

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

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.

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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

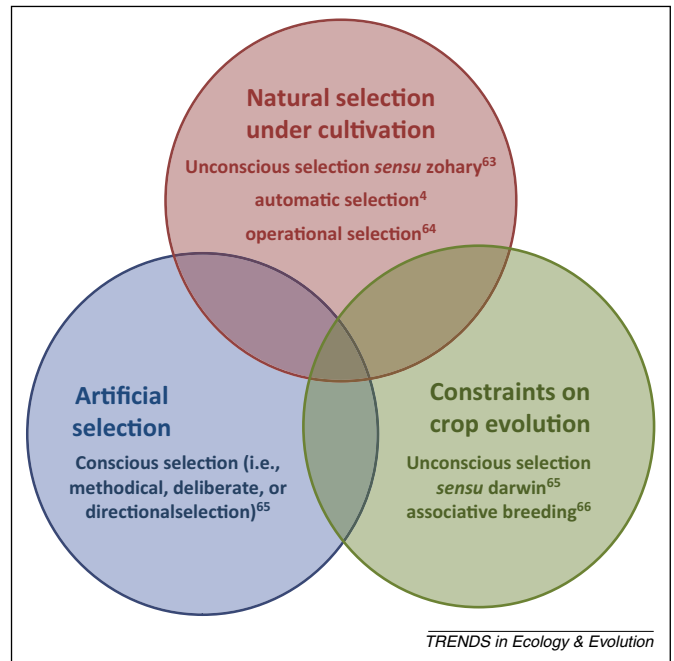


Figure 1. Schematic representation of three drivers of crop evolution, with synonymous terminology. Overlapping areas allow for interactions among drivers. For example, the evolution of seed size, a key trait in domestication research, can be affected by both deliberate and natural selection, and by 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.

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.

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

Box 1. Putative effects of domestication at three biological levels

Studying domestication through an ecological lens leads to new concepts on how traits should change during crop evolution and on the effects that such changes exert over ecosystems and co-occurring biotas. Ecological theory provides diverse frameworks to develop concepts and derive testable hypotheses in this regard. Tools of modern ecology offer multiple complementary techniques to test those hypotheses, using observational, experimental, statistical, and modeling approaches. In [Figure 1](#), we enumerate likely changes in crop phenotypes in response to natural selection under cultivation. A few of

these shifts have been investigated recently but most remain understudied. Subfields of ecology, such as dispersal ecology or ecological strategy theories, provide hypotheses on the directionality of predicted changes. Approaches such as the comparative method or phenotypic space analyses can test these predictions. Also, we illustrate several ecological processes whose components or rates might have been impacted by the emergence of new crop phenotypes. Similarly, community or ecosystems ecology can contribute predictions and tools to evaluate the ecological impact of domesticated phenotypes.

