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# **Experimental and modelling evidence for the evolution of competitiveness during wheat domestication**

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## Summary

Crop domestication involved adaptation of wild plants to human exploitation<sup>1-4</sup>, but the underlying selection mechanisms remain unclear<sup>2,4</sup>. Archaeological evidence from the best-studied regions shows domestication occurring across a diffuse region and protracted period of at least 1,000-2,000 years<sup>2,5-7</sup>, consistent with a co-evolutionary process<sup>2,3</sup>. For seed enlargement, both theory<sup>2,6,8-10</sup> and empirical evidence<sup>11-13</sup> indicate an unintentional, evolutionary mechanism, potentially acting via an ecological process such as competition<sup>14-16</sup>, but this remains unproven. Here, we used real and virtual experiments to test the hypothesis that cultivation selected for stronger competitive ability in wheats. First, we compared three independent domestication events across wheat species, showing that domesticated landraces were stronger competitors than their wild counterparts. Model simulations reproduced this finding, showing that competitiveness increased through larger, more erect leaves, and greater apical dominance. A second experiment compared wild, landrace, and elite durum wheats, finding that stronger competitiveness arose early during domestication, but has been reversed by modern breeding. Simulations showed that weaker competitiveness in modern varieties arose from smaller leaves and shorter internodes. Our work indicates that competition selected for domestication traits responsible for wheat canopy growth and architecture, resulting in competitive landrace phenotypes unsuitable for conventional modern agriculture.

199 words

## Results

### Did competitive ability change during crop domestication?

We investigated the evolutionary history of competitiveness in wheat by carrying out two experiments (Figure S1). In the first, we made an interspecific comparison of competitiveness across three independent domestication events in wheat (i.e. emmer, einkorn and Timopheev's wheat), comparing wild plant accessions (W) with early diverging domesticated landraces (EL) in each case (Figure S1; Table S1). Competitiveness was quantified by measuring how the shoot biomass of target plants decreased in response to a range of neighbour densities, applied in a reciprocal design (Figure S1).

Early diverging landraces were stronger competitors in terms of biomass gain across all three domestication events sampled in the interspecific experiment (Figure 1). Across each comparison, the growth of wild wheats was more impacted by interspecific competition from domesticated wheats than *vice versa*. Competitive interactions were density-dependent, such that the relative difference in biomass between domesticated and wild forms increased with more neighbours (Figure 1A). This impact of competition was observed largely in leaf and stem biomass rather than inflorescences (Figure S2), implying that competitive effects occurred during vegetative rather than reproductive growth. The higher competitiveness of early diverging landraces did not translate generally into height (Figure 1B), but did significantly affect tillering; as neighbor density increased, domesticated forms reduced tillering to a lesser extent than wild plants (Figure 1C).

## **Which traits were responsible for changes in competitiveness?**

To gain mechanistic insight into the traits responsible for changes in competitiveness, we simulated each experiment using a functional-structural plant (FSP) model<sup>17</sup>. We first used experimental trait measurements to parameterize the FSP model, to simulate the experimental outcomes on plant performance. Next, we carried out sensitivity analyses, by varying the model parameters that differed between accessions, to understand which traits were responsible for the competitive outcomes.

The FSP model provided *in silico* support for the experimental findings and uncovered trait-based mechanisms. Simulated competitive differences increased with neighbour density in all three comparisons of wild and domesticated forms, with the domesticated wheats being increasingly stronger competitors than the wild ones at higher densities (Figure 2A-C; Table S2). In a subsequent sensitivity analysis, we switched trait values one-at-a-time to test which of them contributed to this outcome. In Figure 2D-O, a loss or reversal of the positive slope indicates that a particular trait played a role, with reversal indicating a stronger influence on competitiveness.

