Commentary

Polyploidy as a mechanism for surviving global change

'The effects of this process have been so far-reaching, and it is so widespread, that anyone who would have a real understanding of species interrelationships and species evolution in the majority of plants must realize the significance and implications of polyploidy and the processes that accompany it'

(Stebbins, 1940)

One of the great paradigm shifts in the plant sciences in the last century has been the recognition of the fundamental role that whole genome duplication (WGD), or polyploidy, has played throughout the evolutionary history of plants. As its name suggests, a WGD event results in a complete doubling of the cell's genomic complement. Confirming G. L. Stebbins' early insights on the immense potential of polyploidy to influence species' evolution, researchers have now found evidence to support the role of WGD in shaping nearly every aspect of plant evolution, from genome and transcriptome structure to gene expression patterns, gene family evolution, and myriad aspects of ecology and physiology (reviewed in Soltis *et al.*, 2014). Much of the work on plant polyploidy has focused necessarily on extant taxa, but phylogenetic approaches have allowed researchers to identify WGDs that occurred putatively many millions of years ago, including in the ancestry of all major land plant and algal lineages examined to date (*One Thousand Plant Transcriptomes Initiative*, unpublished). In this issue of *New Phytologist*, Cai *et al.* (pp. 565–576) extend these insights into the past one step further and identify not only a remarkable number of WGD events in the history of the plant order Malpighiales, but a significant correlation between the timing of these events and periods of global climatic change during the Paleocene–Eocene transition and in the late Miocene, *c.* 56–54 and 7 million yr ago (Ma), respectively.

'... *researchers have now found evidence to support the role of WGD in shaping nearly every aspect of plant evolution ...*'

Cai *et al.* employed a suite of methods to identify and date the occurrence of WGD events across the Malpighiales. These approaches typically use multi-gene data from sequenced genomes and transcriptomes to infer the phylogenetic location and probable

age of polyploidization events. The authors assembled datasets from 36 ingroup taxa belonging to 21 families representing all major lineages across the order (which includes a total of *c.* 16 000 species in 36 families; Xi *et al.*, 2012). They first searched for clusters of orthologous genes in these datasets and then used these ortholog clusters to reconstruct a dated phylogenetic tree using penalized likelihood, and a species tree using a summary coalescent approach. Three distinct methods were then applied to identify WGD events: (1) assessment of synonymous substitution rates among paralogs; (2) gene tree reconciliation; and (3) a gene count technique. These procedures identified 22, 24 and 22 WGD events across Malpighiales, respectively, most of which were supported by all three techniques. A Gaussian mixture model determined that these events were not distributed randomly in time and discerned two significant clusters of WGDs, one around the Paleocene–Eocene boundary, *c.* 56–54 Ma, and one in the late Miocene, *c.* 7 Ma. A majority of the WGD events inferred in Malpighiales (19 of them) occurred during the Paleocene–Eocene cluster, while a group of five WGDs creates the Miocene peak.

Both the Paleocene–Eocene transition and the late Miocene were periods of worldwide climatic upheaval associated with surges in global temperature (Zachos *et al.*, 2001, 2008). The Paleocene–Eocene thermal maximum (PETM) was the warmest point in the most recent 65 Ma of Earth's history and saw expansion of rainforest habitats worldwide (Pross *et al.*, 2012), while the Mid-Miocene climatic optimum (MMCO) was a period of heightened seasonality and aridity with accompanying expansion of grassland habitats globally (Estep *et al.*, 2014). Both periods are associated with rapid diversification in numerous plant lineages (Jaramillo *et al.*, 2006; Graham, 2011), and evidence increasingly suggests that these and other past intervals of dramatic global change were also associated with increases in paleopolyploidy in plants. For example, Kagale *et al.* (2014) and Estep *et al.* (2014) found evidence for clusters of WGD events across the Brassicaceae and in the grass tribe Andropogoneae, respectively, which both sets of authors dated to the mid to late Miocene. Similarly, Fawcett *et al.* (2009) and Vanneste *et al.* (2014) found evidence for numerous independent WGD events across multiple angiosperm lineages that appear to cluster in the early Cenozoic, at or slightly after the Cretaceous–Paleogene (K–Pg) boundary, predating or potentially overlapping the PETM given the uncertainty in age estimates. The K–Pg boundary itself was a period of intense global change associated with the mass extinction event that ended the Age of Dinosaurs; the Chicxulub impactor and its aftermath also had significant impacts on global plant life, with as many as four out of five species of plants thought to have become extinct (Nichols & Johnson, 2008).

Numerous mechanisms have been suggested to explain why WGD may facilitate survival and adaptation during periods of global change (reviewed in Soltis *et al.* (2014) and Van de Peer *et al.* (2017)). Many of these involve genomic plasticity and the potential

for new combinations of genes, genotypes, and regulatory pathways to increase the possible mechanisms by which populations may adapt to rapidly changing environments. Masking of recessive alleles and restoration of appropriate pairing behavior at meiosis can also 'rescue' otherwise sterile hybrids and restore fertility, increasing opportunities for hybridization to contribute to evolution. Myriad studies have documented the extensive nature of genome restructuring that can occur following WGD, with the general consensus being that there are infinite possible ways by which an extra genome can generate new raw materials for selection to shape into adaptation. Empirical research on the distributions of polyploid plant species reinforces the results of these genomic and transcriptomic studies, as polyploids have routinely been found to be present at higher frequency than diploids in disturbed and challenging environments, and amongst invasive species (Mable, 2013; Van de Peer *et al.*, 2017).

