

RESEARCH ARTICLE

Selection for domestication favored taxa characterized by fast growth and tolerance of high intraspecific density

Rafael Rubio de Casas^{1,2}  | Irene Martín-Brull^{1,2,3}  | Ruben Milla⁴  |
Francisco J. Ocaña-Calahorra¹ 

¹Departamento de Ecología, Universidad de Granada – UGR, Granada, Spain

²MNat Scientific Unit, Universidad de Granada, Granada, Spain

³EEAD-CSIC, Zaragoza, Spain

⁴Grupo de investigación en Ecología Evolutiva, Departamento de Biología y Geología, Física y Química Inorgánica, Instituto de Investigación en Cambio Global, Universidad Rey Juan Carlos, Madrid, Spain

Correspondence

Rafael Rubio de Casas, MNat Scientific Unit, Universidad de Granada, Granada, Spain.
Email: rubiodecasas@ugr.es

Funding information

Ministry of Economy and Competitiveness, Grant/Award Number: CGL2016-79950-R

Societal Impact Statement

To understand why certain plants have been domesticated into crops, we need to recognize that the environmental conditions plants experience in wild populations are totally different from those of agricultural fields. In this study, we investigated whether the characteristics that promote growth and survival in these different environments may have influenced domestication. Our results revealed that ancestral crops were selected because they developed better than other plants in dense single-species stands, with selection for increased yield likely occurring after domestication. These insights shed light on the origins of agriculture and offer valuable guidance for future crop breeding efforts.

Summary

- In spite of a large history of research, it is still unclear which functional traits may have mediated plant domestication. Solving this problem requires consideration of the ecological and demographic disparities between natural plant populations and cultivated fields. Since population density tends to be higher in the latter, we hypothesized that traits facilitating growth and survival in dense, monospecific populations might have been relevant for initial domestication.
- We investigated whether functional traits that respond to population density varied across three different domestication stages: undomesticated crop wild relatives, natural populations of crop progenitors, and landraces. To do this, we compared traits influencing competition (lodging; growth rate), resource acquisition (plant height; total aerial and root biomass) and yield (fruit number) in three annual legume crops—lentil, grasspea, and vetch—grown without resource limitation at three different densities.
- Our results showed clear differences among species, likely reflective of the distinct uses of the crops and their domestication pathways. Nevertheless, undomesticated relatives consistently differed from crop progenitors and landraces, producing smaller, slower-growing plants that were more prostrate and allocated less biomass to roots. The effect of selection under domestication on these vegetative

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Plants, People, Planet* published by John Wiley & Sons Ltd on behalf of New Phytologist Foundation.

traits appeared to be largely negligible. Conversely, landraces produced more fruits.

- We conclude that early agriculturalists selected for domestication wild legumes that performed well in dense monocultures and were more effective in resource capture. Later domestication and breeding efforts likely had more significant effects on reproductive traits, such as fruit and seed production.

KEYWORDS

artificial selection, crop ecology, crop evolution, Fabaceae, intraspecific competition, *Lathyrus*, *Lens*, *Vicia*

1 | INTRODUCTION

Our understanding of crop domestication has been changing rapidly over the course of the last decade. Newly available archaeobotanical evidence and new genetic and genomic tools have illustrated a complex, nonlinear process in which some taxa developed into crops while others did not (Cuniff et al., 2014). The reasons for this selection remain obscure, although in all likelihood it was at least partly mediated by functional differences between crop progenitors and other wild relatives (Gómez-Fernández et al., 2024).

The transition from natural ecosystems to crop fields and agricultural landscapes entailed the objectification and the control of (at least) some biological resources (Abbo & Gopher, 2017; Purugganan, 2022). Epipaleolithic and neolithic communities relied on a wide diversity of local plant taxa (Arranz-Otaegui et al., 2018; Bode et al., 2022; Zeder, 2012). The exploitation and harvesting of these various food sources were coupled to the manipulation of the environment in which they were found, often in connection to animal husbandry (Spengler & Mueller, 2019; Terrell et al., 2003; Weide et al., 2022). Subsequently, the early breeders might have selected the elements of these ancestral “tamed” communities most amenable to farming and increased their productivity (Allaby et al., 2022; Asouti & Fuller, 2013).

Although the ultimate degree of human agency remains controversial (Clement 2022; Gremillion et al., 2014), it is clear that these processes entail a profound divergence in ecological and demographic conditions. Crop fields have a reduced environmental heterogeneity and much lower interspecific diversity (often reduced to a single species) compared to natural communities. This is usually correlated with an increase in population density of the focal species, generally higher under cultivation (Denison, 2016; Donald, 1968). Thus, the functional traits that facilitate growth and survival in biological communities characterized by low diversity (i.e., monospecific) and at high population densities are likely to have been relevant for domestication.

Phenotypes able to establish and thrive in spatially and biologically homogeneous environments can be largely assimilated to Grime's competitive strategy (Grime, 1977). This strategy typically emerges in response to social environments, where the presence of neighbors triggers signals that shape specific phenotypes

(Novoplansky, 2009; Padilla et al., 2013). Successful competitors exhibit rapid and vertical growth, high production of biomass, and high capacity for resource capture (Fréville et al., 2022; Grime, 1977). These traits are potentially advantageous for crops and may have been enhanced through selective breeding following domestication (Abbo et al., 2014; De Wet & Harlan, 1975; Donald, 1968).

However, at the same time, agricultural environments reduce the need for competition, creating “luxury” settings for crops (Weiner, 2019). Still, phenotypic adjustments to the social environment remain essential, as intraspecific interactions are unavoidable in dense, monospecific stands (Zhang & Tielbörger, 2020). Consequently, modern cultivars likely result from a combination of human selection for wild phenotypes and breeding—intentional or not—for performance in high intraspecific density. Teasing apart the effects of these two processes is crucial to improve our understanding of crop evolution.

Simultaneously, selection for phenotypes with high performance in dense crop fields may have entailed selection for phenotypic plasticity to population density. For instance, some authors suggest that reduced phenotypic plasticity in response to stand density may increase tolerance to crowding, making it a (potentially indirect) target of breeding (Fréville et al., 2022; López Pereira et al., 2017). If this is true, it could challenge the idea that artificial selection increased crop competitiveness, as universal adaptive strategy theory predicts higher plasticity in competitors (Callaway et al., 2003; Crick & Grime, 1987; Grime et al., 1991). However, at this point, we still know little of how domestication may have influenced crops' plasticity to biotic factors such as population density (Milla, 2023). If crops exhibit similar or lower plasticity to factors like high intraspecific density compared to their wild ancestors, it may suggest that these responses were actually “pre-adaptive” and facilitated domestication in the first place (Piperno et al., 2015).

Not all crops are used for the same purposes, a fact that has influenced their domestication pathways (Asouti & Fuller, 2013; Fuller et al., 2023). Even closely related taxa or even cultivars or forms of the same species were and are selected for different uses (e.g., *Brassica oleracea*; Mabry et al., 2021). This is likely to affect conditions of propagation and cultivation and therefore the adaptative value of different traits. Whether a plant is bred for grain or as forage could

ultimately determine how it diverges from its wild type. However, it is also possible that traits that facilitated growth and survival under ancestral “agricultural” conditions (i.e., deliberate maintenance and exploitation of plant populations by humans) might be consistently favored across domestication events.

