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Plant domestication through an ecological lens

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Our understanding of domestication comes largely from archeology and genetics. Here, we advocate using current ecological theory and methodologies to provide novel insights into the causes and limitations of evolution under cultivation, as well as into the wider ecological impacts of domestication. We discuss the importance of natural selection under cultivation, that is, the forces promoting differences in Darwinian fitness between plants in crop populations and of constraints, that is, limitations of diverse nature that, given values for trait X, shorten the range of variation of trait Y, during the domestication process. Throughout this opinion paper, we highlight how ecology can yield insight into the effects of domestication on plant traits, on crop feedback over ecological processes, and on how species interactions develop in croplands.

Approaches to studying crop domestication and the domestication syndrome

Domestication (see Glossary) of plants progresses through evolutionary divergences, whereby one or several populations of founder gene pools gradually acquire variable degrees of geographical or genetic isolation from their wild relatives [1]. After divergence, plant reproduction and geographical spread of crops becomes increasingly dependent on humans. Under cultivation, selective forces differ strongly from those prevailing in the wild and include both strong directional selection by humans and natural selection caused by cultivation conditions (i.e., availability and nature of resources, and intensity and frequency of disturbances) [1]. In this opinion paper, we discuss the idea that a stronger focus on natural selection and constraints, guided by ecology, would greatly improve our understanding of domestication.

Archeological and genetic research has provided formidable insights into how domestication has progressed for major crop plants (see, for recent syntheses, [2,3]). This body of research has shown that prominent traits have a tendency to converge as a 'domestication syndrome' in major cereals and several pulses [4]. Those traits include increases in the size of harvestable organs, loss of seed dispersal mechanisms, promotion of erect growth habits, or loss of photoperiod sensitivity [2]. Domestication traits tend to be influenced by a small number of regulatory genes, which facilitate rapid evolution [2,5].

Although genetics and archeology have and will continue to advance our understanding of crop evolution, here we contend that complementary and novel insights can be accomplished by studying domestication from an

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Glossary

Constraints on crop evolution: biophysical, physiological, developmental, or genetic limitation that, given values for trait X, hinders the expression of the potential range of variation of trait Y. Constraints can limit crop phenotypic expression to a variable degree, depending on the nature and tightness of the connections. Directed artificial selection on trait X might imply indirect selection on variation in trait(s) Y(s).

Directed artificial selection: intentional breeding for traits, or combinations of traits, that increases the benefit that humans obtain from crop plants. Synonymous terms include 'conscious selection' and 'deliberate selection'.

Domestication: evolutionary interaction where a producer species gains new dispersal mechanisms while its performance is controlled for the benefit (commonly nutritional) of a consumer species. Ants, beetles, humans, and bacteria have evolved that relationship with domesticates as diverse as basidiomycetes, seed plants, and bacteriophages.

Domestication syndrome: the set of phenotypic traits hypothesized to reflect convergent evolution of crops to artificial selection by humans or to natural selection under cultivation. In a stricter sense, only those traits differing between progenitors and the very earliest domesticates descending from a given center of origin are true signatures of domestication.

Evolution under cultivation: changes in allelic frequencies of a focal crop plant after its domestication. It is driven by a diverse range of natural and directed selective pressures.

Functional trait: any morphological, physiological, or phenological character that impacts fitness indirectly via its effects on growth, reproduction, and survival.

Gene pool of a crop: the alleles contained within the boundaries of the taxonomic circumscription of a crop, including those of its closest wild relatives.

Natural selection under cultivation: forces promoting differences in survival and reproduction between individuals of cultivated plant populations. These comprise various selective factors, including selective pressures that differ between growing under cultivation and growing in the wild. Terms such as operational selection, unconscious selection, or automatic selection have been used to partially or wholly account for these factors.

Phenotypic space: a description of the phenotype, conceptualized by analogy with the niche as an *n*-dimensional space defined by *n* independent phenotypic traits.

Plant domestication: the evolutionary process whereby a wild seed plant acquires phenotypic features that make its survival and reproduction dependent on humans. This process occurs in the early phases of cultivation.

Wild progenitor (or wild ancestor): the closest wild relative of an existent crop. For many crop species, domestication was a complex evolutionary process where the assignment of a unique ancestral wild gene pool is problematic.

ecological perspective. In this opinion paper, we illustrate how progress can be achieved by discussing the consequences of domestication in light of ecological theory at three biological levels: individual traits, integrated phenotype, and beyond the plant phenotype. This approach can identify new plant traits that are signatures of domestication, help reveal how and to what extent ecological processes are altered by domesticated phenotypes, assist plant breeders in developing multipurpose crops, and help identify wild species with specific functional profiles that are of use in agriculture.

