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Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops

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Trait-based ecology predicts that evolution in high-resource agricultural environments should select for suites of traits that enable fast resource acquisition and rapid canopy closure. However, crop breeding targets specific agronomic attributes rather than broad trait syndromes. Breeding for specific traits, together with evolution in high-resource environments, might lead to reduced phenotypic integration, according to predictions from the ecological literature. We provide the first comprehensive test of these hypotheses, based on a trait-screening programme of 30 herbaceous crops and their wild progenitors. During crop evolution plants became larger, which enabled them to compete more effectively for light, but they had poorly integrated phenotypes. In a subset of six herbaceous crop species investigated in greater depth, competitiveness for light increased during early plant domestication, whereas diminished phenotypic integration occurred later during crop improvement. Mass-specific leaf and root traits relevant to resource-use strategies (e.g. specific leaf area or tissue density of fine roots) changed during crop evolution, but in diverse and contrasting directions and magnitudes, depending on the crop species. Reductions in phenotypic integration and overinvestment in traits involved in competition for light may affect the chances of upgrading modern herbaceous crops to face current climatic and food security challenges.

1. Introduction

Plant domestication has had far-reaching evolutionary and ecological consequences for both plants and people [1,2]. On the plant side, conscious and unconscious human selection led to the evolution of new phenotypes. More palatable plant organs with fewer secondary compounds [3], larger and/or more numerous fruits or seeds [4], or modifications in vegetative aboveground morphology [5] are examples of allelic variants favourable to human purposes that were selected for in most domestication processes [5]. Other relevant traits also emerged during domestication, but in variable ways, depending on the crop species or functional group. For instance, most cereals lost spontaneous seed shattering, and many other herbaceous crops reduced seed dormancy mechanisms, while woody fruit crops increased allocation to pericarp tissues [6].

In a parallel literature, though largely independently, ecological science found that selective filters operating in the wild consistently caused plants from unproductive infertile ecosystems to differ from those that evolved in more productive sites in a number of plant traits functionally linked to the use of mineral, water and light resources [7,8]. Plant strategies are groups of species that share traits whose variation impacts fitness differently in ecosystems with contrasting availability of resources [9]. Plant strategies, thus considered as sets of functionally interlinked traits [9], are closely connected with the concept of phenotypic integration. Phenotypic integration is the phenotypic covariance structure of multiple characters that bear functional links [10]. The traits of organisms with high phenotypic integration respond in coordinated fashion to changes in the

environment, in contrast to poorly integrated organisms [11]. Plant strategies and phenotypic integration literatures provide specific predictions as to the direction of phenotypic evolution in habitats with contrasting levels of resource supply, which may correspond to the shift in environmental pressures that plants experienced when humans began to raise them in croplands.

Initial domestication and further crop improvement moved plant species from wild habitats, where resources were relatively scarce, to cultivated land, where water and nutrients were generally more predictably available [12,13]. Plant strategy theory would predict a convergence of evolutionary trajectories during domestication towards plant strategies that acquire water, nutrients and light rapidly to support fast growth at the expense of less efficient nutrient retention [7,8]. If this were the case, traits indicative of effective hoarding of light and carbon, and rapid below-ground resource acquisition and growth, would be more characteristic of current crops than of their wild progenitors. Additionally, ecologists have postulated that abiotically less stressful conditions should relax selection for tight coordination among functionally related traits, resulting in plants with less phenotypic integration [10,14]. That postulate, joined to the fact that selection and breeding have focused on a few beneficial traits, rather than on the complete phenotype, might have reduced phenotypic integration during crop evolution. The concept of phenotypic integration is broadly applied from the physiological to the ecological and evolutionary scales, and from coordination of narrowly related functions and structures to the integration of the complete individual [15]. For the purposes of this work, we consider phenotypic integration as the tendency of functionally linked traits of the whole phenotype to evolve in a coordinated fashion after an evolutionary divergence. The focal divergence here is the split of crop genotypes from their wild progenitors during plant domestication.