In the present work, we investigated whether crop domestication may have been facilitated by certain functional traits, specifically those that favor growth under dense monospecific communities using three genera of legumes. For this purpose, we compared the phenotypes of natural populations of wild crop progenitors, undomesticated close relatives, and crop landraces. We assumed that domestication would lead to phenotypic differences between landraces and conspecific wild populations ($\Delta\phi_C$; Figure 1), whereas traits that made a species selected for early domestication would be different between closely related, undomesticated taxa and crop wild progenitors, as the latter would display the phenotypes favored by ancient domesticators ($\Delta\phi_D$; Figure 1). Furthermore, we also explored the potential role of plasticity in mediating the phenotypes expressed under different population density levels. Using this conceptual and experimental framework, we asked (i) whether functional traits associated with competitiveness and resource capture ability vary across stages of the domestication process (i.e., among undomesticated wild relatives, wild populations of crop progenitors, and crop landraces); (ii) what the effect of population density on vegetative or reproductive (i.e., yield) traits is; and (iii) if phenotypic plasticity to population density changed with domestication.

2 | MATERIALS AND METHODS

2.1 | Plant material and experimental design

In our experiments, we used undomesticated wild relatives, wild populations of crop progenitors, and crop landraces of three phylogenetically close and ecologically similar annual legumes: grasspeas (*Lathyrus* spp.), lentils (*Lens* spp.), and vetches (*Vicia* spp.). To avoid confusion, in every case, we used as undomesticated relatives taxa that have never been implicated in the history of domestication of the corresponding crop and that do not hybridize with it. In two instances, this resulted in taxonomic pairs that were the closest possible relatives: *Lathyrus amphicarpos*/*Lathyrus sativus* and *Vicia amphicarpa*/*Vicia sativa* (in fact, the last two are often treated as subspecies of the same species—*V. sativa* subsp. *sativa* L. and *V. sativa* subsp. *amphicarpa* [Dorthes] Asch.; Blanca et al., 2009; Castroviejo, 2020; Schaefer et al., 2012), while in the case of lentils the domesticated and undomesticated taxa were *Lens culinaris* subsp. *culinaris* and *Lens nigricans* (M.Bieb.) Webb & Berthel., respectively. The three crops (lentil: *L. culinaris*; grasspea: *L. sativus*; common vetch: *V. sativa* var. *sativa*) are ancient domesticates; lentil and grasspea in particular have been cultivated since the early Neolithic (Lambein et al., 2019; Zohary et al., 2012). The earliest domestication date of common vetch remains less clear, but it was undoubtedly domesticated and cultivated in Ancient Rome, as described by Varro (37 BCE). The three of them encompass a wide cultivated diversity and can be regarded as multipurpose crops, having been historically used as grain crops for

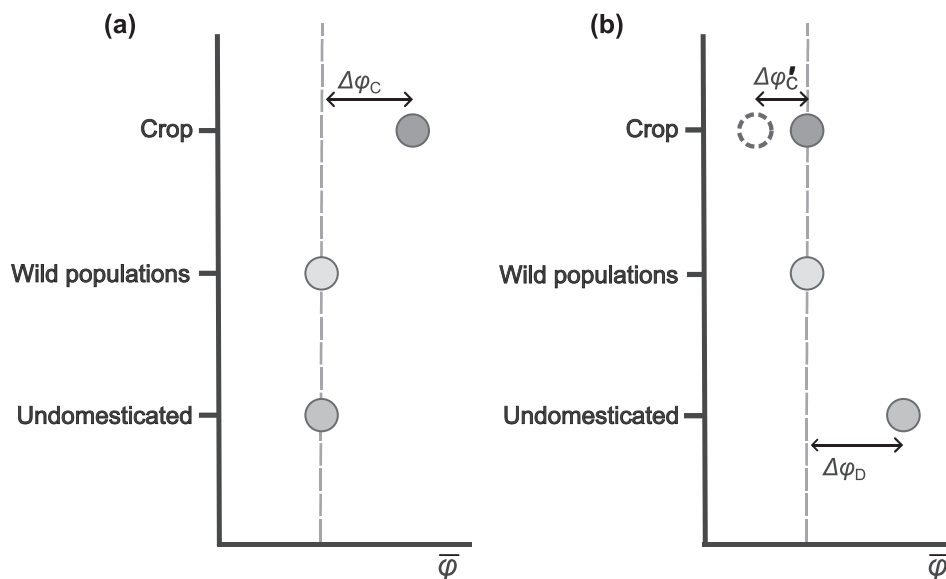


FIGURE 1 Schematic representation of our conceptual and experimental framework. (a) The expected pattern of phenotypic differentiation across the stages of domestication when crop cultivars are phenotypically different from all their wild relatives, that is, different from both the wild progenitor of the crop and other undomesticated wild relatives. We attribute this variation (represented as $\Delta\phi_C$) to selection under cultivation. (b) A case in which the crop and its wild progenitor have similar trait values, but these are clearly different from those of the undomesticated close wild relatives. This phenotypic differentiation ($\Delta\phi_D$) could have therefore been relevant for the ancestral domestication process. Note that this does not preclude that artificial selection (direct or indirect) can result in further deviation in this trait from ancestral mean values ($\Delta\phi'_C$). The horizontal axis represents mean values for a trait of interest ($\bar{\phi}$), and the dotted line corresponds to the mean trait value of the wild populations of the crop progenitor.

human or animal consumption, forage, or even green manure. However, grasspea and lentil have always been predominantly cultivated for their seeds, specially the latter, and *V. sativa* for its vegetative biomass (Cubero et al., 2004). Seeds of the different taxa were obtained from three different genebanks: CRF-INIA (Spain), IPK-Gatersleben (Germany), and the USDA-ARS GRIN service (USA) and/or collected in the wild between 2013 and 2016 (Table 1). To dilute potential maternal environmental effects, we grew one generation of plants in a common environment. In October 2017, seeds of each accession were scarified and sowed in 11 × 11 cm 1-L pots filled with a mixture of 300 mL commercial potting soil (Sustrato Universal Projar), 300 mL vermiculite, 300 mL perlite, and 100 mL of natural soil from a natural community rich in native legumes, mostly *Vicia* spp. and *Lathyrus* spp., to ensure the presence of symbionts (three replicates/accession, two seeds/pot, thinned to one plant/pot after the first pair of true leaves developed). We applied a N-free fertilizer twice over the course of

the growing season (ULTRA-PK NC Booster). Pots were kept moist and randomized every week to minimize microenvironmental effects. In June of 2018, seeds were collected and stored in paper envelopes at room temperature. In October 2018, these seeds were distributed in three different density treatments: control (one plant/pot), intermediate (two plants/pot), and high (five plants/pot). We prepared four replicates of each combination of genus (three levels: *Lathyrus*, *Lens*, and *Vicia*), domestication stage (three levels: landraces, wild population of crop progenitors, and undomesticated relatives), and population density (three levels, total $n = 324$). In order to ensure synchronous germination, all seeds were scarified and placed in Petri plates containing 0.5% agar solution (one plate/pot) and stratified in the dark for 5 days at 4°C. Plates were then placed in a growth chamber set at 21°C with 12-h light cycles (ARALAB, Spain). These conditions have been previously shown to ensure full germination of several of these taxa (Sánchez-Martín et al., 2021). After cotyledon

TABLE 1 Plant material. The table displays the information of all the accessions used in the experiments, including taxonomic assignment (genus; species), accession number (accession), institution of origin of the seeds (institution; USDA-ARS codes USA; CRF-INIA codes ESP; IPK Gatersleben codes DEU; UGR Universidad de Granada), the biological status of each accession according to the EURISCO codes (SAMPSTAT; 100 = wild; 300 = traditional cultivar/landrace) and our own assignment of domestication stage (three levels: undomesticated relatives, wild populations of crop progenitors, and landraces). Before the experiments begun, all accessions were cultivated for a minimum of one generation in the gardens of the Facultad de Ciencias of the UGR to eliminate maternal environmental effects.

