LETTER

Reply to Ross-Ibarra and Gaut: Multiple domestications do appear monophyletic if an appropriate model is used

Ross-Ibarra and Gaut (1) use an inappropriate model with a single wild population, a single genetic locus system, and poor accountability for biological and archaeological data. Their results do not conflict with ours (2) and are easily explained. Our model (Fig. 1) has two structured wild populations, consistent with the current archaeological view of a multiregional agricultural transition (3) and genetic data (4). Our bottleneck uses established biological dimensions (5). In their model the same wild population is domesticated twice, and

the resultant populations are kept separate for 2,500 years, a scenario that has no archaeological basis. Their single-locus system achieves monophyly in ways different from the multilocus systems used in real studies of crop origins and modeled by us. The 60% monophyly they observe results from allele extinction in the wild population. Further monophyly under this system is caused by fixation of derived mutations, this process of allele turnover equal to the mutation rate, in their case taking 2.4-24 million years. Mutation is obviously not a major influence over the relevant timescales, which is why we excluded it from our model. The differentiation of allele frequencies between populations, which causes monophyly in multilocus systems, is absent from their approach. Their artificially small wild population does not reflect the barley metapopulation that stretches from western Turkey to Pakistan but has a dramatic effect on the outcome of their simulation by making wild allele extinction an influential process when it should be negligible; hence, they observe monophyly by artifact.



Fig. 1. Description of population simulation used by Allaby and colleagues (3). Simulations assume that *N* is very large, *N*_b is the bottleneck size, and *k* is the bottleneck severity expressed by *N*_b/*d* where *d* is the number of bottleneck generations.

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LETTER

Multiple domestications do not appear monophyletic

Allaby *et al.* (1) investigate the phylogenetic consequences of crop domestication using forward simulations to mimic the domestication process. Their results suggest that monophyly of crop accessions is not a reasonable criterion for differentiating between multiple and single domestication events. Their simulations also produce the nonintuitive result that multiple domestication events more often result in monophyly than do single domestication events. We believe that these results are a function of their population-genetic model, which employs arbitrary population frequencies, excludes mutation, assumes unrealistically small effective population sizes, and incorporates neither their own protracted domestication model nor evolution of the wild population.

Here we present coalescent simulations (2) with entirely contrary results. We simulate codominant data with recombination, convert the data into dominant genotypes, and follow the phylogenetic methods outlined in ref. 1. We investigate a single domestication event, independent domestications with admixture (akin to ref. 1), and independent domestications with migration (Fig. 1). Under these models, single domestications are much more likely to appear as monophyletic (Fig. 1). Moreover, additional simulations (data not shown) suggest that our results are independent of the size of the domestication bottleneck and the model of population growth after domestication. Like Allaby et al. (1), we find that multiple domestication events appear monophyletic more often over time, but this process occurs much more slowly than claimed: To double the proportion of monophyletic phylogenies under the admixture model requires increasing the age of domestication by an order of magnitude (from 4N to 40N generations following the nonstandard scaling of ref. 1).



Fig. 1. Coalescent models and observed monophyly. Simulations assume $\theta = 0.017$, equivalent to N = 625,000 and $\mu = 6.8 \times 10^{-9}$. Time is shown on the *y*-axis as thousands of years (Kya) before present. (A) Single domestication. (B) Two domestications with admixture. (C) Two domestications with migration. (D) Proportion of 1,000 simulations in which all domesticated taxa appear monophyletic.

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