The genetic expectations of a protracted model for the origins of domesticated crops

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Until recently, domestication has been interpreted as a rapid process with little predomestication cultivation and a relatively rapid rise of the domestication syndrome. This interpretation has had a profound effect on the biological framework within which investigations into crop origins have been carried out. A major underlying assumption has been that artificial selection pressures were substantially stronger than natural selection pressures, resulting in genetic patterns of diversity that reflect genetic independence of geographic localities. Recent archaeobotanical evidence has overturned the notion of a rapid transition, resulting in a protracted model that undermines these assumptions. Conclusions of genome-wide multilocus studies remain problematic in their support of a rapid-transition model by indicating that domesticated crops appear to be associated by monophyly with only a single geographic locality. Simulations presented here resolve this conflict, indicating that the results observed in such studies are inevitable over time at a rate that is largely influenced by the long-term population size. Counterintuitively, multiple origin crops are shown to be more likely to produce monophyletic clades than crops of a single origin. Under the protracted transition, the importance of the rise of the domestication syndrome becomes paramount in producing the patterns of genetic diversity from which crop origins may be deduced. We identify four different interacting levels of organization that now need to be considered to track crop origins from modern genetic diversity, making crop origins a problem that could be addressed through system-based approaches.

domestication | phylogenetics | protracted transition | simulation

The domestication of crops is a model example of evolution under changing climatic conditions that has been at the heart of evolutionary thought since Darwin (1, 2), who recognized that an understanding of the evolutionary dynamic of this process gives a prime source of insight to evolution itself. This fundamental value of domestication is still true today (3). Until recently, domestication in the Near East had been viewed as a rapid process in three principal steps that closely followed the climatic transition between the Pleistocene and Holocene (see Fig. 1), with little predomestication cultivation (4), a rapid rise of domesticated crops, and an explosive expansion of agriculturists out of centers of origin (5).

The rapid-transition model has the major corollary of biological significance that the artificial selection pressure provided by cultivation practices that led to the fixation of the domestication syndrome traits quickly dominated the natural selection pressures to which the wild crops were subject. This corollary appeared to be reasonable based on the rapid appearance of crops in the archaeological record, classic field experiments that demonstrated the possibility of domestication in 20 years or so (6), and the notion that cereals could not have survived in the Near East until after the dry conditions of the Younger Dryas (7). The rapid-transition model supported the notion of the Neolithic Package (8), which implied that the various different crops were brought into domestication by the same group of early farmers. In turn, the Neolithic Package provided a cornerstone to an interdisciplinary paradigm about agricultural spread by elite dominance, in which European populations are largely the genetic (9) and linguistic (5, 10) descendants of farmers from the Near East.

The rapid-transition model has largely driven the debate about crop origins by stating that if the Neolithic Package is true then domesticated crops should be monophyletic (11), because there would be little need for the same group of farmers to redomesticate crops. If domestications were multiple and widespread, then under the rapid-transition model crops should appear polyphyletic because the short timescales involved would mean that separate domestications would be genetically independent. Extensive work has therefore been carried out over the past couple of decades to establish the monophyly versus polyphyly of crops. The genetic evidence has followed three principal lines of investigation. Firstly, the number of times a crop has been domesticated should be apparent in the number of different mutant alleles that give rise to domestication-syndrome traits, such as the tough rachis (11). It is assumed that such mutations occur within cultivated crops because they would be rapidly removed through purifying selection from wild populations, and so independent domestications would select independent mutations. In many crops only one tough rachis mutant is known, supporting a single origin on this evidence, although barley is an unusual case in that two mutants are known (12, 13). The second line of inquiry has considered the reduction in genetic diversity associated with the domestication bottleneck. Typically, modern crops retain $\approx$70% of the genetic diversity of their wild progenitors (14), which, although apparently high, does not preclude a single origin because modeling experiments have demonstrated that an effective population size of only 1,500 individuals can explain the diversity seen in modern crops such as rice and maize (15, 16), which seems consistent with a single origin. The third genetic approach has been phylogenetic. According to gene phylogenies, some crops, such as flax, show evidence of monophyly (17), whereas others, such as rice and barley, are polyphyletic (18, 19). Similarly, allozymes have also been used to establish polyphyly in crops such as lentils (20, 21). Genome-wide surveys using multilocus systems, such as AFLP, have indicated that crops such as einkorn (22), barley (23), and others (24–26) are monophyletic, suggesting a single origin with the domesticated clade closely associated with wild forms from a narrow geographical range, interpreted as rapid, localized invention of agriculture (27). Although the genome-wide evidence has been