Leaf insertion angle was the most influential trait (Figure 2D-F), such that steeper leaf angles made domesticated plants stronger competitors at high neighbourhood densities by enabling them to overtop neighbours during vegetative growth. The other traits acted differently across domestication events, either reversing the advantage of domestication, or removing that advantage to make landraces similarly competitive to wild wheats. A greater potential leaf biomass (i.e. maximum leaf size without resource limitation) was important for light capture in emmer and einkorn, reversing the competitive advantage of landraces over wild plants (Figure 2H-I). Reduced internode length/biomass ratio and greater apical dominance were also

important in these species, reversing the competition results in a density-independent manner (Figures. 2K-L, 2N-O). Competitive outcomes in Timopheev's wheat arose from a combination of several weaker trait effects, which each eliminated the advantages of EL in the sensitivity analysis and did not make W stronger. In this species, greater leaf biomass, apical dominance and internode length/biomass ratio all contributed to competitive advantages of the EL by enabling it to become taller than W (Figure 2G, J, M; Table S2).

The other two traits that distinguished wild and domesticated forms had limited effects across the three domestication events. The number of phytomers on the main stem (i.e. modules comprised of leaves plus internode) had no influence on competitive outcomes (Figure S3G-I), while potential internode biomass was important for Timopheev's wheat (Figure S3D), with a smaller impact in einkorn (Figure S3E), and no effect in emmer (Figure S3F).

#### **At what stage during crop history did the changes in competitiveness occur?**

A second experiment focused on an in-depth intraspecific comparison within one of these domestication events, evaluating how competitive ability changed during emmer wheat diversification, by comparing multiple accessions of wild progenitors (W), early diverging (emmer) landraces (EL), late diverging (durum) landraces (LL) and improved durum wheats (I) (Figure S1; Table S1). Durum landraces are free-threshing forms derived from domesticated emmer landraces, while improved durum varieties were produced by modern selective breeding programmes. To ensure a manageable design for the four-way comparison among multiple accessions, we measured competition in the intraspecific experiment by investigating how the shoot and root trait values of target plants decreased in response to competition with a common weed (*Lolium multiflorum*) (Figure S1).

The intraspecific experiment showed how the competitiveness of wheats derived from domesticated emmer changed during landrace improvement and modern breeding of elite varieties (Figure 3). Early diverging landraces (*T. dicoccum*, EL) were all hulled emmer wheats, while late diverging landraces (*T. durum*, LL) were all naked-grained durum wheats. In agreement with the interspecific experiment, EL were more competitive than wild emmer (*T. dicoccoides*, W) (Figure 3A-B). However, subsequent landrace improvement and modern breeding reduced competitiveness again, making improved modern varieties (*T. durum*, I) less competitive than EL (Figure 3A-B). Despite this reduction, modern I varieties remained stronger competitors than wild W forms (Figure 3A-B). There was significant variation in competitiveness among the eight EL and eight LL accessions, with at least one EL accession no more competitive than the wild type (Figure S4).

The experiment elucidated a number of traits consistently associated with the biomass response to domestication, and eliminated others that were not. In particular, relative growth rate (RGR) increased consistently when faced with competition (Figure 3C). Elite I wheats had the fastest RGR under competition (Figure 3C). However, EL competitiveness also arose from a larger leaf canopy area, achieved through greater allocation to leaf biomass (LMF; Figure 3E) and a smaller investment in leaf biomass for a given leaf area (LMA; Figure 3D). Conversely, LL and I varieties of durum achieved greater competitiveness than wild forms through greater biomass allocation to stems (SMF; Figure 3F).

FSP model simulations reproduced the competitive ranking of the intraspecific experiment, such that EL were the strongest competitors, followed by LL, I, and finally W (Figure 4A). We inferred the traits responsible using a sensitivity analysis, in which all traits were held constant at their wild values, except for a target trait, which was given values corresponding to each domesticated type. In the corresponding plots (Figure 4B-F), positive responses to competition

show that a target trait confers stronger competitive ability, while negative responses show the trait undermines competition.

Sensitivity analysis showed that competitive ability in EL arose from the larger potential size of individual leaves (Figure 4D) and lower LMA (Figure 4E), consistent with experimental inferences (Figure 3D, E) and the interspecific experiment (Figure 2I). Larger leaves were less important for LL and I (Figure 4D), while LMA played a role for LL, but not I (Figure 4E). Simulations also revealed important roles in competition for potential internode biomass (Figure 4C) and individual seed mass (Figure 4F). However, in contrast to the interspecific experiment (Figure 2M, N, O), apical dominance had no influence (Figure 4G). For LL and I, higher values of potential flower biomass undermined competitive ability (Figure 4B), consistent with theory about the impacts of selective breeding on internal resource allocation between grains and leaves.

