

Gene doubling shapes the world: Instant speciation, biodiversity, and the root of our existence

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What do seedless watermelon, salmon, and strawberries all have in common? Unlike most eukaryotic multicellular organisms that have two sets of chromosomes and are diploid, these organisms are all polyploid, meaning they have three or more sets of chromosomes—seedless watermelon and salmon have 3 and 4 sets of chromosomes, respectively, and strawberries have 10! While this might seem surprising, in fact most plant species are polyploid. Polyploidy, or genome doubling, was first discovered over a century ago, but only recently, with the development of molecular tools, has it been revealed just how ubiquitous it is. Polyploidy is being increasingly recognized as an important evolutionary force that can facilitate positive adaptations, lead to instant speciation, and increase biodiversity.

Just as the names Watson and Crick are associated with the double helix and Darwin with evolution, so the name G.L. Stebbins is with polyploidy. Polyploidy, when entire sets of chromosomes are duplicated, can occur when organisms self-fertilize or through sexual reproduction. Polyploidy was first recognized in plants in 1907; in 1911 it was suggested that an ancient genome duplication may have occurred in maize (*Zea mays*); and soon thereafter it was proposed that duplication of whole sets of chromosomes could lead to new species. However, much of the development and importance of polyploidy for plant evolution wasn't recognized until the work of George Ledyard Stebbins, a leading botanical researcher in the 20th century.

As part of the *American Journal of Botany's* Centennial Review series, Douglas Soltis, Clayton Visger, and Pamela Soltis (University of Florida: Dept. of Biology, and Florida Museum of Natural History) review the history of polyploidy and the role that Stebbins played in facilitating its recognition as an evolutionary force. They also describe an emerging paradigm, arising with the advent of new technological advances such as DNA-based phylogenies and [genome sequencing](#).

"Genome doubling has shaped the biological world more than any other process," comments Doug Soltis. "Some might consider this an overstatement, but in the plant world, genome doubling, or polyploidy, rules. It is common in most plant lineages—and it is also crucial in many animal lineages, as vertebrates are the result of two ancient events. It is common in fish, some invertebrate lineages, and we humans are ancient polyploids!"

So, even if polyploidy (duplicate sets of genomes) is the norm rather than unusual, what makes that interesting? One reason is that genome doubling can lead to instant speciation.

As Soltis explains, "If two plants with 12 chromosomes hybridized, you would expect the offspring to have 12 chromosomes, right? What if the offspring had 24 chromosomes? That is genome doubling—every chromosome, every gene duplicated—wow, 2X the genetic material to work with instantaneously!"

In their review, Soltis and colleagues emphasize that polyploidy and the important role it has played, especially in plant evolution, would not have gained the recognition it deserves would it not have been for its staunch proponent, G. L. Stebbins. In the mid-20th century Stebbins synthesized what was known at that time about polyploidy, classifying different types of ploidy, discussing ancient polyploidy events, and investigating hybridizing species and polyploid derivatives.

However, Stebbins thought that polyploidy would only be an advantage for species in environments that might change rapidly, and that it would not be particularly advantageous in stable ecosystems, or in competition with widespread diploid species. In fact in many cases he viewed polyploidy as an evolutionary dead-end.

In the 1980s a new paradigm on polyploidy began to emerge, especially with the more recent advent of genome sequencing, which started revealing just how many duplicated genes there are in the genomes of many different plant species.

"In our early research using allozymes, we kept trying to use this genetic tool—hot stuff at the time—to investigate plants that were reported to be diploid," recounts Soltis. "But we found complex genetic patterns that could not be diploid. Back to the lab we'd go to make some chromosome counts, and we had found by accident that some of the populations of that species were actually 'polyploid.' This happened over and over again, to the point where we started calling it the polyploidy curse."

However, Pam Soltis notes that this "curse" provided many new opportunities to study polyploids from new perspectives, including an assessment of the relative frequency of diploid and polyploid angiosperms.

Indeed, all of the angiosperm genomes that have been sequenced to date show evidence of ancient polyploidy events—back in the 1950s, Stebbins inferred that polyploidy was common, but genomic studies indicate that it is much more prevalent than he surmised. Recent genetic investigations have found, for example, that a whole-genome duplication event preceded the origin of all extant angiosperms. Moreover, it is highly likely that all eukaryotes have ancient genome duplications in their history.

"This is why we continue to stress to this day that we (scientists) have grossly underestimated the extent of genome doubling in nature," emphasizes Doug Soltis.

Polyploidy is not just an "ancient" event, however. A recent study estimates that 35% of extant flowering plant species are of recent polyploid origins.

Polyploidy can also increase species diversity within groups of organisms. Recent examination of polyploidy events in certain plant families have found that genome duplication events are often followed by bursts of speciation (species richness) in those clades.

Interestingly, the same polyploid species can actually arise multiple times (a [species](#) of *Tragopogon* may have formed up to 20 times), and sometimes even from within a very small spatial area, such as within the same town.

In contrast to Stebbins's view that polyploids have less genetic diversity, the new paradigm is finding that they may have greater genetic diversity, especially given the high likelihood of multiple origins and opportunities for chromosomal and genetic mutations shortly after their formation.

"The biosphere is plant-dependent, as we know," concludes Doug Soltis. "Hence, the foundation of our planet's biodiversity has been largely shaped by this genome-doubling process."

Indeed, [polyploidy](#) is a major evolutionary force that can lead to adaptation, speciation, and diversification.

Soltis and colleagues continue to be fascinated by the flexibility, novelty, and dynamic nature of polyploid genomes. "An organism with a doubled genome is greater than the sum of its parts in the long run," states Doug

Soltis. "Genome doubling opens new opportunities for gene expression and gene regulation that we are only now beginning to appreciate."

More information: Douglas E. Soltis, Clayton J. Visger, and Pamela S. Soltis. 2014. The polyploidy revolution then...and now: Stebbins revisited. *American Journal of Botany* 101:737-753. doi:10.3732/ajb.1400178

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