In this paper, we test (i) whether high-resource-use strategies have evolved during the transition from wild progenitors to domesticated forms of herbaceous crop species, and (ii) whether resource-use traits have evolved in a coordinated fashion during domestication and further crop improvement. We pose those questions to a uniquely large set of 30 diverse crop–progenitor comparisons (table 1; electronic supplementary material S1 and S2, and figures S1 and S2). We further assess, in a smaller subset of six herbaceous crop species, which traits and covariation patterns changed during the early evolution of landraces versus the more intensive later breeding and development of modern crop varieties.

2. Material and methods

(a) Study system

We studied the process of domestication in 30 herbaceous crop species important to human food supply (table 1). These include a diverse array of phylogenetically and functionally different crops with distinct domestication geographies and histories (electronic supplementary material, figures S1 and S2), the ample majority of them being annual species. In an extensive experiment, we compared two accessions for each of the 30 crops: a crop cultivar and a related wild species known to have made the greatest contribution to the gene pool of the crop (hereafter termed ‘progenitor’; electronic supplementary material, table S1). In a second intensive experiment, we compared nine accessions for six of these 30 crops. Three of these nine accessions

were geographically diverse provenances of the putative wild progenitor. Three others were landraces, representative of an initial stage of domestication. The final three were commercial varieties that have undergone modern breeding improvement programmes. The accessions of the intensive experiment were selected to include a broad range of geographical wild provenances (wild), of ethnographically and geographically diverse landraces (landrace) and of varietal diversity for modern crops (improved). The six crop species chosen for the intensive experiment, based on their taxonomic and functional diversity and agronomic relevance, were maize, barley, pea, pepper, sunflower and collard. See the electronic supplementary material, table S1 for accession identifiers, seed donors, domestication status and literature source for wild progenitor assignment of the extensive experiment, and electronic supplementary material, table S2 for the same information for the intensive experiment.

(b) Plant growth and trait measurements

We adopted a common garden approach to document phenotypes of all accessions involved in this project in identical environments. Ten to 20 plants of each accession in the project were grown and measured under two experimental regimes. The first regime was devised to obtain early growth, height and leaf trait data for our 30-species extensive dataset. The second was designed to provide root measurements and total plant dry mass for both datasets, and early growth, height and leaf trait data for the six-species intensive dataset. Plant measurements were carried out to obtain individual scores of each of the following nine traits (see Full materials and methods section in electronic supplementary material for trait selection criteria): seed size (mg), total plant dry mass (g), seedling absolute growth rate (cm d^{-1}), plant canopy height (cm), leaf size (cm^2), specific leaf area ($\text{cm}^2 \text{g}^{-1}$), leaf dry matter content (g g^{-1}), specific root length (m g^{-1}) and tissue density of fine roots (g cm^{-3}). A total of 1562–2618 (depending on traits) plant individuals were phenotyped. See Full materials and methods section in the electronic supplementary material for detailed protocols and procedures.

(c) Statistical analyses

Below we describe the several statistical procedures that we followed to test for the effects of domestication on individual and grouped trait scores, and to test for shifts in inter-trait relationships and phenotypic integration during the evolution of crops. Analytical details of each of the procedures, in-depth explanations for the rationale of the construction of structural equation models and motivation for the choice of Aster models to test for different levels of phenotypic integration are provided in the Full materials and methods section in the electronic supplementary material. Additional supporting analyses are also provided in the electronic supplementary material (items 4 and 5).

(i) Effects of domestication status and crop identity on traits and on groups of traits

Traits were considered separately for analyses, and also in groups of two or three, according to well-known strong physiological or developmental linkages among traits. Grouping of traits for further data analysis was performed through factor analyses. Four principal components analyses (PCAs) were run separately for each of the following four groups of log-scaled traits. First, seed size and total dry mass data were reduced to a first PCA axis intended to represent the organ and plant size variation among individuals (SIZE hereafter). Second, seedling absolute growth rate, plant canopy height and leaf size were reduced to a single PCA axis aimed to synthesize competitive ability for light capture (LIGHT COMP hereafter). Third, a PCA was run on leaf economic traits using specific leaf area and leaf dry matter content (LEAF ECON