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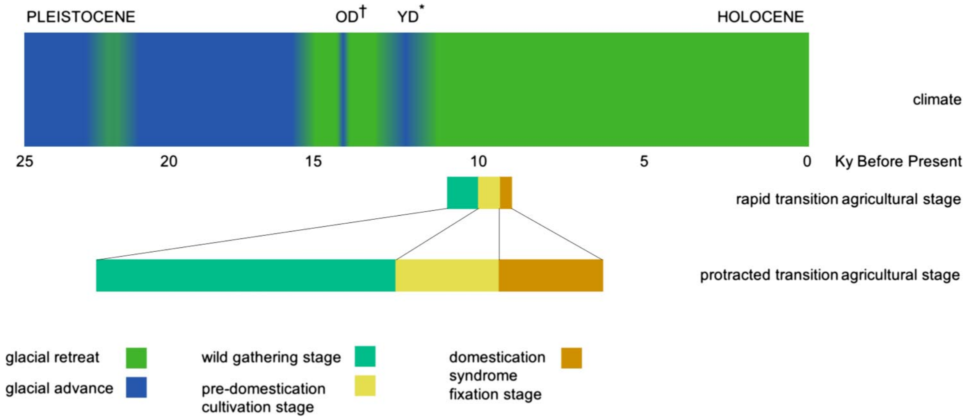

Fig. 1. The timescales of the rapid and protracted transition models of domestication. *, Younger Dryas; †, Older Dryas

interpreted as supporting single origins and the rapid-transition model, it has conflicted frequently with gene phylogeny evidence. Perhaps the most notable conflict is in the case of barley, for which there is a large body of evidence that suggests at least a diphyletic origin (19, 28). This conflict has been the source of some confusion, and its cause has yet to be identified.

Recently, archaeobotanical evidence has overturned the rapid-transition model that crop domestication was initiated and completed in a brief period at the Pleistocene/Holocene boundary (see Fig. 1). All three stages of the domestication process have been extended in timescale. Large plant assemblages have provided evidence for wild-cereal gathering as old as 23,000 years B.P. at Ohalo II (29), some 10,000 years earlier than previously thought. Evidence of predomestication cultivation has been established from 13,000–12,500 years B.P. (30, 31), during the Younger Dryas. Within the predomestication period, there appear to have been numerous beginnings of agriculture, with different species hailing from different localities rather than in a single Neolithic Package (32). The final stage of the domestication process in which the domestication syndrome traits are fixed has also been found to be a slow process; Tanno and Willcox (33, 34) argue that the tough-rachis mutant took over 3,000 years of cultivation to reach fixation and the syndrome traits themselves appeared in slow sequence, not together over a short period.

It is now more appropriate to consider a protracted, rather than a rapid-transition, model for domestication. The extensive timescale of the protracted transition makes gene flow between localities of cultivation more likely and consequently lowers the likelihood that a domesticated crop will be either be exclusively associated with a narrow geographical range or that multiple domestications would be genetically independent. Although it is possible to reinterpret genetic diversity and gene phylogeny evidence within a protracted transition model, it remains problematic that genome-wide surveys appear to support a monophyletic origin of crops that is rapid and localized. A turning point in the interpretation of genome-wide genetic evidence came from modeling studies that demonstrated that it is possible for cultivated populations of hybrid origin to appear monophyletic (35). The model used in this instance was simple in that it assumed complete linkage equilibrium between loci for convenience and hence no concept of chromosomes, which some workers argued made it too unrealistic (24).