## **Discussion**

### **Competition as a domestication mechanism**

Scholars have debated the causes of crop domestication for decades, with a spectrum of opinion between positions considering domestication to be either the result of human choice and manipulation, or the unintended outcome of coevolution between humans and plants through natural selection (reviewed by ref. <sup>18</sup>). Various mechanisms have been proposed to explain how domestication could have arisen as an unintended outcome of co-evolution between people and plants. Notable among these are mutualistic feedback loops<sup>19,20</sup>, reciprocal innovations and behavioral ‘traps’<sup>8</sup>, and ecological release<sup>4,21</sup>.

The action of common underlying selection mechanisms is implied by the convergence of domestication phenotypes across multiple crop species, although these evolved on different timescales in different species<sup>6,22,23</sup>. For example, many cereal species are characterised by the loss of dispersal traits and seed dormancy, greater seed numbers, enlarged seeds and reduced branching in comparison with their wild relatives<sup>1</sup>. Defined by Hammer<sup>24</sup> as the ‘domestication syndrome’, these observations have more recently been augmented with quantitative data, including archaeobotanical evidence, on a greater range of species<sup>6,9</sup>. Competition within crop stands during seedling establishment has long been hypothesized to cause selection for larger seeds and early vigour<sup>1</sup>, and arguments for increased seed size as an unintentional change during domestication have been proposed<sup>2,6,8–10</sup>. Experiments and model simulations focusing on seed enlargement have inferred an unintentional evolutionary process<sup>11–13</sup>, potentially acting via an ecological process such as competition<sup>14,15,25</sup>.

Our empirical and modelling experiments showed that competitiveness increased across three independent domestication events in wheat (emmer, einkorn, Timopheev’s wheat). Focused analysis of the intraspecific diversification in the emmer lineage indicated that greater competitiveness is present in both early diverging hulled emmer landraces (EL) and later diverging naked durum landraces (LL). This indicates that increased competitiveness evolved either once during the process of emmer wheat domestication, before the divergence of durum, or multiple times in parallel during emmer and durum landrace diversification.

Domestication is documented in the archaeological record as a loss of grain shattering, which began in wheats well before 10,000 yrs BP<sup>22,26</sup>, but was not fixed (i.e. >90% non-shattering) in einkorn until 9,000 yrs BP<sup>6</sup>, emmer 8,500 yrs BP<sup>6</sup> and Timopheev’s wheat 8,000 yrs BP<sup>23</sup>. Since free-threshing forms of durum are first found by 9,000 yrs BP<sup>27</sup>, our data therefore imply that competitiveness in vegetative growth habit may have evolved earlier than non-shattering,

and under different selection pressures. The hypothesis that different selection pressures acted at different times during domestication is supported by archaeological evidence of seed enlargement, which also begins earlier than non-shattering.

Previous work has hypothesised seedling competition as a driver of seed enlargement during domestication<sup>1,2,8–10</sup> and, consistent with this explanation, individual seed mass was important for the competitive abilities of emmer and durum wheats in the intraspecific experiment. However, our results from the interspecific experiment cannot be explained by this mechanism, since we germinated and established seedlings in isolation before transplanting them into the density gradient, and the model reproduced the effects of competition without any differences in seed size. Instead, competition during the established phase (i.e. after seedling establishment) is sufficient to explain the observed effects.

Selection during the established phase could have operated via two mechanisms, which are not mutually exclusive. First, the cultivation of genetically diverse populations at relatively low densities could have led to natural selection for stronger competitors, which reached a larger final size and contributed more seeds to the next generation<sup>1,14</sup>. Competition would have been intensified by soil improvement through organic matter amendments and water management during the Neolithic diversification of hulled and naked wheats<sup>8,28–30</sup>. Secondly, if farmers preferentially saved seed from large plants for the next generation, the association between plant size and competitive outcomes could have indirectly selected for vegetative traits promoting competitive ability. In this case, although seed collection from the most favoured individuals was deliberate, the associated selection for traits conferring competitive ability was unintentional<sup>31,32</sup>.