Table 1. Common and botanical name of each of the 30 crop species of this project, together with that of its assigned wild progenitor and family affiliation. Species in bold were those investigated in greater depth in the intensive experiment. See the electronic supplementary material, table S1 for more detailed information, particularly on bibliographic references used for assigning wild progenitors for each crop.

crop	wild ancestor	family	common name
<i>Avena sativa</i>	<i>A. sterilis</i>	Poaceae	oats
<i>Beta vulgaris</i>	<i>B. vulgaris</i>	Amaranthaceae	chard
<i>Brassica oleracea</i>	<i>B. oleracea</i>	Brassicaceae	collard
<i>Capsicum anuum</i>	<i>C. anuum</i>	Solanaceae	pepper
<i>Capsicum bacattum</i>	<i>C. bacattum</i>	Solanaceae	chili pepper
<i>Cicer arietinum</i>	<i>C. reticulatum</i>	Fabaceae	chickpea
<i>Cichorium endibia</i>	<i>C. intybus</i>	Asteraceae	chicory
<i>Cynara cardunculus</i>	<i>C. cardunculus</i>	Asteraceae	cardoon
<i>Eruca sativa</i>	<i>E. sativa</i>	Brassicaceae	rocket
<i>Glycine max</i>	<i>G. soja</i>	Fabaceae	soyabean
<i>Gossypium hirsutum</i>	<i>G. hirsutum</i>	Malvaceae	cotton
<i>Helianthus annuus</i>	<i>H. annuus</i>	Asteraceae	sunflower
<i>Hordeum vulgare</i>	<i>H. spontaneum</i>	Poaceae	barley
<i>Lathyrus sativus</i>	<i>L. cicera</i>	Fabaceae	chickling vetch
<i>Lens culinaris</i>	<i>L. orientalis</i>	Fabaceae	lens
<i>Lupinus luteus</i>	<i>L. luteus</i>	Fabaceae	lupins
<i>Medicago lupulina</i>	<i>M. lupulina</i>	Fabaceae	black medic
<i>Oryza sativa</i>	<i>O. nivara</i>	Poaceae	rice
<i>Pennisetum glaucum</i>	<i>P. glaucum</i>	Poaceae	millet
<i>Pisum sativum</i>	<i>P. humile</i>	Fabaceae	peas
<i>Secale cereale</i>	<i>S. ancestrale</i>	Poaceae	rye
<i>Sesamum indicum</i>	<i>S. indicum</i>	Pedaliaceae	sesame
<i>Solanum lycopersicon</i>	<i>S. pimpinellifolium</i>	Solanaceae	tomato
<i>Sorghum sudanense</i>	<i>S. bicolor</i>	Poaceae	sorghum
<i>Spinacea oleracea</i>	<i>S. turkestanica</i>	Amaranthaceae	spinach
<i>Trifolium repens</i>	<i>T. repens</i>	Fabaceae	white clover
<i>Triticum durum</i>	<i>T. dicoccoides</i>	Poaceae	wheat
<i>Vicia faba</i>	<i>V. narbonensis</i>	Fabaceae	fava bean
<i>Vigna unguiculata</i>	<i>V. unguiculata</i>	Fabaceae	cowpea
<i>Zea mays</i>	<i>Z. mays</i>	Poaceae	maize

hereafter). The first axis of that PCA was negatively related to structural investment in leaf tissue, which commonly correlates positively with leaf longevity and negatively with carbon fixation rates and mass-based nutrient status of leaves. Lastly, a fourth PCA was run on root economic traits with specific root length and density of fine roots as component variables (ROOT ECON hereafter). First axes of the PCA analyses above explained 64–82% of variance in their component variables (see the electronic supplementary material, table S3) and were thus used as summary proxies of each of the four plant functions considered in this paper. Parameter-free PERMANOVA analyses were then used to assess the effects of domestication status, crop identity and their interaction on trait scores and on PCA axes (see Full materials and methods section in the electronic supplementary material for details).