Genus	Species	Accession	Institution	SAMPSTAT	Domestic.
<i>Lathyrus</i>	<i>amphicarpos</i> L.	Wild sample	UGR	100	Udom. relative
<i>Lathyrus</i>	<i>amphicarpos</i> L.	Wild sample	UGR	100	Udom. relative
<i>Lathyrus</i>	<i>amphicarpos</i> L.	Wild sample	UGR	100	Udom. relative
<i>Lathyrus</i>	<i>sativus</i> L.	LAT 4151	DEU146; DEU159; DEU271	100	Wild progenitor
<i>Lathyrus</i>	<i>sativus</i> L.	LAT 4158	DEU146; DEU159; DEU271	100	Wild progenitor
<i>Lathyrus</i>	<i>sativus</i> L.	PI667254	USA650; USA972	100	Wild progenitor
<i>Lathyrus</i>	<i>sativus</i> L.	BGE027129	ESP004	300	Landrace
<i>Lathyrus</i>	<i>sativus</i> L.	BGE023929	ESP004	300	Landrace
<i>Lathyrus</i>	<i>sativus</i> L.	BGE034204	ESP004	300	Landrace
<i>Lens</i>	<i>culinaris</i> Medik.	PI429369	USA650; USA972	100	Wild progenitor
<i>Lens</i>	<i>culinaris</i> Medik.	PI412922	USA650; USA972	100	Wild progenitor
<i>Lens</i>	<i>culinaris</i> Medik.	PI606655	USA650; USA972	100	Wild progenitor
<i>Lens</i>	<i>culinaris</i> Medik.	BGE001017	ESP004	300	Landrace
<i>Lens</i>	<i>culinaris</i> Medik.	BGE001055	ESP004	300	Landrace
<i>Lens</i>	<i>culinaris</i> Medik.	BGE004251	ESP004	300	Landrace
<i>Lens</i>	<i>nigricans</i> (M.Bieb.) Webb & Berthel.	BGE048992	ESP004	100	Udom. relative
<i>Lens</i>	<i>nigricans</i> (M.Bieb.) Webb & Berthel.	BGE019583	ESP004	100	Udom. relative
<i>Lens</i>	<i>nigricans</i> (M.Bieb.) Webb & Berthel.	BGE019582	ESP004	100	Udom. relative
<i>Vicia</i>	<i>amphicarpa</i> L.	BGE029947	ESP004	100	Udom. relative
<i>Vicia</i>	<i>amphicarpa</i> L.	BGE029992	ESP004	100	Udom. relative
<i>Vicia</i>	<i>amphicarpa</i> L.	BGE029928	ESP005	100	Udom. relative
<i>Vicia</i>	<i>sativa</i> L.	BGE001054	ESP004	100	Wild progenitor
<i>Vicia</i>	<i>sativa</i> L.	BGE024714	ESP004	100	Wild progenitor
<i>Vicia</i>	<i>sativa</i> L.	BGE024716	ESP004	100	Wild progenitor
<i>Vicia</i>	<i>sativa</i> L.	BGE001468	ESP004	300	Landrace
<i>Vicia</i>	<i>sativa</i> L.	BGE004221	ESP004	300	Landrace
<i>Vicia</i>	<i>sativa</i> L.	BGE025285	ESP004	300	Landrace

expansion, seedlings were transplanted to pots analogous to those used to grow the maternal generation. Control treatment plants were sown in the center of the pot, intermediate-density plants were placed on diagonal corners of the square pots (approx. distance between plants ~ 12 cm), and plants in the high-density treatment were placed one in each corner and one in the center of the pot (focal plant, average distance to each companion ~ 5 cm). These planting distances match common planting densities for pulse crops (Cubero et al., 2004). Pots were randomized every week, ensuring that they were far apart to avoid interactions across pots and fertilized monthly with N-free fertilizer.

Traditionally, it has been assumed that plants could only sense their neighbors passively by detecting changes in resources (light, water, and nutrient) caused by other plants. However, a growing body of research has shown that plants do actively detect their neighbors and actively respond by altering their growth or behavior relative to a “no-neighbor” scenario, independently of resource availability (Bilas et al., 2021; Chen et al., 2015). At the same time, changes in resource availability will result in phenotypic changes. For instance, declining nutrient availability at high population densities may result in over-proliferation of roots (Gersani et al., 2001). Our aim was to evaluate the direct effects of the number of close neighbors (i.e., density) and not the indirect effects caused by changes in resource availability, that is, we wanted to avoid conflating “competitive phenotype” with “phenotype resulting from competition.” To this end, we tried to bypass the confounding effects of variation in resource availability embedded in the traditional competition setup (i.e., one plant in one pot vs. multiple plants in one pot, given a fixed supply of resources) by ensuring that resources were uncoupled from density and that all plants had access to equal amounts of soil and light resources, independently of density (Becker et al., 2023; Losapio, 2023). Specifically, pots were filled with an inert mixture of washed river sand, vermiculite, and perlite (1/3 each) and an amount of the previous year soil (living soil) proportional to the number of plants in the pot. Control plants were grown in 200 mL living soil + 800 mL inert soil, while intermediate-density pots contained 400 mL living soil and high-density pots 1 L of living soil. The amount of fertilizer was also proportional to the number of plants (i.e., one dose/application/pot in the case of control plants, two for intermediate density, and five for high density). Additionally, when the first flower in each pot was spotted, all plants in the pot were trained on 0.5 m bamboo stakes to minimize competition for light and facilitate fruit harvest. Following this point, plants were inspected every 2 days to count flowers and fruits. All plants were cultivated outdoors in the common garden of the Facultad de Ciencias, Universidad de Granada, under full sun (Mediterranean climate, lat. 37.18043; long. -3.60808).

2.2 | Trait measurements

We measured traits assumed to encapsulate differences in competitiveness, resource capture ability, and yield on each of the focal plants. As competitiveness proxies, we used vegetative characteristics

that can help plants outcompete neighbors: vertical growth, measured as the ratio between plant height and the length of the longest branch after 8 weeks, and growth rate, estimated as the difference between maximum branch length between 4 and 8 weeks. To estimate resource capture ability, we measured aerial and root biomass at the end of the experiment and calculated their ratio, as higher biomass allocation to roots (RMF) is indicative of higher resource capture ability under high irradiance conditions (i.e., when carbon is not limited and aboveground competition minimal; Fukano et al., 2020; Gedroc et al., 1996; Wang et al., 2014). When $\sim 75\%$ of the focal plant of each pot was yellow (late May to mid-June, 2019), we harvested all plants in every pot, cutting the aerial parts. We separated all fruits and oven-dried all stems and leaves at 70°C for 48 h and weighted them with a precision scale (aerial biomass). In parallel, we washed the roots by immersion, carefully separated those of the focal plants and dried (60°C for 48 h) and weighted them (root biomass). Since this measurement was unavoidably destructive, especially in the high-density treatment, we verified that our data were not biased by comparing root biomass of focal plants of this treatment with the average root biomass of the remaining plants of the corresponding pot. This value was obtained as the total weight of all the dry roots of a pot divided by the number of accompanying plants in the pot (usually four). Yield was approximated as the total number of fruits produced. Fully developed fruits on each focal plant were counted weekly after the first one was spotted in each pot and continued until plant harvest.