## **Implications for crop improvement**

Competition within cereal stands has been discussed widely in the context of modern crop improvement. Notably, Donald argued that yield is maximized when plants are weak competitors, since intense competition depresses reproductive allocation within genetically uniform monocultures<sup>33</sup>. Mechanistically, this arises because investment in greater leaf area and taller stems trades-off against grain production<sup>34</sup>. The theoretical phenotype for maximal yield should have the genetic potential to reach a large plant size, a minimal ecological neighbourhood for competition, and maximal efficiency of resource-conversion to yield<sup>35</sup>. However, selection of the most productive individuals in a genetically mixed stand favours individual fitness at the expense of population yield<sup>33</sup>.

Increasing planting densities made an important contribution to raising cereal yields during the Green Revolution, and necessitated breeding of shorter plants with smaller, more erect leaves, which invest proportionately more biomass into grain<sup>36</sup>. This limited competition among individuals within crop populations<sup>37</sup>, and our work showed a corresponding weakening of competitive ability in improved durum wheat varieties, although they remained more competitive than their wild progenitors.

## **Mechanisms responsible for competition**

Our experiments showed that the stronger competitiveness of domesticated forms was caused by several morphological traits, with both commonalities and differences across independent domestication events. Steeper leaf insertion angle had substantial effects across all species, while leaf biomass, apical dominance and internode length-to-mass ratio were less consistently important. In durum landraces and modern varieties, competitiveness was diminished by

decreasing leaf and increasing flower sizes. Breeding for reduced competitiveness is usually discussed in terms of steeper leaf angles leading to more compact growth forms with a smaller ecological neighbourhood<sup>33,34</sup>. Our work shows an unexpected interaction between leaf angle and leaf size, such that steeper leaves only limit competition when paired with small leaves, while the opposite occurs when leaves are large.

The mechanistic basis for leaf insertion angle is well-understood for cereals such as wheat. Leaf angle is set during development of the joint between leaf lamina and sheath<sup>38,39</sup>, which is regulated by auxin and brassinosteroids<sup>40</sup>. Consequently, leaf angle is influenced by auxin and brassinosteroid biosynthesis<sup>41,42</sup>, and the signaling controlling these plant growth regulators<sup>40,43</sup>. The potential size of wheat leaves is also under genetic control but, in common with many size-related traits, is influenced by multiple genes with small effects<sup>44</sup>. Since the key traits responsible for the evolution of competitive ability in wheat are highly polygenic, we hypothesize that evolution is likely to have been convergent, involving different genes in each wheat lineage. Mapping populations based on natural or artificial crosses between wild and domesticated varieties<sup>45–48</sup> offer the potential to establish genes responsible in each case.

Competition occurred in established plants among shoots for light rather than among roots for nutrients. Although wild wheats invest significantly in roots<sup>49</sup> to counteract soil depletion of nutrients and water, domesticated wheats evolved in cultivated soils in which people maintained soil quality through organic matter additions and irrigation<sup>28–30</sup>. However, in our experiments, wild forms were always weaker competitors than their domesticated counterparts, suggesting that root competition was not decisive. Indeed, our modelling reproduced experimental outcomes without simulating nutrient fluxes or root competition. Instead, across multiple domestication events, competitiveness arose from traits that preempted aboveground space and light interception by producing taller vegetative shoots constructed from steeper,

larger leaves and/or taller, more robust stems<sup>50</sup>. Since comparisons were made after controlling for biomass, these traits increased the extent of the ecological neighbourhood for domesticated wheats relative to wild plants, independently of plant size.

## **Conclusions**

Our results provide a comprehensive picture of the changes in competitiveness during the evolution of domesticated wheats. Real and virtual experiments indicate that competition caused convergent trait evolution during wheat domestication, leading to landrace phenotypes unsuitable for modern conventional agriculture. The work provides empirical evidence for natural selection or indirect selection as mechanisms responsible for competition-related vegetative traits in wheat.

## 260    **Resource Availability**

### 261    **Lead contact**

262    Further information and requests for resources should be directed to and will be fulfilled by the  
263    lead contact, Colin Osborne ([c.p.osborne@sheffield.ac.uk](mailto:c.p.osborne@sheffield.ac.uk)).