To investigate the reason behind the apparent conflict between multilocus system data, gene phylogenies, and the protracted transition evident from the archaeological record, we designed a new, considerably more sophisticated model system to simulate the domestication process. The aim was to explore the effects of linkage and a protracted period of cultivation under single- and multiple-domestication scenarios. This model is comprised of virtual plants, each with their own set of virtual chromosomes carrying biallelic markers, capable of random segregation and meiotic recombination, which are subject to population dynamics associated with the domestication process. The model begins by generating a phylogeny for each chromosome and ascribing a population frequency to each genotype described at each node of the tree. A small number of wild individuals representing the domestication bottleneck are then drawn from the population by selecting chromosomes. The wild individuals represent predomestication cultivation. These wild individuals then produce gametes through random segregation, with or without the possibility of meiotic recombination, which are used to generate subsequent crop generations. After the bottleneck period, the cultivated population undergoes an expansion and may then be amalgamated with another population under a multiple domestication scenario or not for single domestications. The populations were then left to cycle through varying numbers of generations to ascertain the effects of protraction. Individuals were drawn from the resultant wild and cultivated populations and subjected to a phylogenetic algorithm to determine whether or not the cultivated population formed a monophyletic cluster.

Results and Discussion

Each set of simulation conditions was repeated 100 times, resulting in 6,100 simulations and analyses (see Fig. 2). Seven different domestication scenarios were considered. In five of these, the long-term size of the cultivated population after expansion was 100 individuals. In two of these, a crop was domesticated from either a single or double origin without meiotic recombination. The other three repeated the double-origin scenario, but with increasing probabilities of meiotic recombination (all of the other scenarios had a zero probability of such recombination). The remaining two scenarios also repeated the double origin, but with long-term population sizes of 50 and 150, respectively.

In each scenario tested, the frequency with which a monophyletic clade of cultivated individuals was obtained increased over time, giving a typically S-shaped curve. In the scenario of the cultivated crop of double origin, size 100, with no meiotic recombination, the midpoint of the S curve approximated 50% of simulations, resulting in monophyly and 100 generations. By 200 generations, the curve had formed a plateau with 90% of simulations resulting in monophyly. To establish whether the curve was an asymptote, the same set of conditions were repeated for 500 generations which resulted in 100% of simulations showing a monophyletic clade for the hybrid population

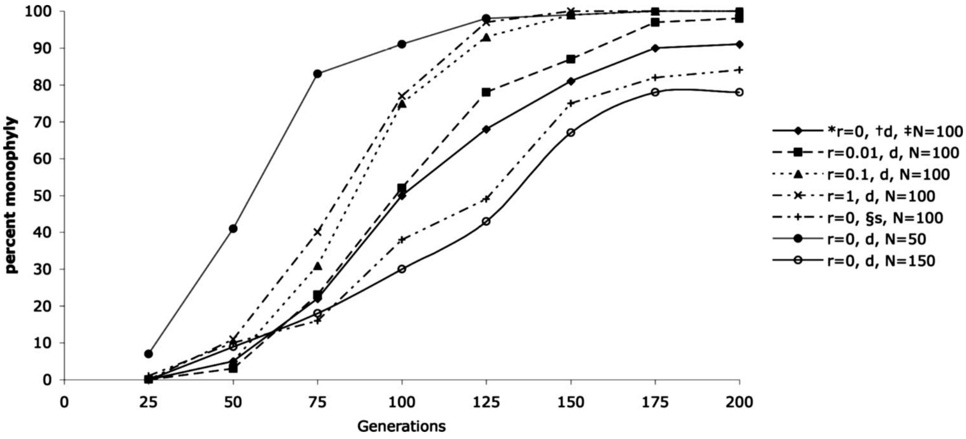

Fig. 2. Percentage of simulations that led to a monophyletic clade of cultivated plants over time. *, meiotic recombination probability; †, double origin of cultivated plants; ‡, long-term population size; §, single origin of cultivated plants.