2.3 | Statistical analyses

Our experiments included three crops that differ in their use and probably followed largely different domestication pathways (Fuller et al., 2023). Moreover, the three genera present very conspicuous morphological differences (Blanca et al., 2009). Therefore, data were analyzed assuming differences across genera in trait means. Our statistical models included each of the phenotypic characteristics used to approximate competitiveness, resource capture ability, and yield as dependent variables and domestication stage and population density as fixed predictors and considering that intercepts and slopes would differ across genera. Full models were of the form

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_{ij(k)} + \epsilon_{ijk} \quad (1)$$

where Y is the response variable (subscript ijk indicates that the response is indexed by the levels of the three factors considered: genus, domestication, and density), μ is the overall mean; α_i is the effect of the i th level of domestication stage (three levels: wild relative, wild populations of crop progenitor, and landraces); β_j is the effect of the j th level of the density treatment (three levels: control, one plant/pot; intermediate, two plants/pot; high, five plants/pot); $(\alpha\beta)_{ij}$ is the interaction effect between levels i and j of both factors; $\gamma_{ij(k)}$ is the effect of the k th level of genus (three levels: *Lathyrus*, *Lens*, and *Vicia*) nested within the combination of levels i and j of the other two factors; and ϵ_{ijk} is the random error term. In these models,

differences in plasticity to population density across stages of domestication are measured by the interaction term $(\alpha\beta)_{ij}$. To establish whether the effects of this term were indeed relevant to understand phenotypic responses, we compared the fit of models including the interaction with reduced additive models of the form

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_{ij(k)} + \epsilon_{ijk} \quad (2)$$

Model parameters were estimated using the “brms” package in R v. 4.3.1 (Buerkner, 2017; R Core Development Team, 2023). To select the model with the best fit to the data, we run the full and additive models for each variable with default priors and using four chains with 2000 iterations, a warm-up of 500, and thinning = 1. The definitive models had normal priors for the global intercept and that of the random factor (i.e., genus) centered around the means calculated with the preliminary runs and a SD = 100. They had four chains that were run for 20,000 generations, of which 10,000 were discarded as burn-in and thinning = 2. In every case, we also used the preliminary model runs to investigate the distribution of the response variable and transformed it as necessary to meet normality for the final run (natural logarithm for growth rate, nat. log. +1 for root biomass and fruit number and square root for aerial biomass). The variables that took values between 0 and 1 (erectness, root/shoot) were fitted using beta-regression models (Ferrari & Cribari-Neto, 2004; Geissinger et al., 2022), while in the other cases, variables were assumed to follow a normal distribution after transformation. MCMC convergence was verified with trace plots and the Gelman–Rubin statistic (\hat{R}). To quantify the explanatory power of the interaction term (i.e., plasticity),

we compared the fit of the full and additive models using their respective leave-one-out estimates of the expected log-pointwise predictive density (ELPD; Vehtari et al., 2017). Graphs were plotted with the packages “ggplot2” (Wickham, 2016) and “bayesplot” (Gabry & Mahr, 2022).

3 | RESULTS

3.1 | Phenotypic and taxonomic differences

We observed a wide variability in all phenotypic traits (Figures 2 and S1), and much of this variation can be attributed to differences among genera. These taxonomic differences were quantified by our models as the proportion of variance explained by the random term “Genus.” All models had good performance and explanatory power ($\hat{R} = 1$; $R^2 \in [0.37, 0.75]$; Table S1), but those that considered both the fixed and the random factors had a better fit to the data than models that did not include the random factor (conditional $R^2 >$ marginal R^2 ; Table S1). For two of the traits considered, fruit number and vertical growth, differences between genera explained most of the observed variance (conditional $R^2 \approx 10 \times$ marginal R^2 ; Table S1). For these two traits *Lens* spp. plants had much higher mean values overall than the other two genera, particularly a higher number of fruits. Conversely, *Vicia* spp. had a much higher growth rate (Figure S2). In spite of the taxonomic differences, domestication stage and population density had clear and consistent effects on all traits (Table S1 and Figures 3 and S2).

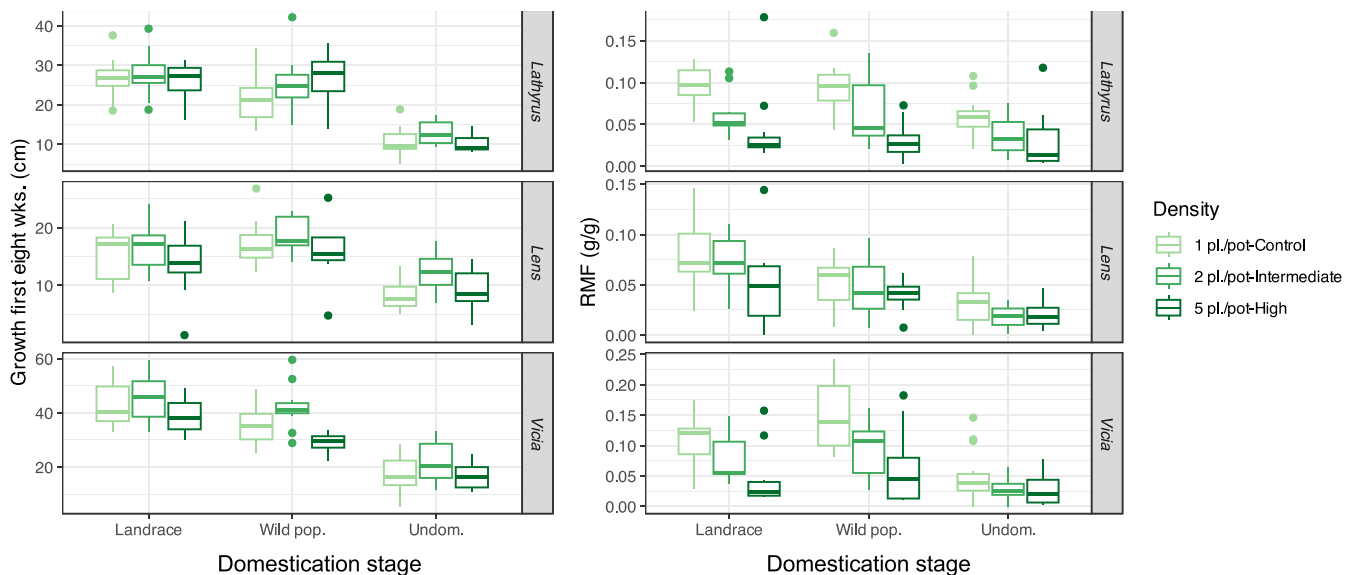


FIGURE 2 Example of the phenotypic diversity observed in the experiment. The graphs represent growth rate (growth in the first 8 weeks; left panel) and biomass allocation to above or below-ground organs, measured as root mass fraction (RMF; right panel) across genera (facets), stages of domestication (x-axis: crop landraces, wild populations of the crop progenitor and undomesticated relative), and population densities (shading; control: one plant per pot; intermediate: two plants per pot; high: five plants per pot). The plots represent the medians (central bars), first and third quartiles (the 25th and 75th percentiles; boxes), and ± 1.5 interquartile range (IQR) (whiskers). Observations beyond those values are represented by outlying dots. The values of the remaining variables (vertical growth, number of fruits produced, aerial and root biomass) are shown in Figure S1.

