REVIEW

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Phenotypic evolution of agricultural crops

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Abstract

1. Food crops are a vital source of nutrition for humans and domestic animals, with an estimated 4 billion metric tons of food produced per year. Crops do not only provide yields, but their traits also play a significant role in regulating the ecosystem processes of croplands, affecting local biotas, water balance, nutrient and carbon cycling. Domestication has led to significant changes in crop traits, making it important to understand the recent evolution of crops and how they differ from wild plants.

2. In this paper I review the evidence on how the ecological traits of herbaceous crops have evolved during and after domestication. Loss of seed dispersal mechanisms, increased plant and organ sizes, high rates of consumption by herbivores and fast decomposition of residues by decomposer microbes in the soil, all have evolved independently in domestication processes of different crops.

3. I also point out types of traits for which we have not identified common responses to domestication, be it because domestication processes of the different crop species are disparate, or because of lack of strong evidence. Those traits include resource acquisition rates of leaves and roots, and whole-plant growth rates. Then, I discuss research gaps in the field, including how to advance knowledge for those traits that show apparently idiosyncratic responses to domestication.

4. Finally, I emphasize the importance of understanding the interactions of crops with other organisms and the environment to breed crops that deliver yield and other services required from croplands. To this end, I introduce an ideotype for sustainable agriculture, which might inspire the breeding of multipurpose herbaceous crops, in the same way than the ideotypes of the Green Revolution inspired the breeding of elite varieties to foster yields under conventional agriculture.

KEYWORDS
crop ecology, crop evolution, crop traits, domestication, herbaceous crops, ideotype, sustainable agriculture

1 | INTRODUCTORY PARAGRAPH

Food crops are the subset of plants that support the nutritional needs of humans and our domestic animals. It is difficult to overstate the relevance of crops. Crops yield ca. 4 billion metric tons of food per year, either as reproductive output or as vegetative tissue (FAOSTAT, 2022). The phenotypic traits of crops mediate the ecosystem processes occurring in croplands, including impacts on the local biotas, water balance, and nutrient and carbon cycling (Martin & Isaac, 2015). Crop traits have changed substantially during and after crops´ domestication. Thus, understanding the ecological performance of crops implies investigating their recent evolution and how crops differ from wild plants. In this contribution I will synthesize commonalities and disparities in the reactions of plants to a history of cultivation and agricultural use. I will focus on herbaceous crops because of their agricultural importance and the fact that most of the current knowledge on the effects of domestication on ecological performance is available for herbaceous crops. I make the point that understanding the ecological performance of agricultural plants—crops´ interactions with other organisms and with the abiotic environment—is key to breed crops that not only deliver yields, but also other ecosystem services demanded from croplands.

2 | CROPLANDS AND CROP PHENOTYPES

Stands of crops take over 10%–15 % of the land surface and are unevenly distributed across most ice-free areas of the globe (Kopittke et al., 2022). Thus, croplands are an important type of ecosystem, with a remarkable influence on pressing environmental concerns like climate change, biodiversity loss and environmental pollution (IPBES, 2019; Tilman et al., 2001). Agricultural management largely drives the productivity and functioning of croplands. But crop traits are key modulators of yield and other functions of agricultural fields. For example (1) carbon sequestration in croplands is higher if plants are deep rooted, produce more litter or deliver more rhizodeposits (Kell, 2011; Williams et al., 2022); (2) diversity of plant traits in agricultural fields tends to raise productivity, and this can happen under diverse management and input options (Li et al., 2020); (3) pollinator-dependent crops feed the communities of local pollinators, or otherwise impact on the performance of wild pollinators if colonies of domestic bees are supplied (Aizen et al., 2020; Mashilingi et al., 2022). Therefore, crop traits contribute to multiple dimensions of agriculture, including but not solely, to harvestable yields.

Crop traits are key to explain variation in harvestable yields and the adaptation of crops to changing environments (Condon, 2020; Wu et al., 2019). Yet, crop attributes are rarely used directly to face agricultural challenges. Agricultural problems are addressed through research and policies linked to management practices. FAO recommends reducing tillage and using organic fertilizers to mitigate climate change through soil carbon sequestration but does not state clearly the types of crops that might promote this function (FAO & ITPS, 2021). Even for optimizing yields, more attention is paid to

management than to crop traits (Rizzo et al., 2022). This is so despite evidence that plant traits are also an important driver of ecosystem functions and services (Bagousse-Pinguet et al., 2021; Happonen et al., 2022). A solid understanding of the ecological roles of crops could thus make a hitherto underexplored contribution to foster a more sustainable and productive agriculture (Brooker et al., 2021).