264

### 265    **Materials availability**

266    This study did not generate new, unique reagents.

267

### 268    **Data and code availability**

269    The original, unprocessed experimental and modelling data are available to download from  
270    Mendeley Data DOI:10.17632/dpwyvvt66j.1. The code needed to run the FSP model is  
271    available from: [https://git.wur.nl/jochemevers1/FSPM\\_BASIC](https://git.wur.nl/jochemevers1/FSPM_BASIC). The code used to analyse the  
272    data reported in this paper is available from the lead contact upon request.

273

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281

## 282 **Author contributions**

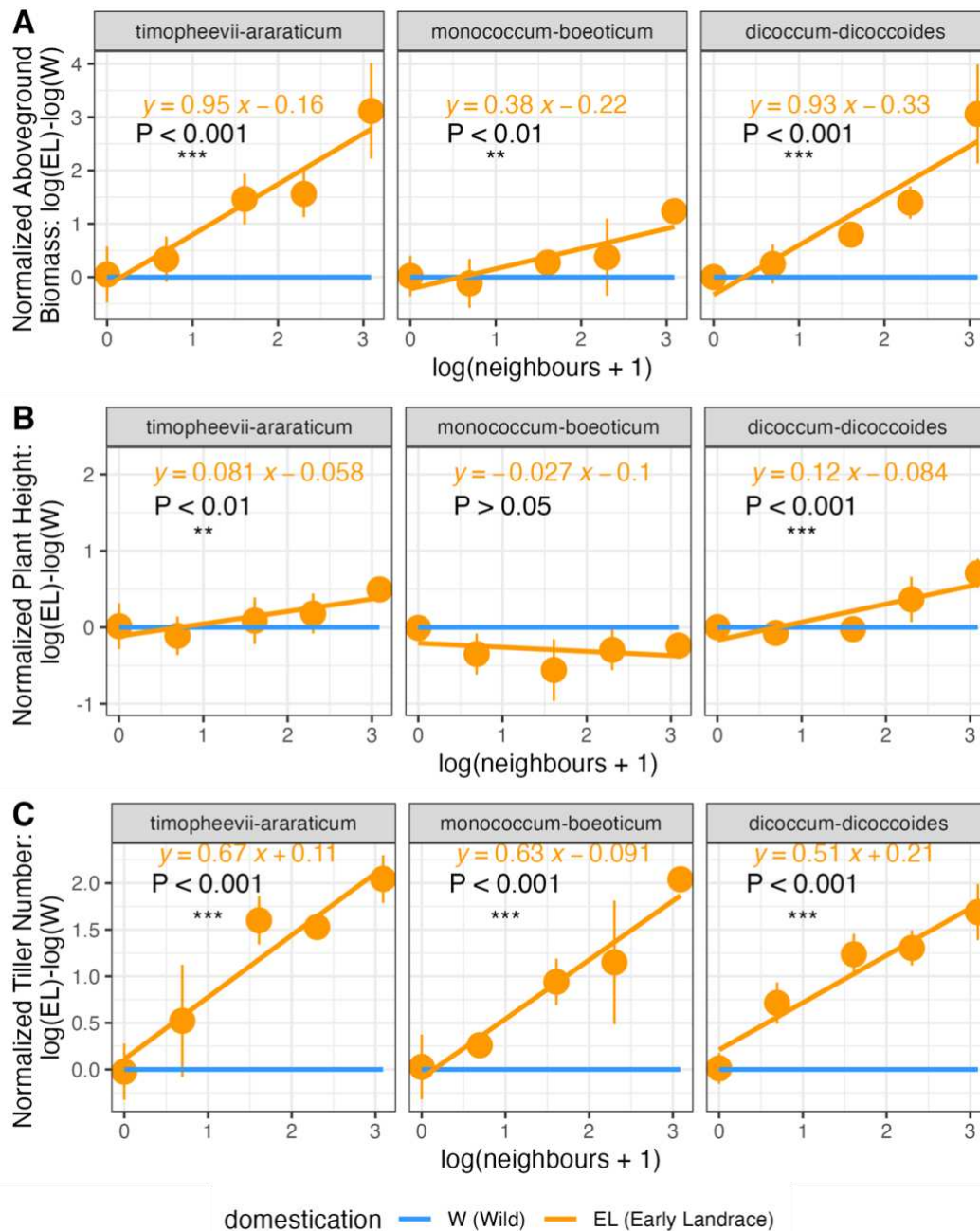
283 YS, AGF, RM and CO wrote the first draft of manuscript. YS, AGF, RF, RM and CO designed  
284 plant growth experiments. YS, JE and CO designed computer simulation experiments. YS and  
285 AGF carried out the experiments, collected and analysed data. All authors contributed to data  
286 interpretation and revisions to the manuscript.

