

## Inappropriate model rejects independent domestications of *indica* and *japonica* rice

In PNAS, Molina et al. (1) argued for a single origin of cultivated rice based on a demographic analysis of SNPs detected from 630 genes on three rice chromosomes. Although hypotheses for both a single origin (snowballing model) and independent origins (combination model) of rice were previously proposed (2), Molina et al. (1) did not provide conclusive evidence to support the single-origin hypothesis.

Molina et al. (1) used an inappropriate model for independent domestications (double-founder model), in which they assumed that *indica* and *japonica* cultivars originated from homogeneous ancestral populations that diverged for an interval between the two domestication events (figure 1b of ref. 1). However, previous studies have shown that substantial differentiation had occurred among populations of the wild progenitors *Oryza rufipogon* and *Oryza nivara* (or the annual form of *O. rufipogon*), particularly between *O. rufipogon* populations of China and the remaining in the world (3, 4). In fact, in Molina et al.'s STRUCTURE analysis, two subpopulations within *O. rufipogon* were identified at  $K = 4$  and  $K = 5$  (figure S1 of ref. 1). These results indicated that there was a strong population structure within the wild progenitors.

Having overlooked the population structure, the double-founder model (Fig. 1B of ref. 1) underestimated the divergence time between *indica* and *japonica*. In other words, the time of divergence between the wild populations giving rise to *indica* and *japonica* could have considerably exceeded that assumed in the model, which was restricted to the interval of the two domestication events ( $\tau$  in Fig. 1 of ref. 1). This is plausible given that *indica* might have been domesticated from *O. nivara* in the southern Himalayas and *japonica* could have been domesticated from *O. rufipogon* in China (2, 3). Consequently, the likelihood of the data fitting the double-founder model must

have been low, and the single-origin model gained relatively high support.

The second line of evidence used by Molina et al. (1) to support the single-origin hypothesis came from the phylogenetic analyses of several published datasets. In their reanalyses, four datasets, each with sequences of more than five loci, yielded trees on which cultivars tended to form a monophyletic group. The other two datasets that supported independent origins were discounted because they each contained sequences from fewer than five loci. This cutoff is arbitrary, especially when the samples of phylogenetic markers are all relatively small. Furthermore, it has been shown that phylogenetic analyses of sequence data could easily group together cultivars with independent origins, particularly when cultivars were domesticated from genetically diverged wild populations and there has been gene flow between cultivars following their independent domestications (4, 5). Both of these situations were very likely to be the case during rice domestication (2). Therefore, neither line of evidence provided by Molina et al. (1) was convincing. The question of whether rice was domesticated once or at least twice remains open.

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