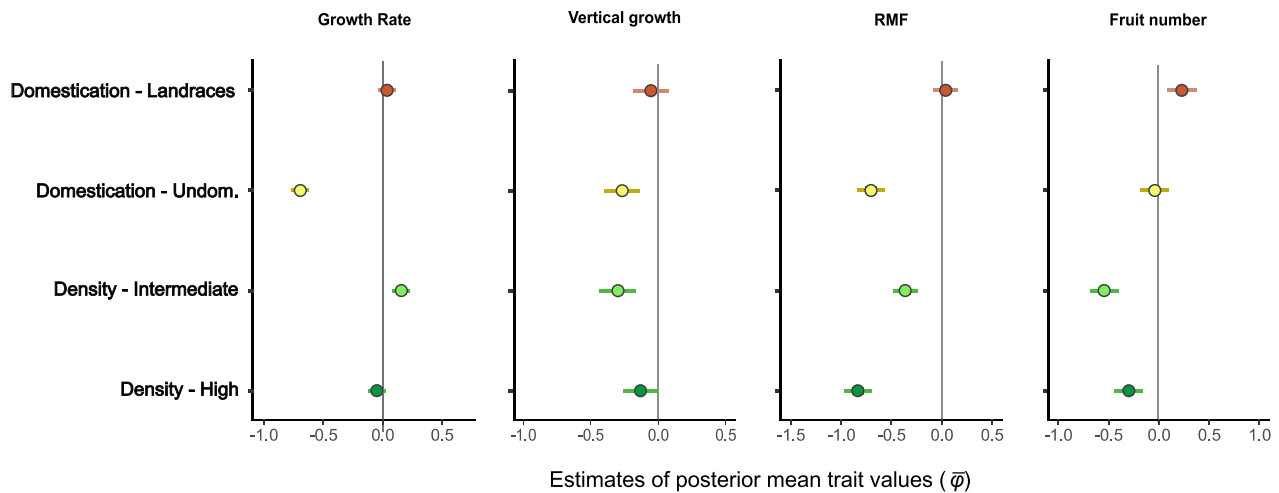


FIGURE 3 Differences in mean trait values across domestication stages and population density levels. The plots represent the estimates of the posterior distributions of trait means for the different treatments relative to that of the reference level for each factor, set by convention at 0 (dotted line). Reference values were the posterior estimates of the mean of each corresponding trait for wild populations of the progenitor of the crop (factor “domestication”) and control (one plant per pot; factor “density”). Dots indicated the 0.5 probability density of the posterior distribution, and the horizontal bars the 0.9 probability density. Factor levels for which posterior density intervals do not overlap 0 (i.e., fall outside of the region of practical equivalence [ROPE]) can be interpreted as resulting in trait means different from those of the reference level of the corresponding factor. All results were obtained by fitting additive models (described by Equation 2) to the data using brms (Buerkner, 2017; see main text for details). Detailed numerical results of all models are presented in Table S1. Figure S2 shows the effects plots for aerial and root biomass.

3.2 | Growth rate and vertical growth

Undomesticated taxa had a lower growth rate and produced less erect plants in the early stages of growth than either the crop progenitors or the landraces (Figures 2 and S1). The effect of population density was stronger under intermediate levels (i.e., two plants per pot), when plants tended to grow faster and less vertically, while plants grown at high densities were more similar to those of the control treatment (Tables S1 and S2 and Figure 3).

3.3 | Plant biomass and RMF

Plants of undomesticated taxa were clearly smaller and produced less biomass than those of wild progenitors or landraces of crops. In fact, we failed to detect an effect of selection under cultivation on plant biomass, that is, plants of wild populations and landraces were of comparable size (Figures 2, S1, and S2; Tables S1 and S2). Plant biomass was mostly determined by aerial biomass (aerial biomass \approx 5–10 \times root biomass; Figure S1). Population density did not seem to affect aerial biomass (Table S1 and Figure S2). Conversely, subterranean biomass differed considerably with domestication and population density (Figures 2 and S2; Tables S1 and S2). Plants of undomesticated taxa had much smaller roots whereas wild and landrace crop populations had very similar root sizes. Population density caused a reduction in root size, with higher densities resulting in smaller roots (Tables S1 and S2; Figure S2). As a consequence, biomass allocation to roots (RMF) decreased with density level, regardless of

domestication status, that is, it was higher in the control plants, lower at intermediate levels of density and lowest at high density and was always smaller in undomesticated taxa (Figure 2). Pearson correlation between focal plant root biomass estimates and average root biomass was significant (0.37; $p < .0001$), indicating that our results were not due to artifactual loss of root biomass in the high-density treatments.

3.4 | Fruit number

The effects of domestication and population density on fruit number deviated from those observed in vegetative traits. We did not observe differences between undomesticated relatives and wild populations of crop progenitors, but between the latter and landraces, which produced more fruits (Figure 3 and Tables S1 and S2). Population density was deleterious for individual fruit production, and plants tended to produce less fruits when grown with neighbors (Figure S1).

3.5 | Phenotypic plasticity to population density

Visual data exploration did not indicate the existence of an interaction between domestication stage and population density on phenotypic responses (Figures 2 and S1). Moreover, in every case, additive models had better or comparable explanatory power than the full models that included the interaction term (Table S3). Our metric of model fit—Bayesian leave-one-out (loo) estimates of the expected log-pointwise predictive density (ELPD)—was higher for the additive,

reduced model for all traits except growth rate, and in this case, the difference between l_{00} -ELPD values was very small (<2 ; Table S3). Therefore, our experiments do not support the existence of differences in phenotypic plasticity to population density across stages of domestication.

4 | DISCUSSION

Our findings revealed that crop wild progenitors consistently differ from closely related undomesticated species in their functional vegetative traits. These differences may be linked to greater competitiveness and resource acquisition in the progenitors. At the same time, crop progenitors and undomesticated taxa yielded fewer fruits per plant than crop landraces. We observed these patterns across three closely related Fabaceae genera that encompass crops with distinct uses and probably also disparate domestication trajectories, grasspeas, vetches, and lentils. Taxonomic differences in growth, architecture, and fruit production were clear and may reflect the primary use of the crop. For instance, lentils (*Lens* spp.), commonly used only as a grain crop, produced a much higher number of fruits per plant than either grasspeas or vetches, whereas for the latter, a common forage and fodder crop grew clearly faster. Accordingly, inter-genus differences explained a big proportion of the observed phenotypic variation.

4.1 | Variation in functional traits across the domestication process

Even after accounting for taxonomic differences, undomesticated taxa exhibited consistent and significant deviations in vegetative traits from crop progenitors and landraces (the kind of shift represented as $\Delta\phi_D$ in Figure 1). Conversely, the number of fruits produced varied more within species between crop progenitors and landraces ($\Delta\phi_C$ in Figure 1). We take these results as evidence that evolution under domestication has had comparably limited effects on vegetative traits and stronger effects on reproductive output.