287

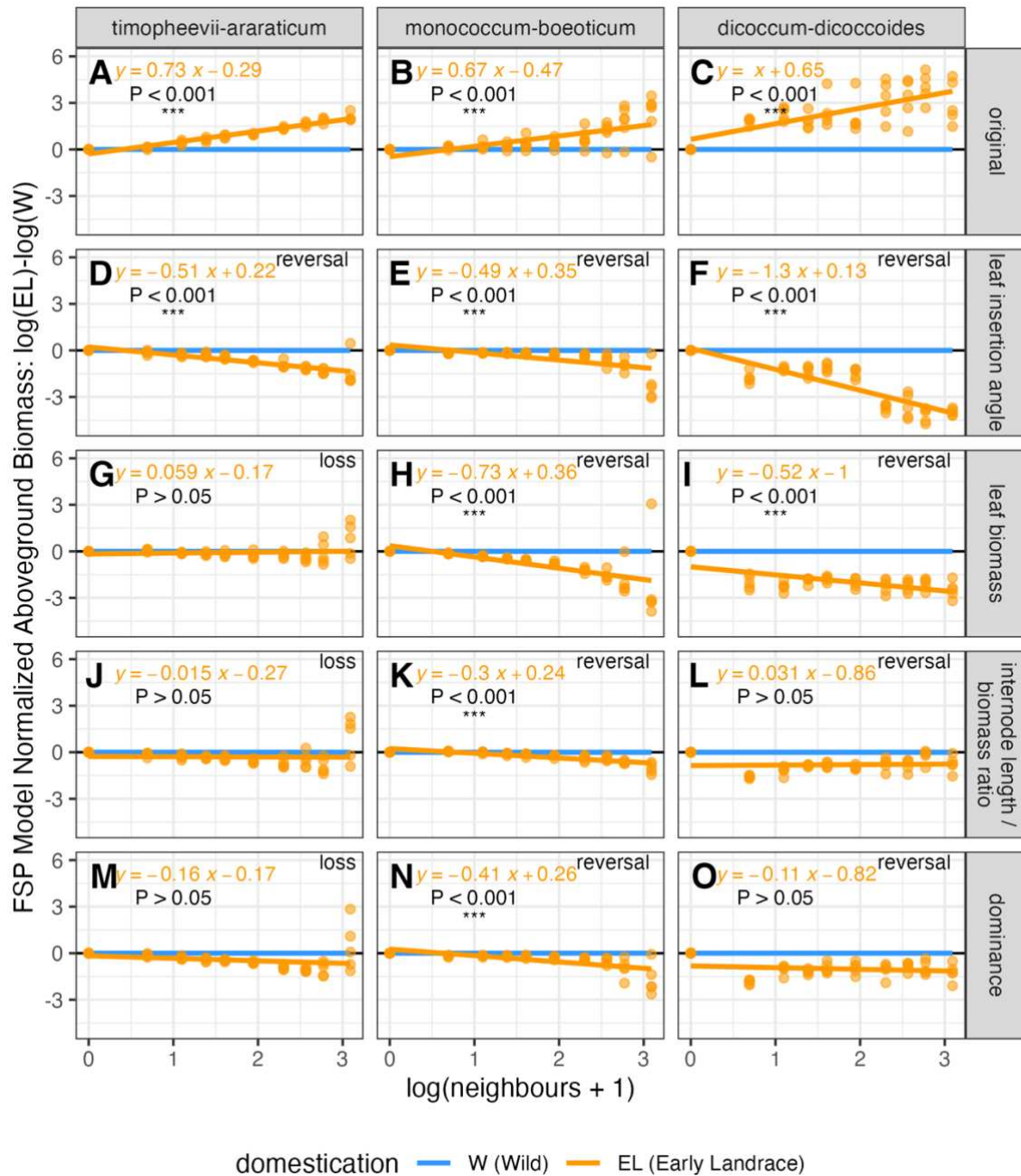
## 288 **Declaration of Interests**

289 The authors declare no