Viewing natural selection under cultivation through an ecological lens

The action of directed artificial selection exerted by humans is diverse and is driven by cultural idiosyncrasies, crop peculiarities, or geographical context [6], all of which might promote diversity in domestication syndromes. Some major crop species, mainly Poaceae, conform to the classical domestication syndrome. However, recent work has revealed that the concept of a common convergent domestication syndrome weakens when tested across a large and diverse set of >200 crops [6]. Classical domestication traits, such as variations in ploidy level or loss of shattering, are rarer within this diverse set of species. Indeed, the average number of typical domestication traits that show shifts during crop evolution is only 2.8 for most species [6]. In light of this result, the classical domestication syndrome might be reformulated such that diverse domestication syndromes can be identified and assigned to subsets of crops on the basis of criteria such as taxonomy, geography, and agricultural purposes.

All crop species experience both directed artificial selection and strong natural selection caused by cultivation conditions (Figure 1). Humans have modulated almost every ecological process occurring in habitats where populations of early domesticates thrived. These changes included supplying nutrients and water, protecting crops from herbivory and weed competition, and regularly harvesting biomass. Such human interference has affected ecological processes such as soil fertility [7], the mode, frequency, and intensity of disturbances [8,9], and the presence, abundance, and dynamics of organisms other than crops [10,11]. Moreover, crop evolution is also driven by indirect selection of traits correlated with either human targeted features or with environmental adaptations, mediated by the ecophysiological and biophysical laws that drive allometric constraints and phenotypic integration. It can be implied from these trait correlations and constraints that phenotypic changes caused by selection will impact the expression of other traits. In Figure 1, we provide a simplified diagram of the drivers of crop evolution with some common synonymous terms that are frequently cited in the literature.

Given the breadth of selective forces and drivers other than directed artificial selection, the traits that differ between domesticated and wild relatives are probably more diverse than those comprising the classical domestication syndrome. In Box 1, we illustrate how the application of ecological theory, at three different levels, should help understand how natural selection under cultivation and indirect selection has molded crop phenotypes, as well as the impact of such evolutionary change on ecosystems. In the following section, we discuss the most relevant topics included in Box 1 in more detail.

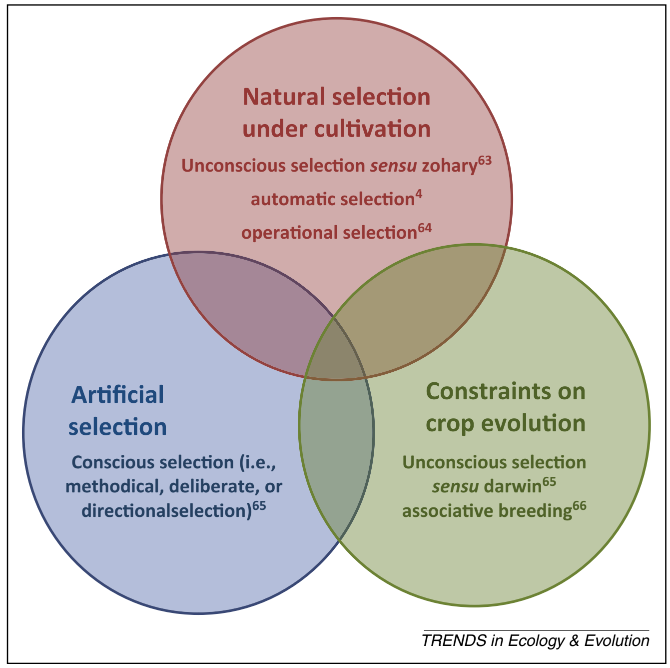

Figure 1. Schematic representation of three drivers of crop evolution, with synonymous terminology. Overlapping areas allow for interactions among drivers. For example, the evolution of seed size, a key trait in domestication research, can be affected by both deliberate and natural selection, and by constraints between size and number of offspring. The relative importance of each driver to explain patterns of seed size evolution under domestication remains unknown. References [4,63–66] are in superscript.

Trait-based ecology

Inspired by comparative biology and early research on ecological strategies, trait-based ecology attempts to characterize the ecological responses and effects of plants on the basis of their functional traits [12,13]. One of the most pervasive tenets in trait-based ecology is that nutrient-poor habitats promote selection for traits allowing efficient resource conservation, while nutrient-rich environments select for species with acquisitive trait profiles [14,15]. For example, in high nutrient environments, plant species tend to bear soft and short-lived leaves, with high nitrogen content, and roots with low specific dry mass investment per unit of root volume [16,17]. Those traits make plants fast growing. Cultivation generally leads to higher and more predictable nutrient and water supply rates [7,18,19]. Thus, it is reasonable to hypothesize that a shift from resource-conservation towards resource-acquisition trait profiles has occurred in parallel with domestication, and that species with resource-acquisition profiles would be preadapted for cultivation. In this regard, some recent studies have tested hypotheses on changes in functional profiles with crop evolution. For example, progenitors of several cereal crops allocate more biomass to leaves and height growth than other wild grasses that were used by hunter-gatherers, but never domesticated [20]. Additionally, humans selected cover crop species from the acquisitive, high growth end of the resource-use spectrum [21]. This