Like those of any other organism, crop phenotypes evolve. Crops have thrived in agricultural lands for the latest millennia of their evolutionary history. Evolution under cultivation should have selected for variants that meet the nutritional needs of humans, are amenable to agricultural production, and are adapted to the agricultural environments. Such selection pressures seem to be common, directional and strong enough to have resulted in convergent evolution of crop traits. Indeed, certain types of crops show reactions to evolution under cultivation that are common across species (Denham et al., 2020; Meyer & Purugganan, 2013). Other traits, and other types of crops, show inconsistent responses to domestication (Meyer et al., 2012). For yet other traits, particularly for traits linked to the ecological relationships of crops like plant–plant interactions and the recruitment of soil microbes, or for phenotypic plasticity, we still know little on how they have reacted to domestication (Milla et al., 2015).

3 | CROPS AND THEIR WILD PROGENITORS DIFFER IN SEED DISPERSAL MECHANISMS, PLANT SIZE, SUSCEPTIBILITY TO HERBIVORES AND A FEW OTHER CRITICAL TRAITS

3.1 | Nonshattering and classical domestication traits

Major crops have evolved several commonalities under cultivation, which seem key to their adoption as crops. Classical domestication traits include upright plants, large seeds, increased biomass allocation to the harvest organs, and stands with high phenological synchrony (Meyer & Purugganan, 2013). Critically, fully domesticated seed crops have fruits that either do not disarticulate, or remain closed at maturity (Lin et al., 2012), which allowed early farmers to harvest stands before most of the seed yield fell onto the ground (Purugganan & Fuller, 2009). Nonshattering became dominant in the agricultural stands of cereals, even though it is maladaptive in the wild. In fact, nonshattering fruits is a diagnostic trait that has been used to distinguish wild from domesticated plant remains (Fuller & Allaby, 2009). This is because domesticates, by definition, are populations which reproduction is under the control of the domesticator to a large degree (Purugganan, 2022). Therefore, loss of spontaneous seed dispersal is indeed the trait that formally qualifies a seed crop to be fully domesticated. The evolution of nonshattering under domestication is a classic example of rapid evolution. However, current evidence shows that classical domestication traits, including nonshattering, became dominant at a slower pace than formerly

thought, and through more complex modes of evolution (Allaby et al., 2022; Chacón-Sánchez, 2018).

3.2 | Plant size

We have less evidence concerning the evolution of traits indicating the ecological performance of crops—that is, traits linked to resource-use strategies of plants, to interactions between plants and with other organisms, and to effects of plants on ecosystem processes. This evidence comes from comparative phenotyping of crop landraces (as the best surrogate of early domesticates) versus current-day representatives of their wild progenitors. A few ecological traits seem to react consistently to evolution under cultivation. Selection in cultivated lands promoted large plants, which have large organs and yield large seeds (Jones et al., 2021; Milla et al., 2014). This pattern has consequences relevant to the performance of crop stands. Large plants tend to overinvest in support tissue at the expense of productive organs (Poorter et al., 2012). Overinvestment in support might have evolved in response to the intensified levels of intraspecific competition in agricultural stands. Competitive phenotypes maximize the hoarding of resources by individual plants, but penalize reproductive allocation at the stand level, and increase the risk of lodging (Anten & Vermeulen, 2016). During the Green Revolution, breeding of semidwarf varieties helped to overcome that inconvenient legacy of domestication for a few major seed crops. This has resulted in decreased phenotypic plasticity to varying stand density, and therefore increased tolerance to plant crowding and increased yield at high planting density, but low capacity to suppress weeds when grown at low density (Tokatlidis & Koutroubas, 2004; Wu et al., 2021). However, for most crops there are no shortened varieties (Hedden, 2003).

3.3 | Relationships with herbivores, decomposers and mycorrhizal fungi

Another widespread legacy of domestication is the evolution of high susceptibilities to herbivore damage. Crops suffer on average 430% more herbivore damage than their wild progenitors, and herbivory takes ca. 30% of harvestable yields (Fernandez et al., 2021; Oerke, 2006). Despite its magnitude and relevance, the mechanisms of this evolutionary change remain elusive. This is because it is difficult to establish a link between crop defences and the levels of herbivore damage. The amounts of constitutive defence compounds—that is, secondary metabolites and defensive physical structures expressed even in the absence of herbivores (Walters, 2011)—evolved in diverse ways after domestication, depending on the crop species and organs considered, and independently of the evolution of their susceptibility to herbivores (Whitehead et al., 2016). For example, the fruits of domesticated blackberries have way less flavanol glycosides than its wild progenitor´s, while cultivars of raspberries have more of this constitutive defence chemical than its wild counterpart (Whitehead et al., 2016).