Historically, yield was considered to be the primary breeding target of the first farmers (Abbo & Gopher, 2017). However, growing evidence suggests that early selection for domestication may have favored traits that allowed plants to thrive in human-managed environments, with increases in yield emerging later as a result of human control over crop reproduction (Allaby et al., 2022; Asouti & Fuller, 2013; Zeder, 2012). Early domesticators may have preferentially used taxa that grew reliably and performed well in uniform, dense stands despite not necessarily yielding more seeds per unit area (Preece et al., 2018). These traits remained beneficial in crop fields and thus underwent minimal change over time. Meanwhile, breeding and selection efforts focused increasingly on enhancing yield (Martín-Robles et al., 2019; Preece et al., 2015). Our results support these predictions. Undomesticated relatives produced smaller, more prostrate plants with lower biomass allocation to roots and slower growth rates

compared to wild populations of crop progenitors, which exhibited a more competitive strategy overall. However, both undomesticated relatives and wild populations of crop progenitors produced fewer fruits per plant than crop accessions (landraces). We hypothesize that this increase in fruit number in landraces may have resulted from directional selection for yield during later stages of crop development.

4.2 | Effects of population density on vegetative and reproductive traits

We also observed strong effects of population density on all traits. Our experiments were designed so as to measure changes due to density rather than to its consequences (i.e., changes in resource availability; Losapio, 2023). In order to reduce competition to a minimum, fertilizer and symbiont inoculum (living soil) were dosed proportionally to density and plants were staked to avoid shading (Gedroc et al., 1996; Zélé et al., 2018). The resulting biomass production patterns were congruent with reduced or no competition: Root biomass and RMF were negatively correlated to the number of plants per pot, while vegetative aerial biomass remained relatively constant (Chen et al., 2021; Rehling et al., 2021; Robinson, 2023; Wang et al., 2014; Weiner & Freckleton, 2010). We did not control for soil volume, an important factor for root-shoot allocation. When the physical space for root development is limited, the first response is a reduction in aerial (shoot) growth (Chen et al., 2015; McCaughay & Bazzaz, 1991; Wheeldon et al., 2021). In our experiments, aerial biomass did not change across different population density levels. Therefore, we believe that the phenotypic differences we observed were caused by a response to the biotic conditions of the experiment, specifically the changes in direct plant-plant interactions brought on by variations in population density. These interactions led to reduced root growth and lower reproductive output under higher densities. These phenotypic adjustments indicate that plasticity to population structure was important in every instance.

4.3 | Phenotypic plasticity to population density and domestication

Although both domestication and population density had strong phenotypic effects, we did not observe any clear interaction between both factors. In other words, response to density was similar in undomesticated taxa, crop progenitors, and landraces. Several authors have predicted that crop response to population density should differ from that of their wild relatives (Denison, 2016; Murphy et al., 2017; Zhu & Zhang, 2013). However, we failed to detect any trend that could confirm this thesis. This result may indicate a connection between ancestral plasticity and domestication in our experimental taxa, as has been described in other systems (e.g., *teosinte-maize*; Piperno et al., 2015). Our experiment did not account for phenotypic changes imposed by recent breeding, and it is possible that Green Revolution cultigens have a different response to demographic conditions than traditional

landraces (López Pereira et al., 2017; Roucou et al., 2018; Zhu & Zhang, 2013). At this point, we cannot rule out the possibility that the response to stand density may vary in modern cultivars. Future research should evaluate the potential effect of the different stages of artificial selection on crop plasticity to population density including wild taxa, landraces, and modern cultivars.

5 | CONCLUSIONS

Crop development processes are complex and case dependent. As a result, existing landraces are likely reflective of different selection pathways across taxa and cultivars. However, our results indicate that early selection for domestication might have consistently favored taxa with vegetative phenotypes particularly suited to growth in dense, monospecific populations and more effective in resource capture. Following initial domestication, selection may have had a strong effect on reproductive traits, leading to gains in yield.

AUTHOR CONTRIBUTIONS

Rafael Rubio de Casas and Ruben Milla formulated the original concept. Rafael Rubio de Casas, Francisco J. Ocaña-Calahorro, and Irene Martín-Brull designed and carried out the experiments. Francisco J. Ocaña-Calahorro and Irene Martín-Brull collected and processed the data. Rafael Rubio de Casas conducted the statistical analyses. All authors contributed to the different iterations of the manuscript and approved the final version.

ACKNOWLEDGMENTS

The authors thank Nuria García Díaz, Luis García García, and Jonathan Abraham Parrilla for their help generating and cleaning the data. This work was made possible by the financial support of the Spanish Ministry of Economy and Competitiveness (grant no. CGL2016-79950-R). Funding for open access: Universidad de Granada / CBUA.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

ORCID

Rafael Rubio de Casas  <https://orcid.org/0000-0003-4276-4968>

Irene Martín-Brull  <https://orcid.org/0000-0003-2357-0367>

Ruben Milla  <https://orcid.org/0000-0001-8912-4373>

Francisco J. Ocaña-Calahorro  <https://orcid.org/0000-0003-1048-9746>

REFERENCES

- Abbo, S., & Gopher, A. (2017). Near eastern plant domestication: A history of thought. *Trends in Plant Science*, 22, 491–511. <https://doi.org/10.1016/j.tplants.2017.03.010>