(ii) Coordinated evolution of traits during domestication and further improvement

First, structural equation modelling (SEM) was used to investigate functional links among multiple traits, and their putative

coordinated evolution during domestication [16]. Here, we briefly describe the datasets we used to build the several SEMs. In the electronic supplementary material (Full materials and methods section), we also explain the rationale for model construction and provide statistical details on the estimation of goodness of fit and on the statistical significance of model parameters. Finally, in the electronic supplementary material (item 4), we provide results of additional SEM analyses intended to provide further empirical support for the general validity of the *a priori* inter-trait relationship scheme depicted in figure 2a.

SEMs were implemented for two separate types of datasets. First, we put together all log-scaled arithmetic mean trait and PCA scores for each accession present in both the extensive and intensive databases ('complete' dataset hereafter; $n = 114$ accessions). Second, we calculated, independently for the extensive and intensive databases, the magnitude of the domestication status effect over log-trait and PCA scores as follows. For the extensive database, we subtracted the average score of each wild (*W*) accession from that of its crop (*C*) counterpart. This evolutionary change is denoted as $\Delta C - W_{\text{Trait}}$ throughout the paper. For the

intensive database, we calculated an effect of domestication and an effect of subsequent improvement separately. The domestication effect was taken by subtracting the average score of each wild (WI) accession from that of its landrace (LR) counterpart ($\Delta LR - WI_{\text{Trait}}$ hereafter). Since the intensive database included three accessions for each domestication status per crop species, we subtracted every possible combination of wild accession from every landrace for each species separately. This is analogous to common practices in phenotypic plasticity literature making use of relative distance plasticity indices [17]. This procedure yielded nine $\Delta LR - WI_{\text{Trait}}$ scores per crop species included in the intensive database. We proceeded in the same way to compute the improvement effect: every score of a landrace (LR) accession was subtracted from each of the three improved (IM) accessions available for each crop species ($\Delta IM - LR_{\text{Trait}}$ hereafter).

The above calculations resulted in four separate datasets: (i) a 'complete' dataset ($n = 114$ log-scaled accession average log-trait and PCA scores); (ii) ' $\Delta C - W_{\text{Trait}}$ ' dataset ($n = 30$ wild-to-crop evolutionary transitions for each trait and PCA score); (iii) ' $\Delta LR - WI_{\text{Trait}}$ ' dataset ($n = 54$ wild-to-landrace evolutionary transitions for each trait and PCA score); (iv) ' $\Delta IM - LR_{\text{Trait}}$ ' dataset ($n = 54$ landrace-to-improved evolutionary transitions for each trait and PCA score).

After that, based on previous knowledge and on the patterns of trait correlations that we observed in our study, we designed an overall causal conceptual structure that linked our four groups of variables in a model (see Full materials and methods section in the electronic supplementary material for details). Considering the conceptual model, we generated several tentative specific models with our empirical variables, and the specific model receiving the highest statistical support for our 'complete' dataset was selected as a baseline model capturing common covariation patterns among the several traits involved in this study. This model was further validated with an independent dataset from the literature (electronic supplementary material, item 4). Then, the ' $\Delta C - W_{\text{Trait}}$ ', ' $\Delta LR - WI_{\text{Trait}}$ ' and ' $\Delta IM - LR_{\text{Trait}}$ ' datasets, representing trait shifts during crop evolution, were fitted to the baseline model (see Full materials and methods in electronic supplementary material for details).

Finally, statistical comparison of phenotypic integration levels among datasets in figure 4 was carried out using log-likelihood ratio tests of Aster models, robust to bimodality of dependent variables (see Full materials and methods and table S8 in the electronic supplementary material).