Pooling together generalist and specialist defences in comparative analyses might obscure relationships between amounts of specific defences and vulnerability to herbivores. In fact, domestication has tended to deplete defences against generalist herbivores, but not against specialists, which tend to remain part of crops´ accompanying biotas under cultivation (Gaillard et al., 2018). Furthermore, we do not know how the interactions among tolerance, resistance and response to herbivores have evolved in most crops (but see e.g. [Ferrero et al., 2020]). Fortunately, a recent meta-analysis investigated the evolution of a wide array of plant defence strategies in crops, including constitutive, induced and indirect defences (Fernandez et al., 2021). Induced defence is the plastic upregulation of anti-herbivore compounds after herbivore attack, and indirect defence is plant protection through communication with the natural enemies of herbivores (Karban, 2011; Kessler & Heil, 2011). Induced and indirect defences have decreased consistently after domestication in most crops (Fernandez et al., 2021). Unexpectedly, Fernandez et al. also found that crops tend to have less micro- and macro-nutrients, carbohydrates and proteins than their wild progenitors, and therefore have lower nutritional value for herbivores. Low nutritional quality might force herbivores to eat more to meet their stoichiometric demands, and thus elicit more damage (Fernandez et al., 2021). This interesting hypothesis needs experimental testing against alternative explanations of increased herbivore susceptibility in crops. Aside from herbivore susceptibility, a decrease in the nutritional value of crops is worrying also for human nourishment. For example, the concentration of carotenoids in the seeds of beans, peanuts and soybeans is ca. half of that of their wild progenitors (Fernández-Marín et al., 2014). This is because early selection and modern breeding of major crops have focused on securing calorie supply, at the expense of nutritional quality (Ku et al., 2020). Thus, breeding for nutritional quality is needed to counteract domestication effects and achieve more balanced human nutrition.

Crop tissues not only became more palatable for humans and herbivores after domestication, but their residues are also more accessible to decomposers (García-Palacios et al., 2013). Crop residues tend to be physically softer and have less lignin and carbon than those of their wild progenitors, which makes them more labile (García-Palacios et al., 2013). The physical and chemical traits of plant residues impact relevant soil functions, including carbon and nutrient cycling, and the composition and functioning of soil biotas (Dias et al., 2017). In fact, soil respiration increases, and nutrient cycling accelerates, when experimental soils are amended with crop residues, as compared to adding residues of crops´ wild progenitors (García-Palacios et al., 2013). Thus, it should perhaps be a priority to breed crops which residues are more diverse and recalcitrant to decomposers. This could help to mitigate the positive feedback between global warming and soil respiration, which is a major contributor to climate change (Bradford et al., 2016).

Another relevant ecological interaction is mycorrhiza, which are key to plant nutrition (Smith & Read, 2010). Agricultural soils tend to host

scant, poorly diverse, and ruderal communities of mycorrhizal fungi, which also are less mutualistic and more parasitic in soils with high nutrient levels (Chagnon et al., 2013; Edlinger et al., 2022; Johnson, 1993). Mycorrhizal interactions might thus be impaired after evolution in agricultural fields. Studies on the effects of domestication on mycorrhizal mutualisms have yielded mixed results (Bryla & Koide, 1990; Koide et al., 1988; Liu et al., 2020). However, a wide screening of 27 crops in a common garden found that domesticated varieties tend to benefit less from mycorrhiza than wild progenitors when grown under high soil nutrient availability (Martín-Robles et al., 2018). Therefore, under the specific conditions of high input agriculture, current crops are less proficient than their wild progenitors on using mycorrhiza, which feedbacks on increased crop dependency on fertilizers.

4 | OTHER RELEVANT TRAITS, LIKE RESOURCE UPTAKE AND GROWTH RATES, SHOW IDIOSYNCRATIC RESPONSES TO DOMESTICATION

4.1 | Photosynthesis in leaves

Links among traits, environment and plant performance are commonly idiosyncratic (Sobral, 2021). In this line, several prominent traits show idiosyncratic reactions to evolution under cultivation. This includes the fact that the leaves of some crops increased their maximum carbon exchange rates (CER) after domestication, while those of other crops remained similar or provide lower photosynthetic profit than their wild progenitors (Evans, 1993; Lei et al., 2022; Matesanz & Milla, 2018; Pujol et al., 2008).

Even if crops tend to have higher CER than other wild herbs (Huang et al., 2022; Nadal & Flexas, 2019), the direct wild progenitors of crops might probably be high CER species to start with (Chapin et al., 1989; Evans, 1993). And there are limitations to ever-increasing CER. In species with high CER, like crops and probably their wild progenitors, photosynthesis is colimited by mesophyll and stomatal conductance to gas exchange and by photochemistry (Gago et al., 2019). Escaping colimitation has proven difficult and could constrain the evolution of higher CER in crops (Flexas & Carriquí, 2020). This hypothesis is supported by the fact that crops have not increased CER after domestication, despite a more even distribution of stomata between both leaf sides (Milla et al., 2013), which should boost stomatal and mesophyll conductance, and therefore CER (Wall et al., 2022; Xiong & Flexas, 2020). The fact that CER has not increased consistently after domestication supports either a colimitation scenario (Gago et al., 2019), or saturation of effective stomatal conductance (Mott et al., 1982).

