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The contribution of genetic and genomic approaches to plant domestication studies

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The application of genomic approaches to the phenomenon of plant domestication promises a better understanding of the origins of agriculture, but also of the way plant genomes in general are organized and expressed. Building on earlier genetic research, more detailed information has become available on the organization of genetic diversity at the genome level and the effects of gene flow on diversity in different regions of the genome. In addition, putative domestication genes have been identified through population genomics approaches (selective sweeps or divergence scanning). Further information has been obtained on the origin of domestication syndrome mutations and the dispersal and adaptation of crops after domestication. For the future, increasingly multidisciplinary approaches using combinations of genomics and other approaches will prevail.

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Introduction

The importance of the Neolithic revolution, which took place some 12,000–10,000 years ago, cannot be overstated. At that time, the human species embarked on a radical change in the way it had procured its food and other products for millions of years. In addition to the transition from hunting-gathering to plant (and animal) agriculture, other major changes were taking place more or less simultaneously including sedentism, the formation of villages, and the introduction of ceramics. Eventually, these developments led to the formation of more hierarchical societies and states and the development of civilizations [1,2]. The Neolithic revolution had a tremendous impact on the biosphere and human societies, consequences that still affect us today. This transition took place in several areas of the Earth and often gave rise to a complementary group of crops that satisfied human needs, not only nutritionally but for other uses as well (Figure 1).

One of the key technological elements of the transition to agriculture is domestication. The cultivation of plants represents an important change in their environment. These changes set in motion several evolutionary processes that led to major morphological and physiological changes, such that often crop plants became quite different from their wild progenitors and, in the most pronounced cases of domestication, could not survive without human intervention [3].

Domestication draws attention from several viewpoints. In addition to its role in human cultural evolution, it is also an experimental system for the study of biological evolution. In addition, many of the differences between wild and domesticated types are important traits or processes in basic biology such as plant development, reproduction, and adaptation [4]. Furthermore, the efficient utilization of crop genetic resources for varietal breeding depends on detailed information about genetic relationships in these collections, which were affected in large part by the domestication process [5,6].

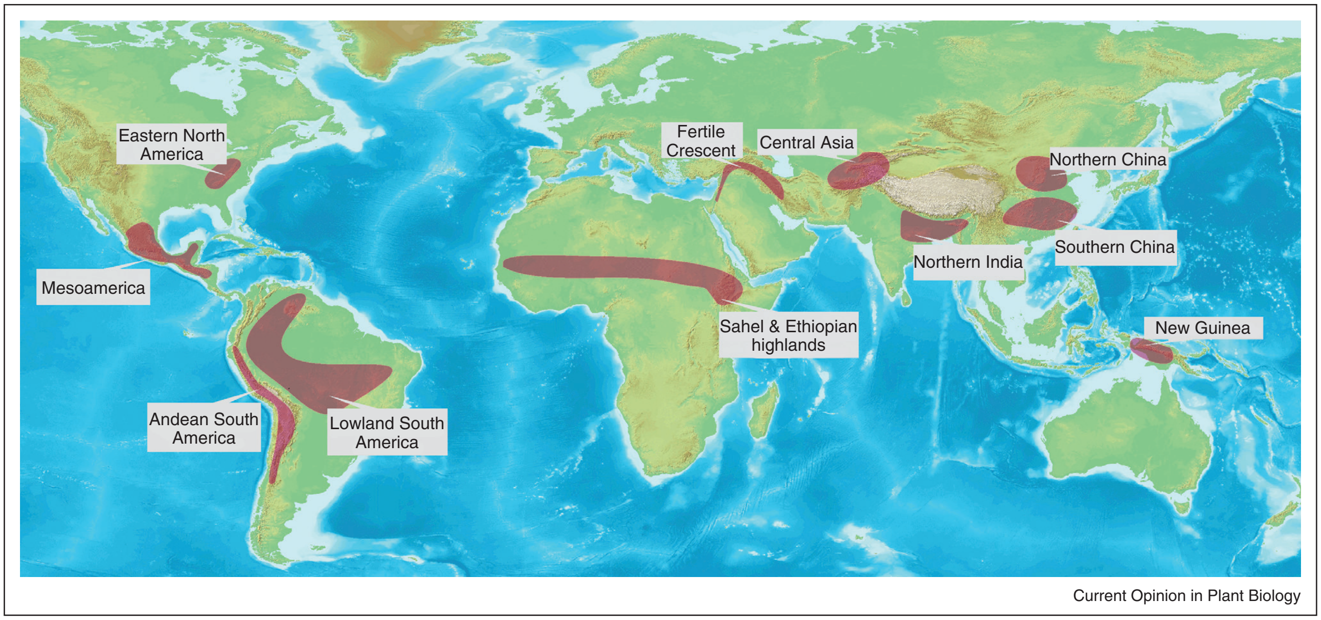
Elucidating the transition from hunting-gathering to agriculture has always been a multidisciplinary research endeavor (e.g. [7–13,14•,15]; for a recent e.g.: [16•]). As science has progressed, new approaches have been incorporated (molecular biology: [17,18•]; bioinformatics: e.g. [19]).