3. Results

Seed and plant sizes generally increased with crop evolution, as did proxies for light competitive ability such as leaf size, plant canopy height and early absolute growth rates of seedlings (figure 1a; electronic supplementary material, figure S3). Traits related to resource-acquisition rates of leaves and roots, such as dry mass content of leaves or specific root length, changed in diverse directions, depending on the crop species (figure 1a; electronic supplementary material, S3). For six crop species, we dissected the crop evolution process into an early domestication and a later improvement stage. Early domesticates, represented by landraces, were larger plants and more effective light competitors, but were similar to progenitors in their leaf and root resource-acquisition traits (figure 1b; electronic supplementary material, S4). Modern cultivars, however, did not differ consistently from comparable landraces in any measured trait (figure 1c; electronic supplementary material, S5). For all traits and evolutionary comparisons, we found significant domestication status $\times$ crop identity effects (electronic supplementary material,

tables S5–S7), signalling crop specificity (see the electronic supplementary material, figures S3–S5).

To analyse patterns of coordinated evolution of traits we first devised a model of inter-trait relationships, based on previous knowledge (electronic supplementary material, Full materials and methods section; figure 2a). Goodness of fit of the model to the data collected on all accessions was high (figure 2b), validation with independent datasets yielded remarkably similar covariance structures (electronic supplementary material, Full materials and methods section), and inter-trait correlations were generally strong. This supports the validity of our *a priori* model. We then used this baseline trait-syndrome model to investigate interlinked shifts in plant traits in response to initial domestication and to crop improvement. Note that path or correlations coefficients $< |0.05|$ were constrained to be zero to achieve model identification in all SEM models (e.g. $\text{SIZE}_{\text{PCA}} \rightarrow \text{ROOT ECON}_{\text{PCA}}$ in figure 2b).

The general strength and pattern of inter-trait coordination weakened when the *differences in trait scores* between wild and crop accessions were the underlying measured variables, rather than the values of traits themselves. This means that a given change in a trait or group of traits (e.g. increased seed size) did not necessarily entail a parallel shift in otherwise inter-connected traits (e.g. increase in seedling absolute growth rate; figure 3a). Note that *differences in trait scores* were widely different among traits and crop species (see Supplementary phenotypic integration analyses section in the electronic supplementary material), so we reject homogeneity of $\Delta C - W_{\text{Trait}}$ scores as the reason for the weakening of coordinated coevolution of traits. This weakening of trait correlation was supported by formal analyses of phenotypic integration (figure 4). Coordinated evolution of traits (i.e. integration), measured jointly as the magnitude and significance of Spearman's correlation coefficients between plant traits, was low when transiting from wild progenitors to domesticated forms of the 30 crops studied here (figure 4b).

We then looked at coordinated evolution in more detail for our subset of six crop species. We found that early domestication retained several of the strong trait-to-trait relationships that we had previously identified from literature and our own data (figure 3b). This includes allometric relationships between size traits and ability to compete for light and coordinated evolution of leaf and root economic traits (figure 3b). However, later crop improvement reduced covariation among most of these traits (figure 3c). Direct comparison of trait covariance matrices between early domestication and later breeding confirmed that changes occurring during more recent crop improvement took place with little coordination among traits (figure 4c–d).

4. Discussion

We found that, despite multiple crop-specific peculiarities, during crop evolution plants changed towards larger and more effective competitors for light, with poorly integrated phenotypes, in our set of herbaceous crop species. Enhanced competitive ability for light occurred during early domestication, whereas decreased phenotypic integration took place later, during recent crop improvement. No consistent phenotypic reaction to domestication was detected as regards leaf and root resource economy traits. These patterns have several important implications. First, increased size and capacity to

Figure 1. Shifts in traits during crop evolution. Direction and magnitude of (log)trait divergences (a) during the evolution of 30 crop species, (b) during early domestication of six species and (c) during further improvement of the same six species for the nine traits studied (white boxes), and for the four PCA axes summarizing trait covariation in figures 2 and 3 (grey boxes). Reference line: crop = wild (a); landrace = wild (b); or improved = landrace (c). Seed size (seed mass), TDM (total plant dry mass), AGR (absolute growth rate of seedlings), HEIGHT (canopy height), LEAF SIZE (projected leaf area), SLA (leaf area per leaf dry mass), LDMC (leaf dry matter content), SRL (root length per unit root mass), ROOT DENS (root tissue density). Crop identities were collapsed for clarity (crop-wise plots in the electronic supplementary material, figures S3–S5). Asterisks, domestication status significant at $p = 0.05$.