Although polyploidy is now recognized as a common mechanism of speciation in plants, discussion continues about the relationship between WGD and net diversification rate. One way to characterize the question at the heart of this debate is whether polyploidy should be seen on average to be an evolutionary 'dead end' or as a facilitator of diversification. The ever-greater numbers of ancient WGD events identified across the plant tree of life, and frequently in the ancestries of diverse clades, increasingly seem to suggest the latter, but a compromise position between the two perspectives is likely more accurate. Polyploidy may perhaps best be characterized as a 'Las Vegas strategy', with WGD events, like bets in a casino, occurring frequently throughout evolution and most often ending in loss, or extinction. However, those events and lineages that 'hit it big' will win the evolutionary jackpot and experience subsequent increases in net diversification. These increases may lag behind the initial WGD event in evolutionary time, a pattern seen frequently enough that Schranz *et al.* (2012) formalized it as the 'Radiation Lag-Time' model of increased diversification following, but separated from, a polyploidy event by up to several million years. While not all major bursts of diversification in plant evolution are associated with polyploidy, the correlation is too strong to ignore the legacy of WGD in shaping plant diversity through time. While Cai *et al.* did not test directly for a relationship between WGD and changes in net diversification rate across Malpighiales, they do note that overall there appears to be a strong association of WGD with the most diverse clades in the order.

In summary, the results presented by Cai *et al.* have implications for numerous areas of interest in the ever-growing field of plant polyploidy research. The relationship between WGD and the success of lineages during periods of global change is a particularly compelling avenue that deserves further attention across the plant tree of life. This study on Malpighiales and the multi-pronged approach that Cai *et al.* used to identify and date WGD events should serve as a gold standard for other researchers wishing to use genomic and transcriptomic tools to study paleopolyploidy in their clades of interest.

Emily B. Sessa

Biology Department, University of Florida, 876 Newell Drive,
Gainesville, FL 32611, USA
(tel +1 352 392 1098; email emilysessa@ufl.edu)

References

Cai L, Xi Z, Amorim AM, Sugumaran M, Rest JS, Liu L, Davis CC. 2019. Widespread ancient whole-genome duplications in Malpighiales coincide with Eocene global climatic upheaval. *New Phytologist* **221**: 565–576.

Estep MC, McKain MR, Vela Diaz D, Zhong J, Hodge JG, Hodkinson TR, Layton DJ, Malcomber ST, Pasquet R, Kellogg EA. 2014. Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences, USA* **111**: 15149–15154.

Fawcett JA, Maere S, Van de Peer Y. 2009. Plants with double genomes might have had a better chance to survive the Cretaceous–Tertiary extinction event. *Proceedings of the National Academy of Sciences, USA* **106**: 5737–5742.

Graham A. 2011. The age and diversification of terrestrial New World ecosystems through Cretaceous and Cenozoic time. *American Journal of Botany* **98**: 336–351.

Jaramillo C, Rueda MJ, Mora G. 2006. Cenozoic plant diversity in the neotropics. *Science* **311**: 1893–1896.

Kagale S, Robinson SJ, Nixon J, Xiao R, Huebert T, Condie J, Kessler D, Clarke WE, Edger PP, Links MG et al. 2014. Polyploid evolution of the Brassicaceae during the Cenozoic era. *The Plant Cell* **26**: 2777–2791.

Mable BK. 2013. Polyploids and hybrids in changing environments: winners or losers in the struggle for adaptation? *Heredity* **110**: 95–96.

Nichols DJ, Johnson KR. 2008. *Plants and the K–T boundary.* Cambridge, UK: Cambridge University Press.

Pross J, Contreras L, Bijl PK, Greenwood DR, Bohaty SM, Schouten S, Bendle JA, Röhl U, Tauxe L, Raine JI et al. 2012. Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. *Nature* **488**: 73–77.

Schranz ME, Mohammadin S, Edger PP. 2012. Ancient whole genome duplications, novelty and diversification: the WGD Radiation Lag-Time Model. *Current Opinion in Plant Biology* **15**: 147–153.

Soltis DE, Visger CJ, Soltis PS. 2014. The polyploidy revolution then. . .and now: Stebbins revisited. *American Journal of Botany* **101**: 1057–1078.

Stebbins GL. 1940. The significance of polyploidy in plant evolution. *American Naturalist* **74**: 54–66.

Van de Peer Y, Mizrachi E, Marchal K. 2017. The evolutionary significance of polyploidy. *Nature Reviews. Genetics* **18**: 411–424.

Vanneste K, Baele G, Maere S, Van de Peer Y. 2014. Analysis of 41 plant genomes supports a wave of successful genome duplications in association with the Cretaceous–Paleogene boundary. *Genome Research* **24**: 1334–1347.

Xi Z, Ruhfel BR, Schaefer H, Amorim AM, Sugumaran M, Wurdack KJ, Endress PK, Matthews ML, Stevens PF, Mathews S et al. 2012. Phylogenomics and a posteriori data partitioning resolve the Cretaceous angiosperm radiation Malpighiales. *Proceedings of the National Academy of Sciences, USA* **109**: 17519–17524.

Zachos JC, Dickens GR, Zeebe RE. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**: 279–283.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**: 686–693.