4.2 | Resource uptake by roots

Photosynthetic rates in leaves depend on water and nutrient provisioning from fine roots. Fine roots reacted inconsistently to

domestication when traits indicative of fast versus slow rates of resource acquisition—for example, root tissue density, specific root length or root mass fraction—were investigated across multiple crops (Barel, 2018; Martín-Robles et al., 2019). Only the diameter of fine roots tends to be slightly thicker in cultivated genotypes than in their wild progenitors, which seems to be an allometric consequence of the larger plant size of domesticates (Martín-Robles et al., 2019). Compared to other wild herbs, the fine roots of crops´ wild progenitors are noticeably acquisitive, which might preclude further evolution of the acquisitive strategy after domestication (Martín-Robles et al., 2019).

Other scales of root organization might be more reactive to domestication than the morphology and physiology of individual fine roots. The roots of maize and wheat, for instance, develop more seminal roots upon germination than their wild progenitors´ (Golan et al., 2018; Perkins & Lynch, 2021). These extra roots contribute one-third of the nitrogen and phosphorus acquired early in the season (Perkins & Lynch, 2021). However, cultivars of wheat lack seminal roots that stay remnant as primordia during early germination, which compromises recovery from water stress later in the season (Golan et al., 2018). This suggests a trade-off between stress tolerance and acquisitive traits in the evolution of cereal roots during domestication. Also, the roots of modern wheat are less branched, proliferate less in response to neighbours and grow more vertically, than the roots of ancient landraces, indicating further evolution of roots during the diversification of domesticated genotypes (Zhu, Weiner, & Li, 2019; Zhu, Weiner, Yu, et al., 2019). These findings remain to be investigated in other species of cereals and in other types of crops.

4.3 | Whole-plant growth rates

If the rates of resource acquisition by roots and leaves did not react in consistent ways to domestication, enhanced whole-plant growth rates might be also compromised. Fast-growing plants thrive in resource-rich environments, allocate little to defence against herbivores, their leaves and fine roots have fast rates of resource acquisition, low construction costs and high turnover rates (Reich, 2014). These traits boost productivity and therefore would seem adaptive in agricultural fields. However, plant relative growth rates (RGRs, gains in biomass per unit biomass per unit time) did not increase consistently after domestication, in line with reactions of leaves and fine roots (Evans, 1993; Gómez-Fernández et al., 2022). This seems puzzling at first instance, but several explanations might explain this pattern. First, domestication has generally promoted large seeds and large whole plants (Kluyver et al., 2017; Milla et al., 2014). Plants with large seeds display low RGRs (Rees et al., 2010), even when RGRs are measured at similar plant sizes (Gómez-Fernández & Milla, 2022). Second, RGRs of wild progenitors might be high enough to meet agricultural needs. Increasing RGRs further might not improve yields, and might trade-off with other relevant traits (e.g. seed and plant size, or investment in defence). Furthermore, the

reactions of the three components of RGR—physiology, allocation and morphology (Poorter, 1989)—to domestication are diverse, and might cancel each other when combined into a whole-plant level process like RGR (Gómez-Fernández et al., 2022). Clearly, more work is needed to disentangle among those competing explanations and unlock the contribution of growth rates to yield improvements. Finally, the plasticity of physiological and growth rates under different environments and managements might differ between crops and their wild progenitors, but this remains to be investigated in depth.

5 | RESEARCH GAPS AND THEIR RELEVANCE TO SUSTAINABLE AGRICULTURE

Despite the evidence reviewed above, we still do not know how evolution under cultivation influenced most aspects of the ecological performance of crops. Crops are plant populations whose ecological scenarios changed radically after transitioning to agricultural fields, including shifts in disturbance regimes and intensities, in resource supply and in co-occurring biotas (Denison, 2012). Most likely, this transition changed the ecological roles of crops more than what has been evidenced thus far. Below I will highlight areas of crop biology which impacts of domestication we mostly ignore but are key to move towards low input and environment-friendly agriculture.

5.1 | Crops and soil microbes

Microbiotas are key to every aspect of plant performance, and to the regulation of ecosystem functioning (Fitzpatrick et al., 2020). Thus far, microbiotas have concerned agriculturalists chiefly to keep harmful microbes at check. But managing microbial communities to assist in the agricultural practice can bring benefits much further, spurred by advances in environmental DNA sequencing and manufacturing of synthetic microbial consortia (Trivedi et al., 2021). To fully embrace this potential, we need to characterize the microbiotas in and around crops, their functional roles, and their eco-evolutionary relationships with crops and their wild progenitors.

Evolution during and after domestication might have changed plant–microbe recognition and filtering mechanisms (Kiers et al., 2007). For example, wild common beans modify bacterial communities in a different way than cultivated beans, recruiting in their rhizosphere more Bacteroidetes and Verrucomicrobia, but less Actinobacteria and Proteobacteria (Pérez-Jaramillo, 2017). But domestication had little impact on how different genotypes of sunflower filter soil fungi and bacteria (Leff et al., 2016). Interestingly, filtering abilities are heritable and might track domestication genealogies (Abdelfattah et al., 2022). Despite these and other contributions (see e.g. Martínez-Romero et al., 2020), we are still at the infancy of characterizing what changed between plants and their microbiotas after domestication. Similarly, even though we know that crop residues interact with soil microbiotas differently than the

residues of wild plants—for example, by increasing soil respiration (García-Palacios et al., 2013)—we ignore how these interactions impact on the composition and functioning of soil microbiotas in croplands. Finally, the diversity and potentialities of the microbiotas at the habitats of origin of crops´ wild progenitors remain unexplored (Raaijmakers & Kiers, 2022). Prospecting the composition and functioning of those microbiotas, which have coevolved with the genetic ancestry of crops, would provide priceless microbial resources, probably absent from agricultural soils today.