Genomic approaches have become especially important since the introduction of next-generation DNA sequencing [20,21] because these technologies allow for the sequencing of multiple genotypes in a low-cost, high-throughput way, and open new avenues for population, landscape, and ecological genomics [22–25].

Origins of domestication and structure of wild and domesticated gene pools

One of the most generalizable observations in crop domestication studies is the reduction in genetic diversity during and subsequent to domestication, for example, [26–29,30•,31,32,33••,34,35,36•]. This reduction is due to the two-fold action of genetic drift and selection that operate at each stage of the domestication process (Figure 2). Additional factors affect reduction in genetic diversity, including the specific stage of the crop evolution process, with the initial domestication phase usually

Figure 1



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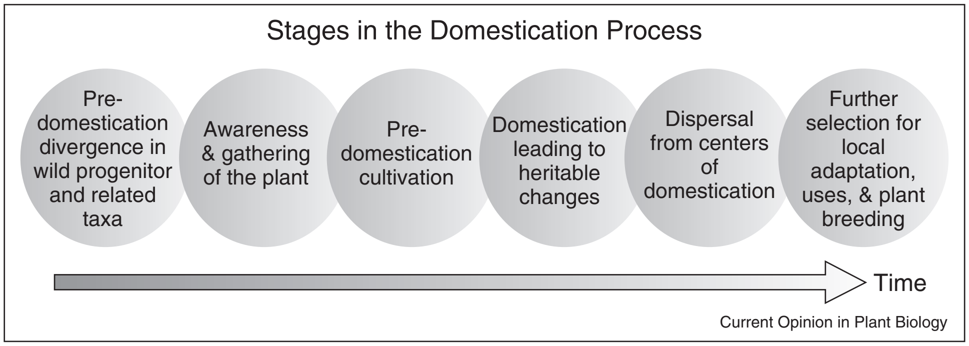
Centers of crop origin and domestication. Shaded regions indicate approximate location of centers of origin and domestication of selected crops. Regions are approximate due to uncertainties in the distribution of the wild progenitors, limited numbers of sites with archaeobotanical remains, and the area of actual domestication. Examples of crops domesticated in their respective centers are: Lowland South America: cassava, sweet potato pineapple, groundnut, cashew, guaraná, peach palm, *Capsicum* peppers; Andean South America: potato, other Andean root crops (e.g. oca, arracacha), common & lima bean, lupin, *Capsicum* peppers, Pima cotton, coca, quinoa, squash; Mesoamerica: Maize, common & lima bean, *Capsicum annuum* pepper, Upland cotton, sisal, papaya, avocado, prickly pear, squash, tomato, vanilla, cacao, amaranth; Eastern North America: sunflower, sumpweed, goosefoot; Sahel & Ethiopian Highlands: African rice, pearl millet, sorghum, cowpea, Bambara groundnut, hyacinth bean, tef, fonio, yam, watermelon, melon, okra, kenaf, coffee, ensete, noog; Fertile Crescent: wheat, barley, oat, pea, chickpea (garbanzo), lentil, faba bean, flax, olive, date palm, grape, onion, lettuce, saffron, poppy; Central Asia: apple, carrot; Northern India: Asian rice (indica), mung bean, pigeon pea; Northern China: broomcorn millet, foxtail millet, Chinese cabbage, soybean; Southern China: Asian rice (japonica), quince, persimmon, litchi, peach, tea; New Guinea: banana, sugar cane.

causing the biggest drop in genetic diversity (e.g. [36•,37]) compared to later steps, including modern plant breeding efforts [32,35,37] (Fig. 2).

Recent genomic studies have improved our knowledge of the fate of genetic diversity in two ways. First, they have expanded our horizons to other crops than the major cereal crops and grain legumes and provided contrasting views of changes in genetic diversity. Next-generation sequencing, various forms of reduced representation libraries, and synteny combined with considerable bioinformatic analyses make it now easier to directly sequence

Figure 2



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Successive stages in the transition from wild-gathered to domesticated plants. The actual duration of the transition may depend on the crop plant and center of domestication, but is thought to have lasted from several 100 to several 1000 years.