[supporting information (SI) Fig. S1]. We conclude that the curve does not asymptote. The effect of the long-term population size was explored by repeating the scenario with a long-term value of 50 and 150 respectively. In these scenarios, the midpoint of the log phase occurred at 50 and 150 generations, respectively, suggesting a strong influence of population size on the time taken to reach monophyly. This influence was further tested with a much larger population of 500 individuals, which again showed the same pattern of S-shaped curve with 59% of simulations resulting in monophyly by 500 generations and 96% of simulations showing monophyly by 1,000 generations (Fig. S2). These results suggest that in the case of perfectly linked biallelic markers, nearly all simulations result in a monophyletic clade of cultivated by 2N generations. This finding predicts that the effective population size of 1,500 individuals that is observed for cereals (14) should reach monophyly in 3,000 generations. We tested this prediction and found that 98% of simulations (69 of 70) (data not shown) resulted in monophyly, supporting the prediction. The effect of reduced linkage through meiotic recombination was investigated by allowing recombination between homologous chromosomes during meiosis with probabilities of 0.01, 0.1, and 1, respectively, the case of 1 being more extreme than would be expected in nature An increased probability of recombination resulted in a more rapid progression to monophyly, although this effect appeared to be less influential than population size.

The outcome of the final scenario of a single origin was most surprising because these simulations were slower than multiple-origin ones to reach monophyly. Consequently, we reach the superficially counterintuitive conclusion that, when viewed through multilocus systems, multiple-origin crops are actually more likely to result in monophyly than single-origin ones. In fact, it is quite reasonable to suppose that this conclusion might be the case. The underlying reason is that cultivated crops that originate from a single wild population are more similar to their wild progenitor population than an amalgamated cultivated population that will have additional genetic contributions from other wild sources: Crops of multiple origins are, from the outset, more differentiated from their wild sources than crops of a single origin.

Conflict Between Genomic Datasets and a Protracted Transition. Contrary to the conventional expectation, the simulations presented here demonstrate that a monophyletic clade obtained from genome-wide data indicates neither a single origin nor a rapid transition. All of the scenarios showed that any crop, whether of single or multiple origins, becomes monophyletic after a number of generations, with this number principally being a function of the size of the cultivated population. This result is true if markers are in perfect linkage disequilibrium, shown with nonrecombining chromosomes, or not. The results suggest that that a cultivated crop is likely to become monophyletic after approximately 2N generations.

The principal genetic difference between the rapid and protracted transitions is the amount of gene flow that would have been possible. The monophyletic clades obtained with genome-wide data sets are quite compatible with the protracted transition in two ways. Firstly, the simulations show that, both in the presence and absence of a second source of genetic material, monophyly will be reached through gene flow. Secondly, the occurrence of gene flow into the cultivated population actually serves to increase the rate at which monophyly is reached, resulting in genome-wide evidence being even more supportive of a complex rather than a single origin. This finding is in agreement with recent studies of einkorn that conclude that the high level of diversity is consistent with extensive gene flow over time and even multiple domestications (36).

It is interesting to note that the value of 2N for a population of approximately 1,500 individuals (14) giving a time of 3,000 years for an annual to reach monophyly correlates closely with the observed timescale of fixation of the domestication syndrome trait of the tough rachis (32). Such a correlation suggests that domestication-syndrome trait fixation might only have been reached when monophyly had been reached, implying an equable balance in artificial selection of domestication syndrome traits relative to natural selection. Had there been a strong bias for the tough rachis, one might have expected it to reach fixation more rapidly than the neutral population processes differentiating the cultivated and wild populations.

Genetic Expectations in a Protracted Transition. The protracted transition model has profound consequences on the evolution of domestication: Artificial selection did not quickly dominate natural selection. The extent of protraction of domestication is determined by the mode and pace of the fixation of traits of the domestication syndrome. Understanding the rise of the domestication syndrome in evolutionary terms has now become key to understanding the origins of crops through genetic diversity, rather than simplistic analyses which have an interpretation rooted in the rapid-transition model. The agricultural and natural environments provide selection pressures that are frequently diametrically opposed. Illustrative examples include seed size, which is increased by sowing pressure but decreased by wild dispersal pressures (34), and rachis quality where harvesting pressure favors tough but wild dispersal pressures favor brittle. In each environment, contrasting traits are selected for and enriched. Consequently, gene flow between the environments results in a struggle between two diametrically opposed evolutionary paths. The factors that must be considered to understand this process are numerous and interacting over at least four levels of organization. Firstly, the strength of selection of each trait, which determines the pace at which traits will be selected, depends on events and conditions within each environment, such as harvesting strategy or abiotic conditions, such as water availability and biotic stress, such as the presence of competitor species. Secondly, the genetic control of traits may be monogenic (e.g., tough rachis), polygenic (e.g., seed size), or part of a biological gene circuit of interaction (e.g., photoperiod sensitivity or vernalization). Whereas a single mutation is enough to effect a saltatory change in a monogenic trait, which can be equally rapidly lost, a polygenic trait may behave in a stepwise manner resulting in an increased phenotypic stability, and a gene circuit may be rendered dysfunctional in parallel through the accumulation of mutations in different genes. Thirdly, the genomic distribution of domestication syndrome loci affects the ease with which the syndrome can be selected for as a whole (37). Indeed, the colocalization of domestication syndrome loci has frequently been observed (38–40). Fourthly, at the population level, one must consider the effects of gene flow in conjunction with selection pressures. If a trait is enriched in one environment and exported to the other, how long may it persist for a given level of gene flow and strength of selection? For instance, the tough rachis allele may be exported to the wild, where it may persist in brittle/tough heterozygote plants (which behave as normal wild forms) for a length of time long enough to be exported further into other cultivated environments, undermining the assumption that tough rachis mutants are necessarily rapidly removed from the wild.