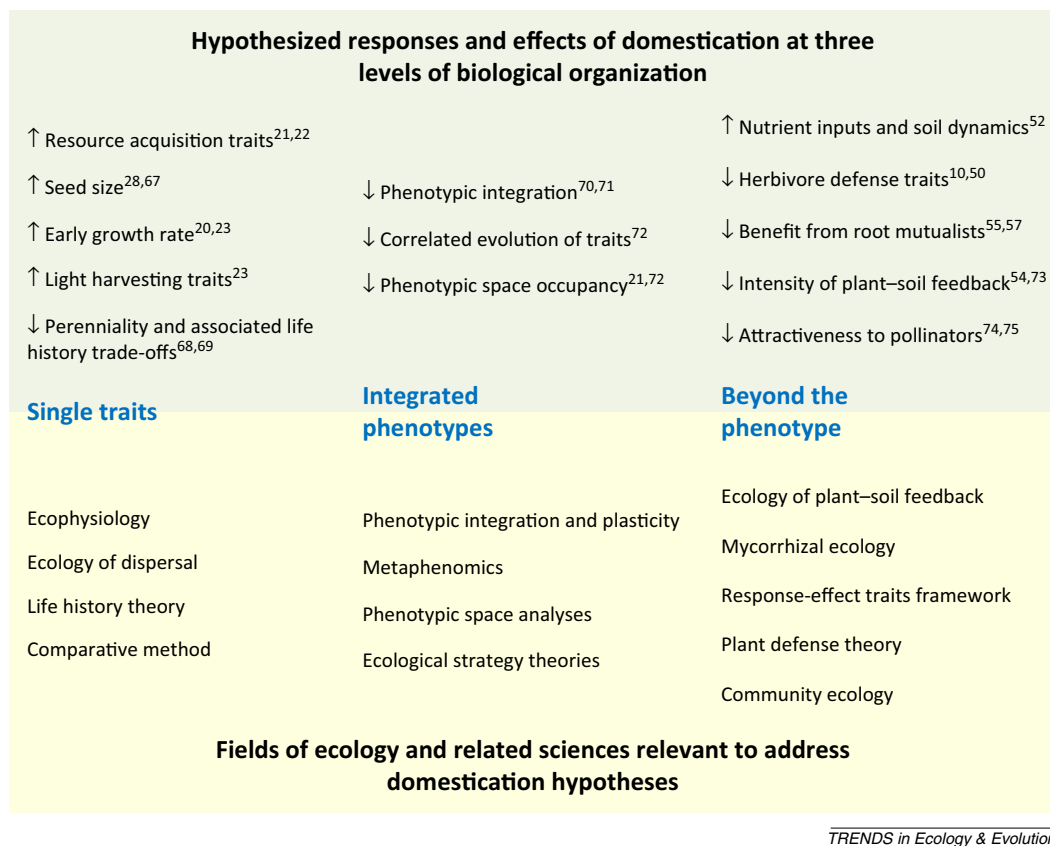


Figure 1. Functionally relevant traits and ecological processes that should be affected by domestication, but have received limited attention in the domestication literature. Directionality of arrows indicates hypothesized effect of domestication, on the basis of ecological theory and/or recent empirical research. References [10,20–23,28,50,52,54,55,57,67–75], for accrediting directionality, are in superscript.

observation is consistent with the fact that most herbaceous crops have experienced an increase in stomatal conductance in the upper leaf side during domestication, indicating a shift towards phenotypes that lose more water to the atmosphere [22]. Also, several traits contributing to competitive ability for light changed during crop evolution, including increased seedling growth rates, maximum canopy heights, and the size of leaf laminae [23], most likely as a result of changes in allocation patterns. However, domestication has not consistently promoted faster photosynthetic rates or higher specific leaf areas [23,24]. This is puzzling given that physiological and morphological traits tend to be more responsive to environmental factors than allocation traits [25]. Overall, we need more extensive comparative work to assess the generality of whether resource use trait strategies have changed during crop domestication in accordance with the expectations of trait-based ecology. Moreover, we need further information

on how environmental conditions in croplands have changed over time, particularly for the earlier stages of domestication [18,19].

Another attribute of prime relevance to trait-based ecology is seed size. Seed size is evolutionarily labile and reacts to numerous biotic and abiotic factors [26,27]. Interestingly, seed size is also a crucial domestication trait, especially in grains and pulses. Although domesticated crops generally have larger seed size than their wild progenitors [4,23,28], the selective forces accounting for that increase remain unclear. A recent comparative study failed to support a natural selection mechanism, that is, deeper seed burial in agricultural habitats selecting for larger seeds, as a general force triggering the increase in seed size during the domestication of legumes [28]. Alternative natural selection and constraint based hypotheses remain to be tested (e.g., trade-offs between seed size and number, as affected by direct selection on yield). A greater

understanding of the causes of the evolution of this trait requires more expansive approaches that can jointly test the importance of diverse drivers. Rapid evolution experiments can be devised that will manipulate the relative strengths of natural (e.g., head start in growth) versus directed (e.g., yield or yield stability) selection on changes in seed size. Short-lived model species, like *Arabidopsis thaliana*, are a promising avenue for this approach [29]. A complementary approach would be to statistically disentangle the relative importance of different selection forces using structural equation modeling, as well as selection gradients and differentials, in the context of phenotypic selection analyses [30,31].