- Abbo, S., Van-Oss, R., Gopher, A., Saranga, Y., Ofner, R., & Peleg, Z. (2014). Plant domestication versus crop evolution: A conceptual framework for cereals and grain legumes. *Trends in Plant Science*, 19, 351–360. <https://doi.org/10.1016/j.tplants.2013.12.002>
- Allaby, R. G., Stevens, C. J., Kistler, L., & Fuller, D. Q. (2022). Emerging evidence of plant domestication as a landscape-level process. *Trends in Ecology & Evolution*, 37, 268–279. <https://doi.org/10.1016/j.tree.2021.11.002>
- Arranz-Otaegui, A., González Carretero, L., Roe, J., & Richter, T. (2018). “Founder crops” v. wild plants: Assessing the plant-based diet of the last hunter-gatherers in southwest Asia. *Quaternary Science Reviews*, 186, 263–283. <https://doi.org/10.1016/j.quascirev.2018.02.011>
- Asouti, E., & Fuller, D. Q. (2013). A contextual approach to the emergence of agriculture in southwest Asia. *Current Anthropology*, 54, 299–345. <https://doi.org/10.1086/670679>
- Becker, C., Berthomé, R., Delavault, P., Flutre, T., Fréville, H., Gibot-Leclerc, S., Le Corre, V., Morel, J.-B., Moutier, N., Muñoz, S., Richard-Molard, C., Westwood, J., Courty, P. E., de Saint Germain, A., Louarn, G., & Roux, F. (2023). The ecologically relevant genetics of plant-plant interactions. *Trends in Plant Science*, 28, 31–42. <https://doi.org/10.1016/j.tplants.2022.08.014>
- Bilas, R. D., Bretman, A., & Bennett, T. (2021). Friends, neighbours and enemies: An overview of the communal and social biology of plants. *Plant, Cell & Environment*, 44, 997–1013. <https://doi.org/10.1111/pce.13965>
- Blanca, G., Cabezudo, B., Cueto, M., Salazar, C., & Morales, T. C. (2009). *Flora vascular de Andalucía oriental*. Junta de Andalucía.
- Bode, L. J. K., Livarda, A., & Jones, M. D. (2022). Plant gathering and people-environment interactions at Epipalaeolithic Kharaneh IV, Jordan. *Vegetation History and Archaeobotany*, 31, 85–96. <https://doi.org/10.1007/s00334-021-00839-w>
- Buerkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Callaway, R., Pennings, S. C., & Richards, C. L. (2003). Phenotypic plasticity and interactions among plants. *Ecology*, 84, 1115–1128. [https://doi.org/10.1890/0012-9658\(2003\)084\[1115:PPAIA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1115:PPAIA]2.0.CO;2)
- Castroviejo, S. (Ed.). (2020). *Flora ibérica: Plantas vasculares de la Península Ibérica e Islas Baleares*. CSIC, Consejo Superior de Investigaciones Científicas.
- Chen, B. J. W., During, H. J., Vermeulen, P. J., de Kroon, H., Poorter, H., & Anten, N. P. R. (2015). Corrections for rooting volume and plant size reveal negative effects of neighbour presence on root allocation in pea. *Functional Ecology*, 29, 1383–1391. <https://doi.org/10.1111/1365-2435.12450>
- Chen, B. J. W., Huang, L., During, H. J., Wang, X., Wei, J., & Anten, N. P. R. (2021). No neighbour-induced increase in root growth of soybean and sunflower in mesh-divider experiments after controlling for nutrient concentration and soil volume. *AoB Plants*, 13, plab020. <https://doi.org/10.1093/aobpla/plab020>
- Clement, C. R. (2022). Control is not necessary in domestication. *Trends in Ecology & Evolution*, 37, 823–824.
- Crick, J. C., & Grime, J. P. (1987). Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *The New Phytologist*, 107, 403–414. <https://doi.org/10.1111/j.1469-8137.1987.tb00192.x>
- Cubero, J. I., Moreno, M. T., & Nadal, S. (2004). *Las leguminosas Grano en la agricultura moderna*. Mundi-Prensa.
- Cunniff, J., Wilkinson, S., Charles, M., Jones, G., Rees, M., & Osborne, C. P. (2014). Functional traits differ between cereal crop progenitors and other wild grasses gathered in the neolithic Fertile Crescent. *PLoS ONE*, 9, e87586. <https://doi.org/10.1371/journal.pone.0087586>
- De Wet, J. M. J., & Harlan, J. R. (1975). Weeds and domesticates: Evolution in the man-made habitat. *Economic Botany*, 29, 99–108. <https://doi.org/10.1007/BF02863309>

- Denison, R. F. (2016). *Darwinian agriculture: How understanding evolution can improve agriculture*. Princeton University Press.
- Donald, C. M. (1968). The breeding of crop ideotypes. *Euphytica*, 17, 385–403. <https://doi.org/10.1007/BF00056241>
- Ferrari, S., & Cribari-Neto, F. (2004). Beta regression for modelling rates and proportions. *Journal of Applied Statistics*, 31, 799–815. <https://doi.org/10.1080/0266476042000214501>
- Fréville, H., Montazeaud, G., Forst, E., David, J., Papa, R., & Tenailon, M. I. (2022). Shift in beneficial interactions during crop evolution. *Evolutionary Applications*, 15, 905–918. <https://doi.org/10.1111/eva.13390>
- Fukano, Y., Guo, W., Uchida, K., & Tachiki, Y. (2020). Contemporary adaptive divergence of plant competitive traits in urban and rural populations and its implication for weed management. *Journal of Ecology*, 108, 2521–2530. <https://doi.org/10.1111/1365-2745.13472>
- Fuller, D. Q., Denham, T., & Allaby, R. (2023). Plant domestication and agricultural ecologies. *Current Biology*, 33, R636–R649. <https://doi.org/10.1016/j.cub.2023.04.038>
- Gabry, J., & Mahr, T. (2022). bayesplot: Plotting for Bayesian models.
- Gedroc, J. J., McConnaughay, K. D. M., & Coleman, J. S. (1996). Plasticity in root/shoot partitioning: Optimal, ontogenetic, or both? *Functional Ecology*, 10, 44–50. <https://doi.org/10.2307/2390260>
- Geissinger, E. A., Khoo, C. L. L., Richmond, I. C., Faulkner, S. J. M., & Schneider, D. C. (2022). A case for beta regression in the natural sciences. *Ecosphere*, 13, e3940. <https://doi.org/10.1002/ecs2.3940>
- Gersani, M., Brown, J. S., O'Brien, E. E., Maina, G. M., & Abramsky, Z. (2001). Tragedy of the commons as a result of root competition. *Journal of Ecology*, 89, 660–669. <https://doi.org/10.1046/j.0022-0477.2001.00609.x>
- Gómez-Fernández, A., Aranda, I., & Milla, R. (2024). Early human selection of crops' wild progenitors explains the acquisitive physiology of modern cultivars. *Nature Plants*, 10, 25–36. <https://doi.org/10.1038/s41477-023-01588-6>
- Gremillion, K. J., Barton, L., & Piperno, D. R. (2014). Particularism and the retreat from theory in the archaeology of agricultural origins. *Proceedings of the National Academy of Sciences*, 111, 6171–6177. <https://doi.org/10.1073/pnas.1308938110>
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 111, 1169–1194. <https://doi.org/10.1086/283244>
- Grime, J. P., Campbell, B. D., Mackey, J. M. L., & Crick, J. C. (1991). Root plasticity, nitrogen capture, and competitive ability. In D. Atkinson (Ed.), *Plant root growth: An ecological perspective*. Blackwell Scientific Publications.
- Lambein, F., Travella, S., Kuo, Y.-H., Van Montagu, M., & Heijde, M. (2019). Grass pea (*Lathyrus sativus* L.): Orphan crop, nutraceutical or just plain food? *Planta*, 250, 821–838. <https://doi.org/10.1007/s00425-018-03084-0>
- López Pereira, M., Sadras, V. O., Batista, W., Casal, J. J., & Hall, A. J. (2017). Light-mediated self-organization of sunflower stands increases oil yield in the field. *Proceedings of the National Academy of Sciences*, 114, 7975–7980. <https://doi.org/10.1073/pnas.1618990114>
- Losapio, G. (2023). Contextualizing the ecology of plant–plant interactions and constructive networks. *AoB Plants*, 15, plad035. <https://doi.org/10.1093/aobpla/plad035>
- Mabry, M. E., Turner-Hissong, S. D., Gallagher, E. Y., McAlvay, A. C., An, H., Edger, P. P., Moore, J. D., Pink, D. A. C., Teakle, G. R., Stevens, C. J., & Barker, G. (2021). The evolutionary history of wild, domesticated, and feral *Brassica oleracea* (Brassicaceae). *Molecular Biology and Evolution*, 38, 4419–4434. <https://doi.org/10.1093/molbev/msab183>
- Martín-Robles, N., Morente-López, J., Freschet, G. T., Poorter, H., Roumet, C., & Milla, R. (2019). Root traits of herbaceous crops: Pre-adaptation to cultivation or evolution under domestication? *Functional Ecology*, 33, 273–285. <https://doi.org/10.1111/1365-2435.13231>
- McConnaughay, K. D. M., & Bazzaz, F. A. (1991). Is physical space a soil resource? *Ecology*, 72, 94–103. <https://doi.org/10.2307/1938905>
- Milla, R. (2023). Phenotypic evolution of agricultural crops. *Functional Ecology*, 37, 976–988. <https://doi.org/10.1111/1365-2435.14278>
- Murphy, G. P., Van Acker, R., Rajcan, I., & Swanton, C. J. (2017). Identity recognition in response to different levels of genetic relatedness in commercial soya bean. *Royal Society Open Science*, 4, 160879. <https://doi.org/10.1098/rsos.160879>
- Novoplansky, A. (2009). Picking battles wisely: Plant behaviour under competition. *Plant, Cell & Environment*, 32, 726–741. <https://doi.org/10.1111/j.1365-3040.2009.01979.x>
- Padilla, F. M., Mommer, L., de Caluwe, H., Smit-Tiekstra, A. E., Wagemaker, C. A. M., Ouborg, N. J., & de Kroon, H. (2013). Early root overproduction not triggered by nutrients decisive for competitive success belowground. *PLoS ONE*, 8, e55805. <https://doi.org/10.1371/journal.pone.0055805>
- Piperno, D. R., Holst, I., Winter, K., & McMillan, O. (2015). Teosinte before domestication: Experimental study of growth and phenotypic variability in Late Pleistocene and early Holocene environments. *Quaternary International*, 363, 65–77. <https://doi.org/10.1016/j.quaint.2013.12.049>
- Preece, C., Clamp, N. F., Warham, G., Charles, M., Rees, M., Jones, G., & Osborne, C. P. (2018). Cereal progenitors differ in stand harvest characteristics from related wild grasses. *Journal of Ecology*, 106, 1286–1297. <https://doi.org/10.1111/1365-2745.12905>
- Preece, C., Livarda, A., Wallace, M., Martin, G., Charles, M., Christin, P.-A., Jones, G., Rees, M., & Osborne, C. P. (2015). Were Fertile Crescent crop progenitors higher yielding than other wild species that were never domesticated? *New Phytologist*, 207, 905–913. <https://doi.org/10.1111/nph.13353>
- Purugganan, M. D. (2022). What is domestication? *Trends in Ecology & Evolution*, 37, 663–671. <https://doi.org/10.1016/j.tree.2022.04.006>
- R Core Development Team. (2023). R: A language and environment for statistical computing.
- Rehling, F., Sandner, T. M., & Matthies, D. (2021). Biomass partitioning in response to intraspecific competition depends on nutrients and species characteristics: A study of 43 plant species. *Journal of Ecology*, 109, 2219–2233. <https://doi.org/10.1111/1365-2745.13635>
- Robinson, D. (2023). OPT-ing out: Root–shoot dynamics are caused by local resource capture and biomass allocation, not optimal partitioning. *Plant, Cell & Environment*, 46, 3023–3039. <https://doi.org/10.1111/pce.14470>
- Roucou, A., Violle, C., Fort, F., Roumet, P., Ecnart, M., & Vile, D. (2018). Shifts in plant functional strategies over the course of wheat domestication. *Journal of Applied Ecology*, 55, 25–37. <https://doi.org/10.1111/1365-2664.13029>
- Sánchez-Martín, R., Gómez, J. M., Cheptou, P.-O., & Rubio de Casas, R. (2021). Differences in seed dormancy and germination in amphicarpic legumes: Manifold bet-hedging in space and time. *Journal of Plant Ecology*, 14, 662–672. <https://doi.org/10.1093/jpe/rtab019>
- Schaefer, H., Hechenleitner, P., Santos-Guerra, A., de Sequeira, M. M., Pennington, R. T., Kenicer, G., & Carine, M. (2012). Systematics, biogeography, and character evolution of the legume tribe Fabaeae with special focus on the middle-Atlantic island lineages. *BMC Evolutionary Biology*, 12, 250. <https://doi.org/10.1186/1471-2148-12-250>
- Spengler, R. N. I., & Mueller, N. G. (2019). Grazing animals drove domestication of grain crops. *Nature Plants*, 5, 656–662. <https://doi.org/10.1038/s41477-019-0470-4>
- Terrell, J. E., Hart, J. P., Barut, S., Cellinese, N., Curet, A., Denham, T., Kusimba, C. M., Latinis, K., Oka, R., Palka, J., Pohl, M. E. D., Pope, K. O., Williams, P. R., Haines, H., & Staller, J. E. (2003). Domesticated landscapes: The subsistence ecology of plant and animal domestication. *Journal of Archaeological Method and Theory*, 10, 323–368. <https://doi.org/10.1023/B:JARM.0000005510.54214.57>