5.2 | Polycultures and crop traits

Polycultures and varietal mixtures benefit multiple facets of sustainability (Renard & Tilman, 2021). Importantly, polycultures increase yield stability and tend to yield more than the average of composing monocultures (Renard & Tilman, 2021). Spatial diversification is thus a sustainable strategy to increase crop yields (Li et al., 2020). But crop genotypes are adapted to perform in neighbourhoods of conspecifics, because monocultures provide the bulk of food supplies. In fact, domestication and a history of cultivation in monoculture can impair the ability of plants to perform in polyculture (Chacón-Labella et al., 2019; Stefan et al., 2022; Zuppinger-Dingley et al., 2014). Therefore, breeding crop varieties that are proficient in diversified crop stands is a priority. A first step in that endeavour is to identify and understand the traits that are relevant to the plant–plant interactions underlying biodiversity effects—that is, the effects that underlie the increase in yield brought by increasing levels of biodiversity (Engbersen et al., 2022; Litrico & Violle, 2015). Identification of the molecular basis of biodiversity effects, and application of gene editing technologies to diversify crops, can contribute to speed up this process (Garland & Curry, 2022; Wuest & Niklaus, 2018). At the field scale, we need to characterize trait–performance relationships in polyculture to overcome the constraints set by domestication and historical selection under monoculture. Finally, interactions with agronomic practices are important. For example, selecting for mixtures that maximize overyielding at high planting densities might be key. When plant stands are grown at increasing densities, productivity per unit land area increases up to a plateau, known as constant final yield (CFY; Silvertown & Charlesworth, 2001). Overcoming CFY through the breeding of varieties that increase growth at high densities was key to the success of the Green Revolution´s monocultures. Mixtures also show CFY (Cavalieri et al., 2022), and therefore improving traits for higher tolerance to density might bring enhanced performance of polycultures.

5.3 | Trade-offs among traits and functions

Thus far I have written on individual traits, or types of traits, as if variation in a trait was independent of variation in the rest of the phenotype. This is true to a limited extent. Plants are modular organisms, which confers some independence on trait variation among and

within modules. This is demonstrated by the multiple axes needed to ordinate variation in plant traits—for example, traits like plant size tend to vary orthogonally to mass-based rates of resource acquisition (Díaz et al., 2015; Kramer-Walter et al., 2016; Laughlin, 2014). However, plant hydraulics, source–sink dynamics, ontogeny and hormonal regulation pose limits to the free variation of individual traits. Phenotypic integration and trade-offs among traits and functions are thus widespread in plants (Messier et al., 2017).

In fact, strong trade-offs are a limitation to crop improvement. For example, limited gain of CER during domestication and further breeding, as described in section IV, might be explained by trade-offs with other traits at the whole-leaf and canopy levels. Domesticated cultivars tend to have larger leaves than their wild progenitors (Milla et al., 2014). Larger leaves require more support per unit of leaf area, which comes at the cost of less investment in the photosynthetic machinery (Milla & Reich, 2007; Niklas et al., 2007). Larger leaves also require stronger petioles and stems, which adds to increased allocation to support instead of productive tissue (Milla & Matesanz, 2017). Extended duration of leaf area (e.g. stay-green phenotypes) and upright leaf angles can also trade-off with increased CER, which may render variation in CER of limited agronomic value and unlikely to be targeted by artificial selection for yield (Evans, 1993).

Achieving trade-off-free improvements is key to adapt crops to current challenges (Denison, 2012; Weiner, 2019). Whether crop evolution has freed, or reinforced, trait trade-offs is largely unexplored. In a small set of six crops, it was found that the reactions of disparate traits to domestication occurred coordinately—indicating trade-offs and phenotypic integration—while recent improvement disrupted several of the trait–trait relationships—indicating relaxed trade-offs and less phenotypic integration (Milla et al., 2014). The maintenance of other trade-offs under domestication—for example, between reproductive output and defence (Whitehead & Poveda, 2019) or between growth and stress tolerance (Koziol et al., 2012)—has been reported in several case studies. However, provided its relevance, more research is needed in this realm.