Constraints and the integrated plant phenotype

Many of the pursuits of breeders have been hindered as a result of ubiquitous trade-offs between functionally linked traits (see multiple examples in [7]). This occurs because desired changes in some traits can lead to detrimental changes in other traits. Studying trade-offs, trait syndromes, and phenotypic integration and plasticity will therefore result in improved understanding of how crops have evolved and how breeding efforts can be redirected in the near future. In this regard, the notion of a domestication syndrome is conceptually similar to other multiple trait syndromes more familiar to ecologists, such as plant resource-use traits, defense, and pollination syndromes [15,32,33]. Trait syndromes entail coordinated evolution and trade-offs among the individual traits that contribute to the syndrome. However, the integrative side of the syndrome concept is rarely considered in research on domestication syndrome. This is true despite well-grounded research showing strong correlations among organ size (e.g., fruit size), branching intensity, and other domestication syndrome traits [27,34]. Research on allometry, anatomy, or plant hydraulics [35,36] should be implemented to identify and understand constraints in trait evolution during domestication [37]. Other perspectives include trait coordination within the phenotypic space [38,39], quantification of the intensities of phenotypic integration and plasticity [40–42], or modeling trait interactions through path analyses [31]. For example, integrative approaches have revealed that functional traits, such as seed size and early growth, tend to show coordinated evolution in the wild [23]. However, the degree of coordinated evolution is lower when selection occurs under cultivation [23]. This result suggests that indirect selection of correlated traits might work differently when evolution progresses under cultivation. However, given the relevance of such an assertion to breeding strategies, further work testing the generality of that finding is needed before arriving at transferable conclusions.

Correlated evolution has been studied with a particularly strong emphasis on leaf functional traits. Strong constraints govern the pattern of covariation in leaf traits linked to the resource-use strategy of plants [43,44]. In **Box 2**, we place crop species, and their wild progenitors, within the contextual frame of that covariation pattern. Formal analyses of trait hypervolume occupancy on such covariation planes [39] should help quantify divergences in functional profiles, as affected by constraints and by

evolution under cultivation. In **Box 2**, we illustrate this concept with two features of the leaf phenotype. However, similar explorations could look at other functions of the plant body or, in a more integrated manner, to proxies of the integrated plant phenotype in single joint multivariate analyses [45,46]. Most interestingly, placing crop species within the context of phenotypic variation observed among wild plants could help to pinpoint candidate species for future domestication using quantitative functional criteria. Other extensions of the approach include phenotyping numerous crop gene pools and plotting them against relevant sections of global botanical diversity. This can help investigate the extent of diversity in resource-acquisition strategies within gene pools, and assist breeding towards focalized regions with selected functional profiles.

Beyond the crop phenotype

Shifts in individual traits or phenotypes not only impact plant performance but also interactions with other species in the community and feedback on the functioning of ecological processes. It is, however, scarcely known how those effects have evolved during domestication [10].

Approximately 5% of annual terrestrial primary production ends up in the guts of herbivores, who consume plant organs at diverse rates [47]. It is frequently advocated that crops have evolved reduced defenses against enemies ([10], but see [8]). This is puzzling because rates of herbivory are thought to be higher in croplands than in the wild [48]. Artificial selection and constraints might then be more important than natural selection under cultivation (**Figure 1**) in driving the evolution of crop defense against enemies. First, directed artificial selection frequently focuses on overcoming bitterness or toxicity, as well as increasing nutritional quality [8]. Improving palatability and nutrient content for humans can imply doing the same also for herbivores. Second, investment in defense tends to be lower in high-resource habitats, and based on inducible defenses that are only synthesized in the event of herbivore attack [16]. Since agricultural lands are high-resource environments, they might therefore select for low constitutive defense phenotypes. And finally, plant defense theory predicts that constraints between fast aerial growth and investment in defense partly account for variance in resistance to herbivores [49–51]. In accordance, the loss of secondary chemistry during domestication has been observed for several crops [6,52]. However, when a large-scale comparative study was undertaken and phylogenetically diverse sets of crops were considered, support for the hypothesis that domestication reduces defense was weak at best [8]. Across 29 independent domestication events, Turcotte *et al.* [8] reported that crops did not have lower constitutive chemical and morphological defenses. In addition, crop domestication only partly increased the performance of a generalist leaf-chewer and did not increase fitness of a generalist phloem-feeder [8]. With current data at hand, we have concluded that, for this particular interaction, studies using expectations from ecological theory fail to contribute additional general characteristics to the domestication syndrome. The use of a comparative approach here served to challenge the commonly-held view

