

Multiple domestications of Asian rice

To the Editor — In their recent Correspondence¹ about our study showing that there were three origins of Asian rice², Huang and Han suggest that the methodology that we used to infer multiple domestications was flawed as it did not take account of the strong genetic bottleneck in *japonica*. We agree that the differences in diversity between *japonica* and the other groups present a challenge when comparisons are made, and we explored this issue in some detail in the Supplementary Information of our paper².

Specifically, Huang and Han criticized our choice of a $\pi_{(wild)}/\pi_{(domesticated)}$ threshold of 4 for each of *japonica*, *indica* and *aus*, and implied that a higher threshold would be more appropriate for the detection of selective sweeps in *japonica*. We did, in fact, test the data with such an approach — it is described in the first paragraph of the Methods section of the paper, and the resulting tree is presented as Supplementary Fig. 1². In brief, we compared the sweeps Huang *et al.*³ identified for *indica* at threshold 3 against the sweeps they identified for *japonica* at threshold 14 (Supplementary Section 2 of ref. 3) and extracted genomic regions that are detected as sweeps in both groups ('sweep overlaps'). The resulting tree reveals that even when a much higher sweep threshold is used for *japonica* (to reduce the swept fraction of the *japonica* genome), *indica*, *japonica* and *aus* still form separate clusters. We are therefore

confident that the strong *japonica* bottleneck does not influence our results in the way suggested by Huang and Han¹.

Huang and Han¹ also contend that the presence of similar haplotypes, including identical coding sequences, in cultivated groups for loci such as *sh4* and *PROG1* argues against multiple domestication. In the Supplementary Information of our paper², we explain how selection of similar haplotypes that are geographically widespread within the standing variation can lead to this outcome, and we provide evidence indicating that the *sh4* allele present in domesticated rice was selected from at least two wild sources. We do not believe that the 55 domestication sweeps previously identified by Huang *et al.*³ are validated by the presence within them of 'well-characterized domestication genes', as this assumes that these domestication genes have undergone selection in all groups of *O. sativa*, which has not been established for the majority of those genes. In fact, comparison of the selective sweeps separately detected for *japonica* and *indica* by Huang *et al.* (see Supplementary Tables 10 and 11 of ref. 3) shows that at least some of these genes have not undergone selection in both of these cultivated groups. For example the *gSH1*, *Waxy* and *Rc* genes, as well as various genomic regions associated with quantitative traits such as grain length, number and weight, tiller angle and panicle length, which are

under strong selection in *japonica*, are not found within the selective sweeps of *indica*. This observation questions the use by Huang *et al.*³ of the single *O. sativa* supergroup for detection of the 55 'major domestication sweeps', as many regions passing the threshold can be under strong selection in one group but much weaker selection in another. Huang and Han admit that this happens: "the *indica* group has many allelic combinations at the 55 domestication loci but *japonica* has very few"¹. It is indeed possible that the diversity of *indica* was enriched by *japonica*, but the multiplicity of the allele combinations indicates that these loci have been subject to zero or weak selection in *indica*. This suggests that such gene flow was not critical for the domestication of *indica* and probably occurred after the independent domestication of this group of rice. □

References

1. Huang, X. & Han, B. *Nature Plants* **2**, 15207 (2015).
2. Cíván, P., Craig, H., Cox, C. J. & Brown, T. A. *Nature Plants* **1**, 15164 (2015).
3. Huang, X. *et al.* *Nature* **490**, 497–503 (2012).

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