5.4 | The ecological profiles of crop wild progenitors

Constraints and opportunities for crop adaptation might arise not only from a history of evolution under cultivation, but also from the nature and properties of the gene pool originating domesticated populations, that is, the traits of crop wild progenitors. We largely ignore what wild progenitors have in common, what their ecological profiles are and how their profiles compare to the wider botanical variation (but see, e.g. Cunniff et al., 2014). So much that different authors portray the wild progenitors of major crops as ruderal, competitor or even stress-tolerant types of plants (Abbo et al., 2010; Milla et al., 2015; Spengler & Mueller, 2019). Robust research on the ecological strategies of wild progenitors would benefit crop breeding and neo-domestication of wild plants. For instance,

annual herbs with ruderal profiles prioritize fast growth, small stature, early allocation to reproductive output, and precocious seed set, at the expense of competitive dominance or tolerance to biotic disturbance and abiotic stress (Hodgson et al., 2020). Therefore, obtaining leafy crops from ruderal wild plants that readily shift to reproductive growth might not be good strategy. Similarly, breeding a high-density grain crop out of a wild progenitor that is a strong competitor might be a bad idea, because much of its biomass gain will be invested in outcompeting neighbours (Anten & Vermeulen, 2016; Wille et al., 2017). Identifying the ecological strategies of crop wild progenitors might help to re-focus the capabilities of each crop and to ease breeding for specific yielding purposes. Additionally, setting crop wild progenitors in the phenotypic space of wider botanical diversity would help to target candidate wild species amenable to domesticate crops de novo.

5.5 | The genetic bases of an expanded domestication syndrome

The genetics of classical domestication traits are relatively well known. Early domestication entailed the evolution of key loss-of-function point mutations, which favoured nonshattering, loss of seed dormancy, low branching and other relevant traits (Gross & Olsen, 2010; Meyer & Purugganan, 2013). Later diversification and improvement stages brought changes in traits driven by protein-coding genes (Meyer & Purugganan, 2013). Another genetic pattern accompanying the evolution of crops is the prevalence of hybridization and genome duplication events. In particular, interspecific admixture implying allopolyploidization (Purugganan, 2019), or breeding of F1 hybrids (Kingsbury, 2009), were key to the ancient and recent development of crops respectively. Hybrids provide heterosis—vigorous growth, yield and resistance—and adaptive plasticity for geographic expansion (Purugganan, 2019). Indeed, polyploids were more likely to be domesticated than other wild plants (Salman-Minkov et al., 2016).

Even if we know the basics of the genetic changes accompanying some domestication traits, we ignore how the ecological traits covered in this review arose. For example, even if the genetic basis of variation in leaf litter decomposability has been linked to the genes controlling the composition of cell membranes (Kazakou et al., 2019), we ignore if the highly decomposable litters of crops evolved as side effects of artificial selection on pleiotropic genes, or through other genetic mechanisms. Similarly, there is hints on the genetic bases underlying biodiversity effects (Wuest & Niklaus, 2018; Wuest et al., 2022). But we are far from transferring that knowledge to understand the decrease in performance under polyculture of domesticated varieties (Chacón-Labella et al., 2019). Decomposability, plant–plant interactions, plant size or resistance to herbivores are quantitative traits and have a polygenic architecture. Disentangling how domestication impacted their genomic basis will be a major challenge. Recent findings on the fast evolution of weedy genomes, promoting quantitative variation in growth, and in

stress and disturbance tolerance, might guide this research (Kreiner et al., 2022).

5.6 | How to deal with idiosyncrasy

Finally, a topic that deserves research attention is the idiosyncrasy among crops in their reactions to domestication. Relevant crop traits have reacted to domestication in different ways, depending on the species and genotypes being investigated, and on the environmental context where plants are grown (see Section IV). Often, ecological and evolutionary patterns are overridden by context dependency (Bradley et al., 2020; Fukami, 2015; Schoenle et al., 2018; Sletvold, 2019). Context dependency can arise from poor experimental designs and disparate research approaches between studies, or from true variation in the response (Catford et al., 2022). Thus, a first step to understand context dependency in domestication is to qualify evidence as hard or soft, and then perform further research when idiosyncrasies stem from soft evidence or from evidence that is hardly generalizable. This research should provide results that are more generalizable across crops, that address confounding factors, variation in statistical inference or methodological approaches, and other causes of apparent context dependency identified in previous work (Catford et al., 2022). If evidence is hard, then context dependency might be mechanistic, and a deeper level of enquiry should explore the underlying sources of variation among crops or genotypes. For example, when investigated under common growth conditions, the effects of domestication on leaf nitrogen and phosphorus depend largely on the crop species considered (Delgado-Baquerizo et al., 2016). But part of that variation can be attributed to the biogeographic origins of crops, such that crops originating from high latitudes evolved leaves with more phosphorus, less carbon and lower N:P and C:P ratios than crops from low latitudes (Delgado-Baquerizo et al., 2016). Generally, research on the ecological effects of domestication should aim to increase explained variance by considering wider arrays of covariates and expanded genotype sampling, as far as logistics permit.

