

## Meetings

## Polyploids integrate genomic changes and ecological shifts

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The 13th Congress of the European Society for Evolutionary Biology (Tuebingen, Germany) gave concrete expression to the need for extra crosstalk between molecular and population geneticists. Holistic explanations about biological evolution indeed call for a better integration of molecular details and ecological ramifications. Molecular biologists have described a diversity of genome architectures, leading to the notion of an evolutionarily dynamic genome (Koonin, 2009). They have also shed new light on the genetic architecture of phenotypes and documented many eukaryotic pathways, presenting an unexpectedly 'baroque structure' that involves considerable redundancy (Lynch, 2007b). Indeed, genetic networks commonly consist of a plethora of genes controlling the expression of downstream products, with only a small fraction of genes ultimately having a direct impact on phenotypes. However, we are still far from understanding the origin and the maintenance of such complexity. In particular, we need to further evaluate the consequences of genome variation on fitness in order to assess forces – mainly, the importance of natural selection vs random genetic drift – underlying evolutionary changes.

A symposium entitled 'Polyploid ecological genomics' presented advances supporting the view that polyploidy (i.e. merging of genomes associated with multiplication of chromosome sets) is a revolutionary event, inducing drastic changes in both genome organization and ecological properties of nascent lineages (Fig. 1). As nascent polyploids are expected to go through selection for increased viability and fertility, it is tempting to interpret most variation produced by such drastic reorganization as the result of selection (Fontdevilla, 2011). However, polyploid lineages also start with low effective population size (i.e. polyploidy represents a genetic bottleneck) strongly reducing the efficiency of selection and neutral explanations shall be kept as null hypotheses before invoking adaptive processes (Lynch, 2007a). Accordingly, polyploidy represents a convenient model-process to integrate natural variation in genome architecture, phenotype and fitness into a coherent evolutionary framework.

### Hopeful polyploids

Polyploidy has major evolutionary significance. It is prevalent in plants (Jiao *et al.*, 2011) and, as shown by Mable *et al.* (2011), in animals. An appealing property of polyploid lineages is their

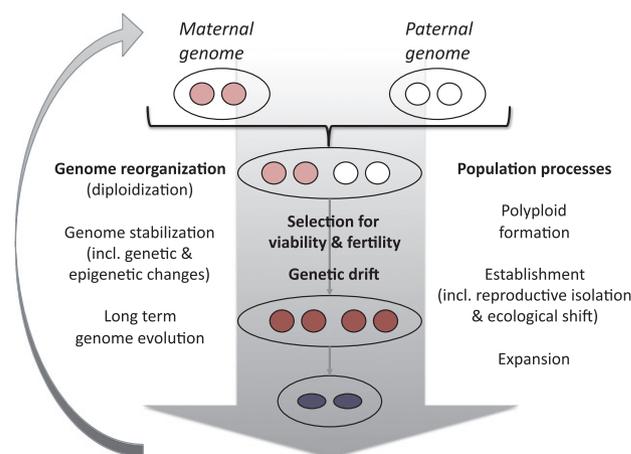


Fig. 1 Polyploid differentiation as a recurrent evolutionary process involving changes at both the genome and the population levels.