compete effectively with weeds for light is an evolutionary trajectory expected in high-resource environments [7,18]. Aggressive light competitors, however, divert resources to heterotrophic tissue (e.g. stems) for outcompeting neighbours [18]. This comes at the cost of diminishing community-level productivity and increasing risks of lodging, which are

undesirable in agricultural stands [12,19,20]. Consequently, several of the major grain cereal crops were bred during the Green Revolution for shorter, more productive plants [12]. This could account for the lack of increased light competitiveness during the latest improvement stage of herbaceous crop evolution, at least for barley (figure 1c). In contrast to our

Figure 2. Baseline structural equation model for inter-trait relationships. (a) Conceptual *a priori* model. Solid and dashed lines are positive and negative relationships, respectively. Double-headed arrows denote uncertain direction of causality. Question marks denote uncertain sign (+ or -) of the relationship. SIZE, LIGHT COMP, LEAF ECON and ROOT ECON signify plant functions. SIZE increases with larger seeds and larger plants. LIGHT COMP increases with increasing leaf size, plant height and aboveground growth rates. LEAF ECON and ROOT ECON are larger for softer and photosynthetically faster leaves and roots with faster uptake rates, respectively. (b) Fit of the current paper's dataset to the *a priori* model. Statistically significant paths ($\rightarrow$) or correlations ($\leftrightarrow$) in bold and denoted as $**p < 0.01$ or $*p < 0.05$. Trait ϵ = unexplained variance of dependent variables. Standardized path or correlations coefficients $< |0.05|$ (e.g. between SIZE and LEAF ECON) were constrained to be zero to achieve identification. Names of variables as in figure 1. (Online version in colour.)

initial hypothesis and the predictions of ecological strategies theory [7], leaf and root traits did not signal a generalized move towards a high-resource-use strategy during crop evolution. This result supports early literature noting absence of a systematic increase in area-based rates of photosynthesis during the evolution of cereals and other major herbaceous crops [21]. In addition, the few previous studies investigating shifts in specific leaf area accompanying crop evolution do not support any consistent pattern of change in this trait under domestication [22–24]. Wild progenitors of current herbaceous crops were probably already high-resource strategists in terms of biomass renewal and resource-acquisition rates. A look at specific leaf area scores of our species in the context of worldwide variation in that same trait supports this view (electronic supplementary material, figure S6). Fostering increases in an already fast strategy might provide diminishing physiological returns [25]. Further archaeo-ecophysiological work, however, is required to test the idea that wild progenitors were faster resource strategists than phylogenetically comparable co-occurring species (but see [26]).

Augmented size and competitive ability for light were not correlated with changes in proxies for leaf and root resource-use strategies (figures 1a and 3a). This is most interesting, and is at odds with previous theoretical and empirical literature highlighting metabolic costs of increases in body size or in heterotrophic tissue [27,28] (but see [29]). Note that decreased levels of coordinated coevolution among those traits occurred mainly during the improvement stage of herbaceous crop evolution, for the subset of six crops investigated more intensively (figure 4d). This suggests that historically recent breeding might explain the decrease in the degree of coordinated evolution of traits (i.e. phenotypic integration) observed for the larger 30-species dataset. During the improvement phase of herbaceous crops, a combination of enhanced understanding of genetics of specific traits and greater human control over the agro-environment may have allowed selection of new trait combinations, which neither succeeded in the wild nor during earlier plant domestication.

Phenotypic integration may arise through strong directional selection, through genetic linkages that promote joint

Figure 3. Shifts in plant trait relationships during crop evolution. Fit of the structural equation model in figure 2b to (a) the magnitude of trait shifts between crop and wild accessions of the 30-crop-species set (Δ_{C-W} trait'), (b) the same shift in traits between wild and landrace accessions during early domestication of six crops (Δ_{LR-W} trait'), and (c) the same shift in traits during later improvement for the same six crops (Δ_{IM-LR} trait'). Symbols and variables names as in figures 1 and 2. (Online version in colour.)