Box 2. Phenotypic space analyses of domestication

Worldwide botanical diversity in leaf functional traits such as nitrogen content or specific leaf area can be arranged along a remarkably tight principal axis of variation [43]. In that axis, acquisitive, fast-growing species tend to cluster at one end, opposite to slow-growing species, while most taxa spread in-between (gray dots in Figure 1A–C). When we embedded data from 36 herbaceous annual crop species into that background, we found that crops tend to overlap with species from the high growth end of the spectrum (Figure 1A). Did humans gain the productive advantage of annual crops by taking into cultivation wild species that were already at this end of the spectrum? Or, instead, have annual crop genotypes moved towards that end of the spectrum as a result of evolution under cultivation, via domestication, selection, and breeding? Figure 1B shows that wild progenitors of the set of crops plotted in Figure 1A were already high-growth species, suggesting that the choices of early farmers exerted a large impact on the functional

profile of current annual crops [20,23,76]. The fact that wild progenitors are fast species is perhaps not surprising, even if this demonstration of the phenomenon is new. A more interesting question would be whether the wild progenitors selected as crops differ from wild relatives of similar growth form or from sympatric species from the same regional species pool. In Figure 1C we plot, in the same traits space, Fabaceae and Poaceae progenitors of panel (B) together with a set of other herbaceous wild species of each family. Progenitors of Fabaceae and C4 Poaceae crops lie within the phenotypic boundaries of their corresponding non-domesticated wild relatives. However, C3 Poaceae progenitors have remarkably higher leaf nitrogen content compared with other C3 grasses (see also [20] for other traits). More nitrogen in leaves, for a comparable investment in dry mass per unit area (i.e., similar range of specific leaf area in Figure 1C), would probably drive greater synthesis of Rubisco and thus higher carbon profit [15].

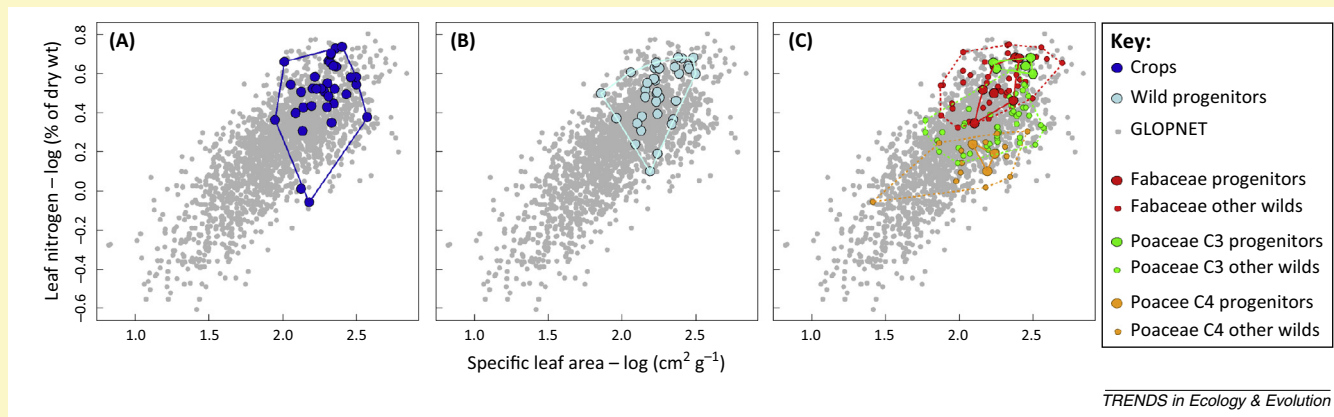


Figure 1. Diverse crop gene pools in the context of botanical diversity of two key leaf traits, specific leaf area and leaf nitrogen content. (A) Herbaceous crops (36 species, blue dots) versus a global dataset of 2157 wild species (gray dots in the background). (B) Recognized wild progenitors of the 36 herbaceous crops depicted in (A) (red dots) versus global wild species (gray dots). (C) Wild progenitors of three selected groups of crop species (large intensely colored) versus cofamilial wild species who were not domesticated (small colored dots), with global wild species in gray background. Convex hulls around each subgroup delineate phenotypic space occupancy. Data on crop and wild progenitors are from [23] and R. Milla (unpublished). Data on other wild species are from the GLOPNET database [43].

that trade-offs should cause plants to reduce resistance to herbivores during domestication. It is possible that changes in resource-acquisition or resource-use efficiency modulated the strength of expected trade-offs.

