992). Accumulating evidence suggests that autopolyploidy may be prevalent under environmental change owing to: increased rate of autopolyploid formation; suitable conditions for establishment because of relaxed competition; polysomic inheritance increasing the likelihood of successful range shifts; the potential of autopolyploids for local adaptation also promoting long-term persistence.

The hypothesis that autopolyploidy is advantageous under environmental change mainly relies on those two traits that are consistently associated with autopolyploidy, namely genic redundancy and polysomic inheritance. In marked contrast to allopolyploids, there is no example of rapid and drastic genome reorganization induced by genome multiplication (Table 1). As neither large genomic structural nor functional changes have been detected after genome doubling *per se* (although only a few studies are available), we hypothesize that divergence among homologous chromosomes is not strongly selected for, supporting maintenance of polysomic inheritance as an immediate adaptive trait in young autopolyploid lineages; and genome multiplication *per se* does not generate substantial genetic diversity upon which selection immediately acts to favor the establishment and range expansion of autopolyploids. Although polysomic inheritance might seem disadvantageous as it counteracts efficient selection, it also immediately increases effective population size and should reduce inbreeding depression in the short term, allowing autopolyploids to cope with climate-induced range shifts. Conversely, genic redundancy and polysomic inheritance seem to be only transient evolutionary stages in the autopolyploid's lifespan. The level of polysomic inheritance is expected to decline in the long-term, restoring disomic inheritance and stabilizing adaptive genetic variation accumulated under genic redundancy. Although we have highlighted the many open questions still remaining to be solved with respect to the evolution of autopolyploid lineages, the recent accumulation of knowledge challenges Stebbins' statement that 'chromosome doubling by itself is not a help but a hindrance to the evolutionary success of higher plants' (Stebbins, 1971: 126).

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