inheritance of traits, through selective sweeps and through genes with pleiotropic effects exerting biochemical control (e.g. response of many traits to abscisic acid) [28,29]. Disruption of genetic and some biochemical linkages among traits offers opportunities to develop varieties with new combinations of desired traits through breeding and genetic engineering. Indeed, that has been the case for the evolution and breeding of many crops, with obvious beneficial effects for humans. What disadvantages, if any, might then result from loss of

coordinated evolution of functional traits during recent crop improvement? Phenotypic integration is promoted by environmental stresses (e.g. drought) that directly select for groups of traits with functional linkage (e.g. low minor vein densities and low maximum rates of photosynthesis) [30]. Previous work has documented increases in phenotypic integration in response to increasing environmental stress [10,14,31]. That literature, however, primarily focused on the plastic response of phenotypes to changes in the environment, rather than the

Figure 4. Decrease in phenotypic integration with crop evolution. Matrices of Spearman's correlation coefficients among the nine log-transformed traits measured in this study (figure 1). When a correlation was non-significant, the coefficient is statistically non-different from zero and was thus denoted as 0.00. Significant correlations are highlighted in bold and in grey background. (a) Correlation coefficients for the current paper's dataset of all accessions. (b–d) Correlation coefficients between shifts in traits (b) during crop evolution of the whole set of 30 crops, (c) due to early domestication of six crops and (d) during later improvement for the same six crops. Different lowercase letters (a, b) among matrices in the same row indicate significant differences in average correlation coefficient scores.

macroevolutionary changes reported here [11]. Although studies of coordinated plant trait macroevolution are abundant [32,33], phenotypic integration levels are rarely explicitly addressed in that research. The fact that annual herbs not only acclimate, but also evolve varying levels of inter-trait linkages as a consequence of crop domestication and breeding, is remarkable. Evolutionary disruption of those linkages might result in varieties that perform effectively in highly controlled environments such as high-input agriculture, but may be more vulnerable to stressful conditions that are expected with climatic change. For instance, ongoing increased aridity is perceived as a relevant threat for the marketability of *Brassica oleracea* L. var *acephala* (cabbage), a major European crop [34]. Cabbage has shown outstanding evolutionary plasticity in food quality characteristics. However, the fact that traits that promote an efficient use of water and mineral resources did not improve during the evolution of this crop (electronic supplementary material, figures S3–S5) may pose limitations on its widespread use in the near future, particularly in southern European countries. More detailed and crop-specific research is needed to understand the balance between benefits and disadvantages, in terms of yield or plant fitness, of diverse levels of phenotypic integration and of plasticity in crop species grown in contrasting environments.

In short, our results show that evolution of herbs under agricultural selective pressures resulted in phenotypes that are larger and more aggressive competitors for light than their wild progenitors, but similar in terms of mass-specific capabilities for root and leaf resource uptake and conservation. The capacity to compete for light was selected during initial domestication, but plants did not grow larger during recent crop improvement. More interestingly, we report that phenotypes did not change in a coordinated manner during crop evolution for traits that are otherwise tightly interrelated in wild habitats. Such decrease in phenotypic integration

occurred in recent times, during breeding of modern commercial varieties.

We suggest that the set of commonly observed traits that accompany domestication should be extended to include traits of direct relevance to plant fitness in the wild. This may contribute to our knowledge of how herbaceous crop evolution proceeded in the past and to our opportunities to re-direct or emphasize those trajectories. Most of the common traits associated with domestication of annual herbs are chiefly made of traits that were selected for their agronomic benefit to humans [4]. Here, we propose that evolution of more effective light competitors should be considered a generalized consequence of herbaceous crop domestication, jointly with other traits previously identified [5]. Additionally, decreases in the strength of inter-trait linkages during crop evolution fit expectations from phenotypic integration literature for evolution under benign environments [10,14,31]. Potential implications of this remarkable result for augmenting crop yields, and for promoting yield sustainability and adaptability to stress factors in a changing climate, should prompt further research in this area.

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Data accessibility. All data used in this manuscript are deposited in Dryad repository (doi:10.5061/dryad.dg85v).

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