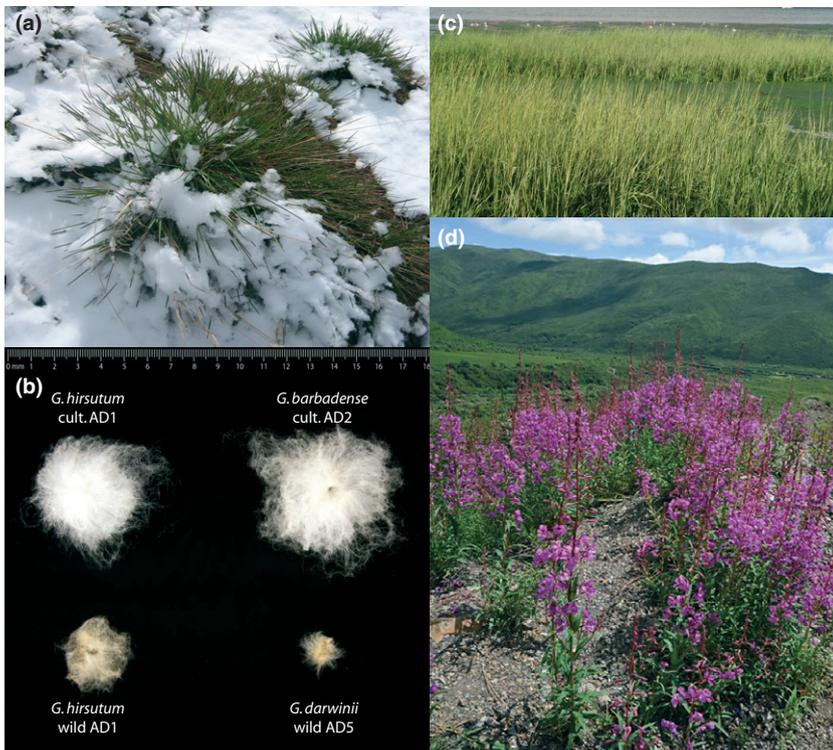
genomic and phenotypic instability, allowing researchers to assess the processes shaping successful genomes (Leitch & Leitch, 2008). Furthermore, the initial stimulus of evolutionary change is straightforward in polyploid systems, offering considerable advantages for exploring the impact of genome reorganization on ecological shifts.

*'Spectacular and repeatable shifts in gene expression commonly accompany polyploidy ...'*

In spite of these advantages, the development of significant polyploid species models has been hindered by the need to comprehensively characterize multiple copy genes (i.e. homologues or homeologues). Griffin *et al.* (2011) showed how to take advantage of new sequencing technologies to overcome such challenges and demonstrated in allopolyploid *Poa* species (Fig. 2a) that 454 sequencing of barcoded amplicon mixtures allows one to characterize all alleles of various homeologous loci. Similar approaches can be used to reliably address phylogenetic relationships within polyploid complexes and will also enable genotyping at the population level. Such advances are promising for assessing the forces shaping the evolutionary trajectories of natural polyploid lineages.

### What is the evolutionary significance of genome changes induced by polyploidy?

A variety of molecular mechanisms affecting polyploid genomes at both the structural and the epigenetic levels have been



**Fig. 2** (a) *Poa*, photograph courtesy of Philippa Griffin; (b) *Gossypium*, photograph courtesy of Jonathan Wendel; (c) *Spartina* (Poaceae), photograph courtesy of Malika Ainouche; (d) *Chamerion* (Onagraceae), photograph courtesy of Brian Husband.

described (see references in Ainouche & Jenczewski, 2010). Spectacular and repeatable shifts in gene expression commonly accompany polyploidy and can result in phenotypic changes. Jonathan Wendel (Iowa State University, USA) presented ongoing work comparing gene expression in two sets of diploid progenitors of allopolyploid cottons with both synthesized and 1–2 million-yr-old allopolyploids (Fig. 2b), and showing that several genes are transgressively up- or down-regulated in allopolyploids (Rapp *et al.*, 2009). In addition, thousands of genes showing differential expression between diploids were characterized by a ‘phenomenon of genome-wide expression dominance, whereby gene expression was either up- or down-regulated to the level of one of the two parents’. Interestingly, the same sub-genome can be either dominant or recessive, depending on the specific genomic combination. Malika Ainouche (University of Rennes, France) showed in the 150 yr-old allopolyploid invasive *Spartina anglica* (Fig. 2c) that hybridization ‘was accompanied by maternal expression dominance’ to a large extent, while this dominance was attenuated after genome doubling (Chelaifa *et al.*, 2010). It is tempting to speculate that genome-wide dominance and transgressive expression are associated with phenotypic variation and might result in ecological changes or the emergence of evolutionary novelties. In line with this hypothesis, artificial selection that accompanied the domestication and the improvement of the fibre of upland cotton radically altered the transcriptional network, affecting the expression of nearly a quarter of the genes (Rapp *et al.*, 2010). However, the origin and evolutionary significance of the rewiring of expression networks remains to be clarified.