Domestication can also alter the contemporary evolutionary dynamics of interacting species. For example, Turcotte *et al.* [53], using experimental evolution on 17 independent domestication events, found that aphid populations evolved more slowly on crops and maintained higher genotypic richness. This finding was partly driven by weaker natural selection and by reduced genetic drift on crops compared with wild relatives [53]. In addition, domestication and cultivation conditions can impact trophic interactions among plants, herbivores, and their natural enemies in complex and unexpected ways (reviewed in [10]). Thus, a full understanding of the biotic impact of domestication will require a combination of expertise from community ecology, trait-based ecology, and evolutionary ecology.

The impact of domesticated phenotypes on interactions expands beyond herbivores. A plethora of plant–microbe interactions are potentially influenced by domestication [54]. These include interactions with root mutualists such as rhizobia or arbuscular mycorrhiza. Several case studies have addressed this issue, under the hypothesis that evolution under domestication should

have reduced the selective pressure for maintaining carbon-expensive mutualisms. The evidence, however, is mixed [55,56]. A meta-analysis using time of release of agricultural varieties as a proxy for timespan of evolution under domestication also showed mixed results [57]. Other relevant interactions with microbes include relationships with growth-promoting microbiota or plant–soil biota feedback mechanisms [58]. There are reasons to expect that natural selection under cultivation affected these plant–microbe interactions in similar ways for different crops and, consequently, analyses might reveal additional components to an extended domestication syndrome. However, there is a lack of systematic screening. Clearly, approaches where multiple independent domestications are investigated under common conditions are needed.

Shifts in resource-use strategy, interaction with herbivores, or plant–microbe interactions affect key ecosystem processes such as litter dynamics, cycling of mineral nutrients, and primary productivity [59,60]. Soil fertility and yield are services of major relevance to agroecosystems, and any impact of domestication can thus have far-reaching consequences. For example, García-Palacios *et al.* [52] have recently documented that, for most of a set of 24 crops, microbes digest domesticated litter faster than litter from their corresponding wild progenitors. As a consequence,

Box 3. Outstanding questions

- Is the domestication syndrome a tenable concept, applicable to most domestication processes? If not, are there other plant traits that might be signatures of domestication and that should be thus investigated?
- How have the environmental conditions that plants have experienced changed during domestication histories?
- Plants exert a strong impact over ecosystem processes and the dynamics of co-occurring biotas. Provided that plant phenotypes have changed during crop evolution, are those impacts of different nature and magnitude now, as compared with those of their wild progenitors?
- Several factors drive the evolution of traits under domestication, including artificial selection, natural selection, and constraints on trait variance. Can we develop experiments to investigate the relative importance of each of them?
- Can we devise methods to pinpoint wild plants that make good candidates for future domestication on the basis of their functional profiles?

nitrate and low-weight organic molecules are returned faster to soils where domesticates thrive [61]. To attribute increased litter decomposability to the effects of directed artificial selection is difficult; instead, this finding seems to be an outcome of natural selection under the cultivation environment. It is consistent with the litter dynamics theory [62], which proposes that genotypes that have evolved under resource-abundant environments (i.e., croplands) should shed litter that is more easily accessible to microbial assemblages than those from resource-scarce habitats (i.e., those of wild progenitors). This is an example of a domestication-driven shift in plant–microbe interactions with important ecosystem level effects, opening up breeding options for crops that promote either fast-open or slow-closed nutrient cycling patterns.

Concluding remarks

Our understanding of domestication is based on highly successful genetic and archeological approaches that will continue to provide significant contributions to this field. Here, we have shown that supplementing this field through an ecological perspective provides a more nuanced understanding of the drivers and consequences of domestication. Some recent discoveries, such as increased competitive ability for light and augmented litter decomposability, are good examples of the benefits of this approach. Most importantly, ecology can take advantage of the global-scale availability of functional data and tools on wild plants to quantitatively identify and evaluate candidates for a new generation of domesticated crops (Box 3). Science-oriented selection and domestication of wild species has been seldom pursued [6], but plant comparative ecology is well placed to lead this search. This could provide invaluable revenue for decades of past and future investment in ecological research.

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