- Varro, M. T. (37 BCE) *Rerum rusticarum libri tres* (Jl Cubero, Tran.). Junta de Andalucía. Consejería de Agricultura y Pesca.
- Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27, 1413–1432.
- Wang, P., Weiner, J., Cahill, J. F. Jr., Zhou, D. W., Bian, H. F., Song, Y. T., & Sheng, L. X. (2014). Shoot competition, root competition and reproductive allocation in *Chenopodium acuminatum*. *Journal of Ecology*, 102, 1688–1696.
- Weide, A., Green, L., Hodgson, J. G., Douché, C., Tengberg, M., Whitlam, J., Dovrat, G., Osem, Y., & Bogaard, A. (2022). A new functional ecological model reveals the nature of early plant management in southwest Asia. *Nature Plants*, 8, 623–634.
- Weiner, J. (2019). Looking in the wrong direction for higher-yielding crop genotypes. *Trends in Plant Science*, 24, 927–933.
- Weiner, J., & Freckleton, R. P. (2010). Constant final yield. *Annual Review of Ecology, Evolution, and Systematics*, 41, 173–192.
- Wheeldon, C. D., Walker, C. H., Hamon-Josse, M., & Bennett, T. (2021). Wheat plants sense substrate volume and root density to proactively modulate shoot growth. *Plant, Cell & Environment*, 44, 1202–1214.
- Wickham, H. (2016). ggplot2: Elegant graphics for data analysis.
- Zeder, M. A. (2012). The broad Spectrum revolution at 40: Resource diversity, intensification, and an alternative to optimal foraging explanations. *Journal of Anthropological Archaeology*, 31, 241–264.
- Zélé, F., Magalhães, S., Kéfi, S., & Duncan, A. B. (2018). Ecology and evolution of facilitation among symbionts. *Nature Communications*, 9, 4869.
- Zhang, R., & Tielbörger, K. (2020). Density-dependence tips the change of plant–plant interactions under environmental stress. *Nature Communications*, 11, 2532.
- Zhu, L., & Zhang, D.-Y. (2013). Donald's ideotype and growth redundancy: A pot experimental test using an old and a modern spring wheat cultivar. *PLoS ONE*, 8, e70006.
- Zohary, D., Weiss, E., & Hopf, M. (2012). Pulses. In D. Zohary, M. Hopf, & E. Weiss (Eds.), *Domestication of plants in the old world: The origin and spread of domesticated plants in southwest Asia, Europe, and the Mediterranean Basin*. Oxford University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: de Casas, R. R., Martín-Brull, I., Milla, R., & Ocaña-Calahorra, F. J. (2024). Selection for domestication favored taxa characterized by fast growth and tolerance of high intraspecific density. *Plants, People, Planet*, 1–11. <https://doi.org/10.1002/ppp3.10596>