Both genetic and epigenetic variation can account for changing gene expression, but their relative contribution to altered

phenotypes has not been sufficiently documented yet. In a symposium devoted to ‘plant epigenetics’, Vincent Colot (École Normale Supérieure, Paris, France) presented an approach using recombinant inbred lines of the diploid *Arabidopsis thaliana* with distinct epigenomes. This work already demonstrated that epigenetic variation is largely heritable through at least seven to eight generations and produces a diversity of complex phenotypic traits that correspond to the phenotypic diversity of natural accessions (Roux *et al.*, 2011). Furthermore, Verhoeven *et al.* (2010) showed that heritable methylation changes between genetically identical triploid dandelions can be induced by different ecological stresses. Transgenerational epigenetic variation alone can account for phenotypic evolution and its role certainly needs further theoretical developments. However, a better understanding of the mechanisms triggering genome reorganization and expression changes seems crucial (Feng *et al.*, 2010). Genetic and epigenetic variation indeed ‘sit on top of each other’: overlapping epigenetic mechanisms control both gene expression and genome structural integrity by repressing transposable elements, while the activation of transposable elements can induce both restructuring and epigenetic repatterning across the whole genome. It is becoming clear that the merging of divergent genomes can reveal conflicts between interspersed transposable elements and their epigenetic repressors, potentially resulting in genome-wide reorganization (Parisod *et al.*, 2010a). Such changes certainly result in the emergence of new steady states across the genome, but we are only just beginning to understand to what extent it accounts for drastic changes in gene expression and phenotypes. As polyploidy induces structural and epigenetic reorganization of both coding and repetitive fractions, young polyploid systems are offering convenient models to further address to what extent such raw material translates into significant evolutionary change.

## Are ecological shifts fostered by polyploidy?

The traditional comparison of extant diploid progenitors with established polyploids has revealed that polyploids commonly occupy larger geographic ranges and different, usually wider, ecological niches than diploids (Parisod *et al.*, 2010b). The challenge now is to assess the impact of polyploidy *per se*, as opposed to the impact of post-polyploidy evolution. Brian Husband (University of Guelph, Canada) introduced one way to tackle this issue by using experimentally synthesized polyploids, mimicking established polyploids of *Chamerion angustifolium* (Fig. 2d). A number of ecological experiments comparing diploids, nascent polyploids and established polyploids of these plants are offering fresh perspectives on the evolutionary consequences of polyploidy. For instance, the great drought tolerance of established tetraploids is not entirely due to genome doubling (Maherali *et al.*, 2009): diploids and synthetic polyploids had nearly the same xylem hydraulic conductivity, which was nearly 30% less than in established tetraploids. Accordingly, tetraploids take longer to wilt and die than both diploids and synthetic polyploids under similar levels of water deficit, indicating that stress tolerance and ecological differentiation evolved after polyploidy. Similarly, pollen from synthetic polyploids is not competitive against diploid pollen as is pollen from established tetraploids, indicating the polyploid siring success probably strengthened after the polyploidy (Baldwin & Husband, 2011). Such evidence suggests that polyploidy might increase the response to selection. Indeed, in a multi-generation selection experiment on flowering time in *C. angustifolium*, synthetic polyploids responded slowly, initially, and then rapidly to selection during the first generations. After a few generations of directional selection, the realized heritability of flowering time was highest in synthetic polyploids and lower in established tetraploids than in diploids. The origin of such discrepancy between nascent polyploids and established polyploids in selection response is yet unknown, but may be associated with genome reorganization.

## Towards an integration of genome reorganization and ecological changes

Genome organization is being increasingly linked to phenotype, but very little work (if any) manages to link those crucial components of variation with fitness (Barrett & Hoekstra, 2011). The study of polyploid species complexes may help to bridge the gap between genomic changes and ecological shifts, towards a better understanding of their causes and consequences. Whether polyploidy-induced genomic instability plays a role in shaping ecological differentiation of nascent polyploids should now be within the reach of multidisciplinary approaches and might help in assessing to what extent polyploid genome flexibility is associated with amplified responses to selection. Ultimately, understanding polyploid evolution requires knowledge to be integrated at the population level, and will have not only to rely on elegant experimental displays, but also on comprehensive surveys of variation at multiple levels. Recent and forthcoming sequenc-

ing advances paint in glowing colours the wealth of genomic data to be soon released in the wild species used as models by evolutionary ecologists. Such valuable resources would be best used in combination with rigorous theoretical developments, allowing the assessment of natural selection under complex demographic scenarios. Accordingly, the challenging integration of genotype, phenotype and fitness variation within a coherent evolutionary framework might become feasible in natural systems in the not too distant future.

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