Another important source of true context dependency is phenotypic plasticity. Genotypes map into different phenotypes depending on the environment. Thus, the phenotypic patterns covered in this review must be considered in the conditions of the environments where trait data were collected. In this context, common gardens circumvent some of the limitations of comparative biology (de Villemereuil et al., 2016). But replicated common gardens, set up under contrasting environments, are rare in domestication research and would help to disentangle the genotypic basis of phenotypic patterns more accurately.

Phenotypic plasticity evolves (Pigliucci, 2005) and might have changed during the recent evolution of crops. For example, the roots of modern varieties of wheat over-proliferate little when encountering neighbouring roots, in contrast with the strong over-proliferation of early landraces and other wild plants, which indicates reduced plasticity in the roots of modern wheats (Zhu, Weiner, & Li, 2019).

Other studies have found limited differences between crops and their wild progenitors in trait plasticity to water and nutrient supply, or in growth form variation in different microenvironments (Matesanz & Milla, 2018; Ménard et al., 2013). However, for a vast majority of traits and species, we largely ignore if crops have wider or narrower reaction norms to environmental variation than their wild progenitors. Provided that domestication commonly entails genetic bottlenecks (Gross & Olsen, 2010), phenotypic plasticity might be a most relevant tool for crop adaptation to changing environments and to management practices like, for example, polyculturing (Yang et al., 2022). Furthermore, recent progress on the epigenetic regulation of plasticity (Bossdorf et al., 2010), and on transgenerational plasticity (Bell & Hellmann, 2019), is moving the field forward in lines that should be relevant to the performance of crops, and that should be investigated in the context of domestication research.

6 | HOW TO USE KNOWLEDGE ON CROPS´ REACTIONS TO DOMESTICATION TO FOSTER SUSTAINABILITY: AN IDEOTYPE FOR SUSTAINABLE AGRICULTURE

We are far from a complete picture on how the evolution of plants under cultivation has impacted the ecosystem services modulated by crops. However, we can speculate on the characteristics of crop phenotypes that would better suit the goals of sustainable agriculture (Figure 1). Such ideotypes are useful as targets for crop breeding. For example, during the Green Revolution the enforcement of agricultural intensification was accompanied by the breeding and adoption of new high-yielding varieties of grain crops (Khush, 1999). These varieties fitted Donald's ideotype, that is, they were small and stiff plants with erect leaves and high harvest indexes (increased ratios of reproductive to vegetative biomass), that maximize yields when grown at high planting density under high input agriculture (Donald, 1968a, 1968b). In this line, we can devise ideotypes of crop plants purposed to maximize multiple ecosystem services.

