

# Recently Formed Polyploid Plants Diversify at Lower Rates

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Polyploidy (or whole-genome duplication) is a widespread feature of plant genomes, but its importance to evolution has long been debated. Polyploids have been postulated to be evolutionary dead ends because of the inefficiency of selection when genes are masked by multiple copies (1). However, most plant species have experienced at least one genome doubling early in their history (2), suggesting that rather than being an evolutionary dead end, polyploidy is a route to evolutionary success. A recent study (3) confirmed the ubiquity of polyploidy, with about 35% of vascular plant species being recent polyploids (“neopolyploids,” having formed since their genus arose), representing 15% of speciation events in flowering plants and 31% in ferns. It remains unknown, however, whether the abundance of polyploids is a consequence of higher diversification rates following polyploidy or of frequent polyploid formation.

We estimated diversification rates of neopolyploids relative to their diploid congeners. We compiled a data set of angiosperm ( $n = 49$ ) and seed-free vascular plant (SFVP, including ferns and lycophytes;  $n = 14$ ) generic-level groups in which ploidy levels could be estimated from cytological and phylogenetic data (4). Over 500 ploidy shifts were inferred with a probabilistic model of chromosome number evolution that accounts for aneuploid and polyploid transitions but not diversification rate differences (5). This allowed us to label all descendants of a polyploidization event as neopolyploids, even when lacking chromosome data.

Likelihood analyses indicated that 33% of the examined species are neopolyploids (609/2043 for angiosperms and 209/458 for SFVPs), matching earlier estimates (1, 3). Polyploidization events were not distributed uniformly across phylogenies but were disproportionately represented on the tips of the tree of life [ $\chi^2_1 = 90.5$  (all data); 48.2 (angiosperms); 45.1 (SFVPs);  $P \ll 0.01$  (4)], suggesting that newly formed polyploid lineages generally fail to persist.

To estimate diversification rates, we used the binary state speciation and extinction (BiSSE) model (6) to coestimate diversification rates associated with diploids versus neopolyploids. Defining polyploids as those lineages that underwent a polyploidization event since divergence from their generic ancestor, the transition rate from polyploidy to diploidy was set to zero [but see (4)]. Across our data set, the speciation rates of neopolyploids were significantly lower than that of diploids ( $P < 10^{-3}$ ;  $t$  test), and their extinction rates were significantly higher ( $P < 10^{-12}$ ). Together, neopolyploid lineages exhibit significantly reduced rates of diversification (speciation minus extinction) ( $P < 10^{-12}$ ) (Fig. 1).

The inferred difference in speciation rates between diploids and polyploids may be driven by a greater propensity of diploids to speciate via polyploidization relative to neopolyploids. We extended BiSSE to allow ploidy transitions only at speciation events (4) and inferred the frequency of diploid speciation events that involve polyploidization and those that do not (heteroploid and homoploid speciation, respectively). Discounting diploids that underwent

heteroploid speciation, the difference in speciation rates between diploids and polyploids was no longer significant ( $P > 0.1$ ). Nevertheless, the diversification rates of polyploids remained significantly lower than that of diploids ( $P < 10^{-6}$ ; fig. S2) because of the higher extinction rate of neopolyploids. The average frequency of heteroploid speciation was 31.7% for all plants, 29.7% for angiosperms, and 38.7% for SFVPs, exceeding previous estimates that ignored extinction rate differences. Our estimates for the rate at which diploids speciate via polyploidization likely represent upper bounds, however, because only phylogenies with variation in ploidy were examined and because ploidy transitions were allowed only at speciation events.

The lower diversification rates of polyploids may seemingly contradict evidence of ancient polyploidization events in the genomes of most angiosperms (2). Yet we find that the expected number of paleopolyploidization events is higher than would be observed if diversification rates were equal (4). Our results indicate that polyploidy is most often an evolutionary dead end, but the possibility remains that the expanded genomic potential of those polyploids that do persist drives longer-term evolutionary success.

## References and Notes

1. G. Stebbins, *Chromosomal Evolution in Higher Plants* (Edward Arnold, London, 1971).
2. Y. Jiao *et al.*, *Nature* **473**, 97 (2011).
3. T. E. Wood *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 13875 (2009).
4. Materials and methods are available as supporting material on Science Online.
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## Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1207205/DC1  
Materials and Methods

SOM Text

Figs. S1 to S3

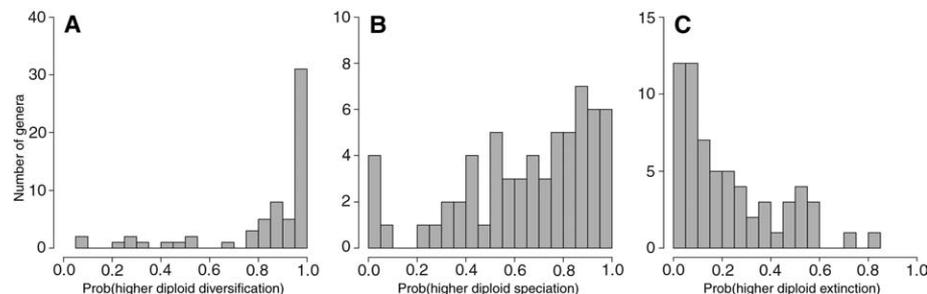
Tables S1 to S3

References (7 to 103)

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**Fig. 1.** The posterior probabilities that diploids exhibit higher rates of (A) diversification, (B) speciation, and (C) extinction than polyploids.

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