The Challenge of Unraveling Crop Origins. The apparently even balance between artificial and natural selection pressures mediated by gene flow raises the possibility that successful domestication may be more likely as cultivated crops are removed from the wild progenitor biogeographical range. An interesting corollary of this possibility is that each human expansion out of the range may have resulted in a domestication, leaving phylogeographic evidence. Evidence for independent expansions has been found for emmer (41, 42) and could perhaps explain the distinctiveness of Ethiopian crops from European counterparts, such as in the case of barley (19). Alternatively, traits may have become fixed within the wild progenitor range, all in one location or in a piecemeal fashion throughout the range. This trait fixation may have led to either a single center of origin from which there was a single rapid agricultural expansion, leading to a facilitation of human expansion by domestication (43) that may be expected to lead to a single phylogeographic signal of crop expansion or a more diffuse origin in which many localities contributed different traits or simultaneously fixed the same traits.

To unravel crop origins, we need to establish what signatures of genetic variation are associated with the various different domestication scenarios possible under the protracted transition. To do so, analyses need to move to a new level that incorporates the four levels of organization of the evolutionary process of domestication. We propose that one way forward is to take systems-based approaches that allow the necessary complex interactions to occur and generate the expected patterns of diversity.

Methods

The simulations were carried out by using a program written by R.G.A. For the program methodology, see *SI Text*. The parameters for the simulations were as follows: Each virtual diploid plant had a complement of 40 chromosomes. A total of 320 biallelic markers were distributed evenly across the genome (resulting in 16 markers per chromosome). In the case of double-origin simulations, the two wild populations generated had an average Fst distance of 0.25 from each other, which is a realistic value given observed distances of natural wild populations (44).

The domestication bottleneck consisted of drawing 20 individual plants from the (infinitely large) wild population, which were used to propagate 10 generations of plants, giving a severity of bottleneck of comparable order to previous estimates (15, 16). The population then expanded to 50, 100, or 150 individuals, and a further 20 generations were propagated, which represented the minimum possible time to generate domesticates (6), although there was no need in this simulation to consider whether the cultivated crops were domesticated phenotypes or not. In the case of double-origin crops, the preceding stages above were carried out in parallel for both crops and, at this point, amalgamated to form a single population of 50, 100, or 150 individuals. Single-origin crops simply proceeded without the amalgamation step. The cultivated crop was then propagated at constant population size for 25, 50, 75, 100, 125, 150, 175, or 200 generations.

After each simulation, a phylogenetic algorithm was performed to determine whether the cultivated crop formed a monophyletic cluster, which was done by using a second program written by R.G.A. Ten individuals were selected randomly from each population: the two wild populations, the two independently domesticated populations, and the amalgamated population or the wild population and the cultivated population in the case of a single origin. A similarity matrix was constructed by using the algorithm of Dice (45), which was inverted to a distance matrix and used to construct a neighbor-joining tree by using NEIGHBOR (J. Felsenstein, University of Washington, Seattle). Each tree file was analyzed to ascertain whether the resulting cultivated individual population occurred in a monophyletic clade or not.

Each set of simulation conditions was repeated 100 times, giving a percentage value of the number of times monophyly was observed for the cultivated crop.

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