Traits composing an ideotype for sustainable agriculture might include the following. (1) Increased levels of indirect defence, and of organ-specific expression of direct defences (e.g. inducible instead of constitutive defence, and response against generalists instead of specialized pests; Chen, 2008; Gaillard et al., 2018). Such phenotypes could minimize pesticide use and could restore plant defence strategies that have weakened during domestication (Fernandez et al., 2021). (2) Phenotypes that maximize performance in diversified and dense stands (Litrico & Violle, 2015) and under heterogeneous environments (Rolhauser et al., 2022). Varietal and species mixtures can increase resource use efficiency and provide more stable harvests in space and time. (3) Root traits optimized for resource use efficiency and for harnessing benefits from interactions with soil biotas. For example, selection for specific profiles of rhizodeposition should help to filter soil microbiotas for the benefit of crop performance (Koprivova & Kopriva, 2022; Preece & Peñuelas, 2020). This is critical to the success of commercial SynComs (synthetic
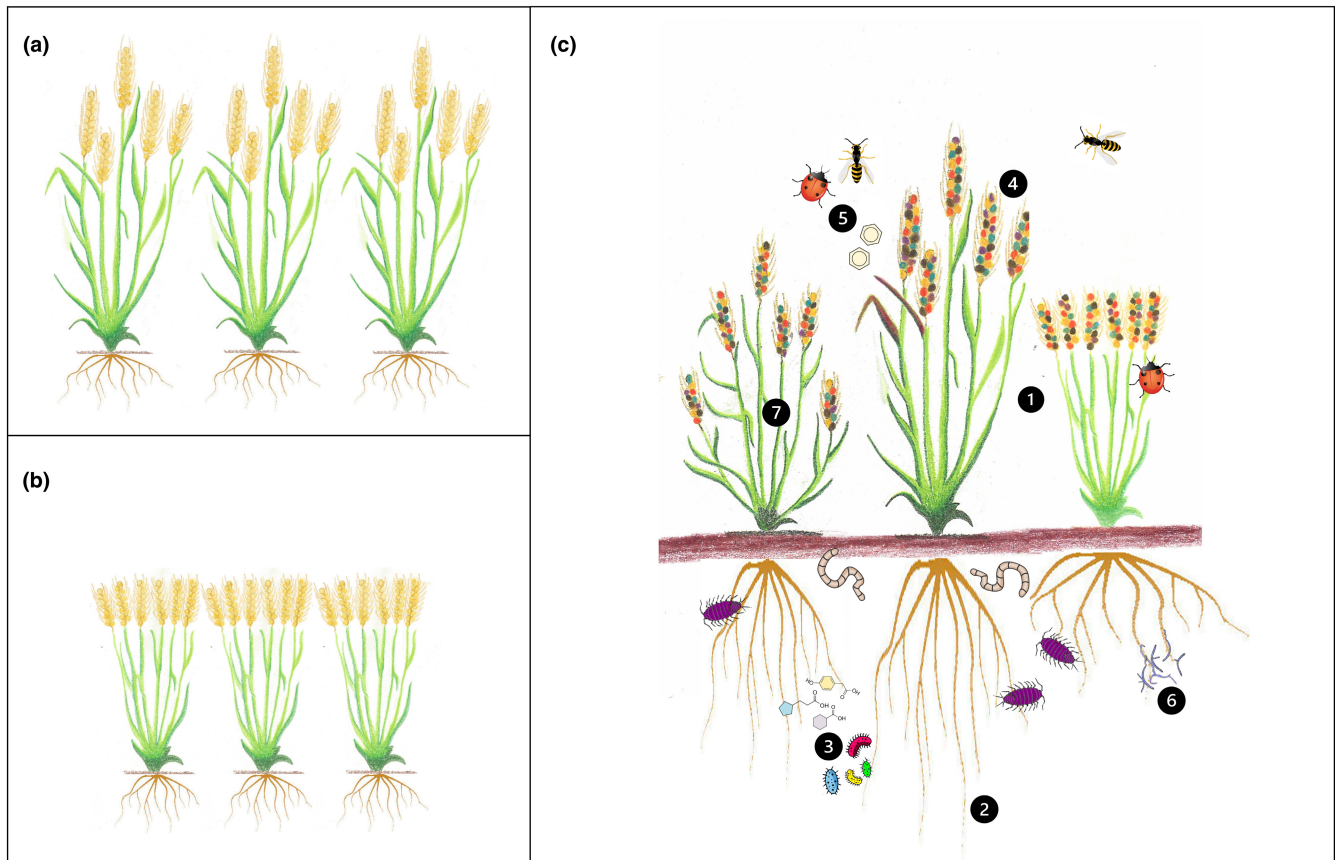
FIGURE 1　Ideotype for sustainable agriculture. (a) Stand of an early domesticate of an herbaceous seed crop, with large plants bearing large organs and seeds. (b) Ideotype for conventional agriculture, fit to perform at high planting density in high input monocultures. Monocultures use plants of short heights, high allocation to reproductive output and high dependence on irrigation, herbicides, pesticides and synthetic fertilizers. (c) Mixture of ideotypes for sustainable agriculture, portraying traits that promote yield, but also nutritional quality and other ecosystem services. (1) Diverse canopies (and roots) that promote complementarity in the use of light, water and nutrients, and suppress a wide range of weeds. (2) Diverse, but collectively deeper and more intensive, roots which promote efficient foraging for nutrients, microbes and water, less soil erosion and more carbon sequestration. (3) Diverse, intense and selective rhizodeposition, so that soil microbes are efficiently filtered to the rhizosphere to improve plant performance and plant protection. (4) Increased diversity and improvement in the nutritional quality of seeds. (5) Plant defence strategy focused on indirect defences, and on organ-specific expression of induced defences. (6) Increased dependency on mycorrhiza for nutrient provisioning and for minimizing runoff. (7) Inclusion of locally adapted landraces in varietal and species mixtures, and in the genetic background of elite varieties through breeding. Plant drawings modified from (Gómez-Fernández et al., 2022).

microbial communities), which usually fail to make it to the rhizosphere (Delgado-Baquerizo, 2022). Furthermore, diverse but extensive and deep root systems should optimize resource use in low input agriculture and contribute to increase organic matter in agricultural soils, fostering many facets of sustainability (Johnston et al., 2009; Kell, 2011). This might be particularly relevant in cover crops. Provided that Earth´s soils have lost ca. 14.000 km^3 of rooted volume due to the agricultural conversion of native habitats (Hauser et al., 2022), it is a priority to breed crop root traits that recover part of this carbon sink. (4) Other dimensions of crop phenotypes that should be targets of sustainability-oriented breeding include improved floral reward for pollinators in pollinator-dependent crops (Garibaldi et al., 2013), local adaptation of traits through backcrossing elite varieties with landraces (Meseka et al., 2015) and breeding for nutritional quality instead of plain calorie supply (Graham et al., 2007).

How to breed crops that promote agricultural sustainability and balance and deal with multiple trade-offs among participating traits seems daunting. But it is worth the effort. In recent decades, research and policy have focused on fostering sustainability through agricultural practices at the field and landscape levels (Gomiero et al., 2011). Sustainable agricultural practices need to be supplemented with crop phenotypes that deliver the diverse services we demand from croplands. A first step to inspire this endeavour is to understand how crops became what they are through the early selection of wild progenitors, domestication and further evolution under cultivation.

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