competing interests.

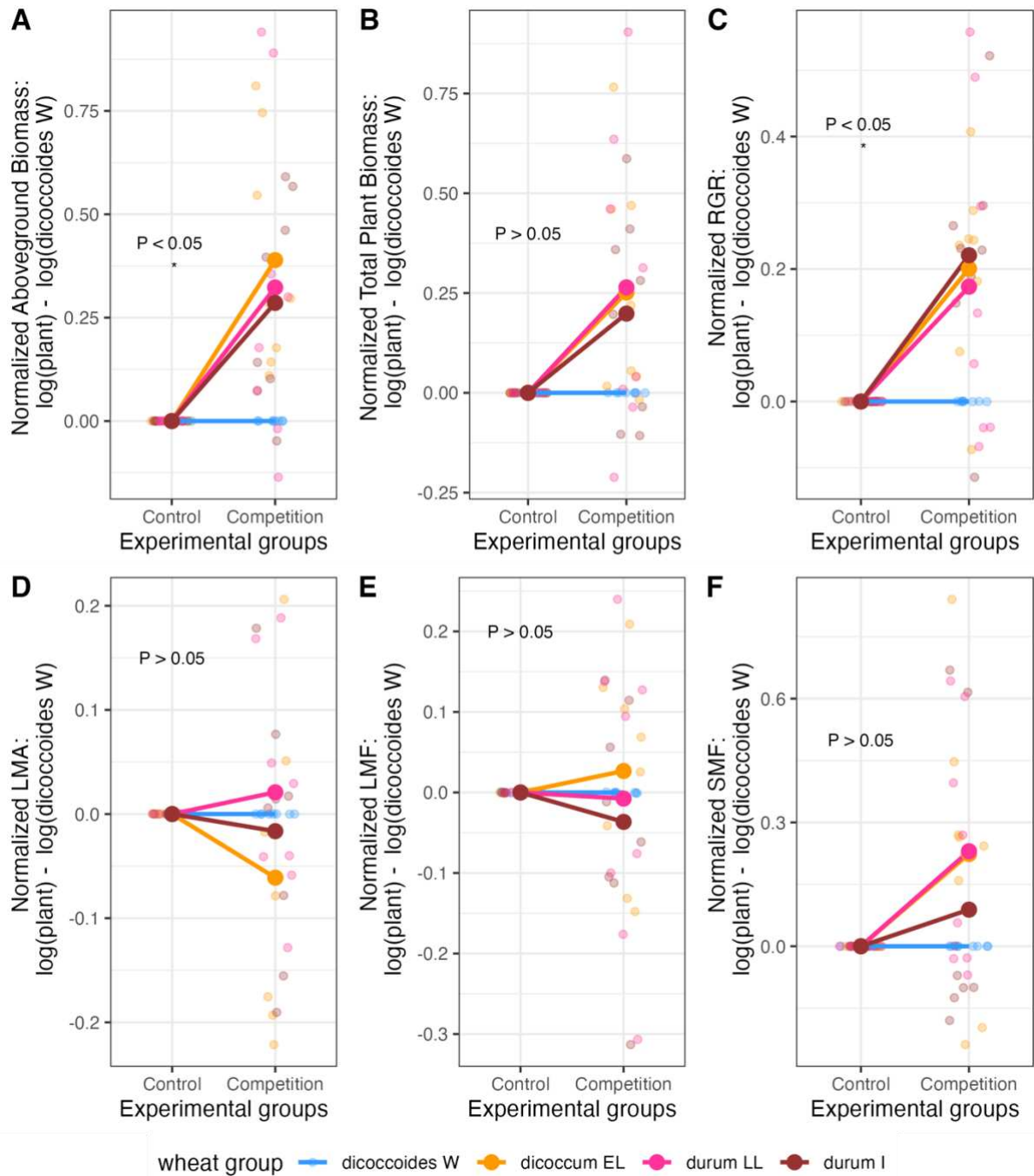
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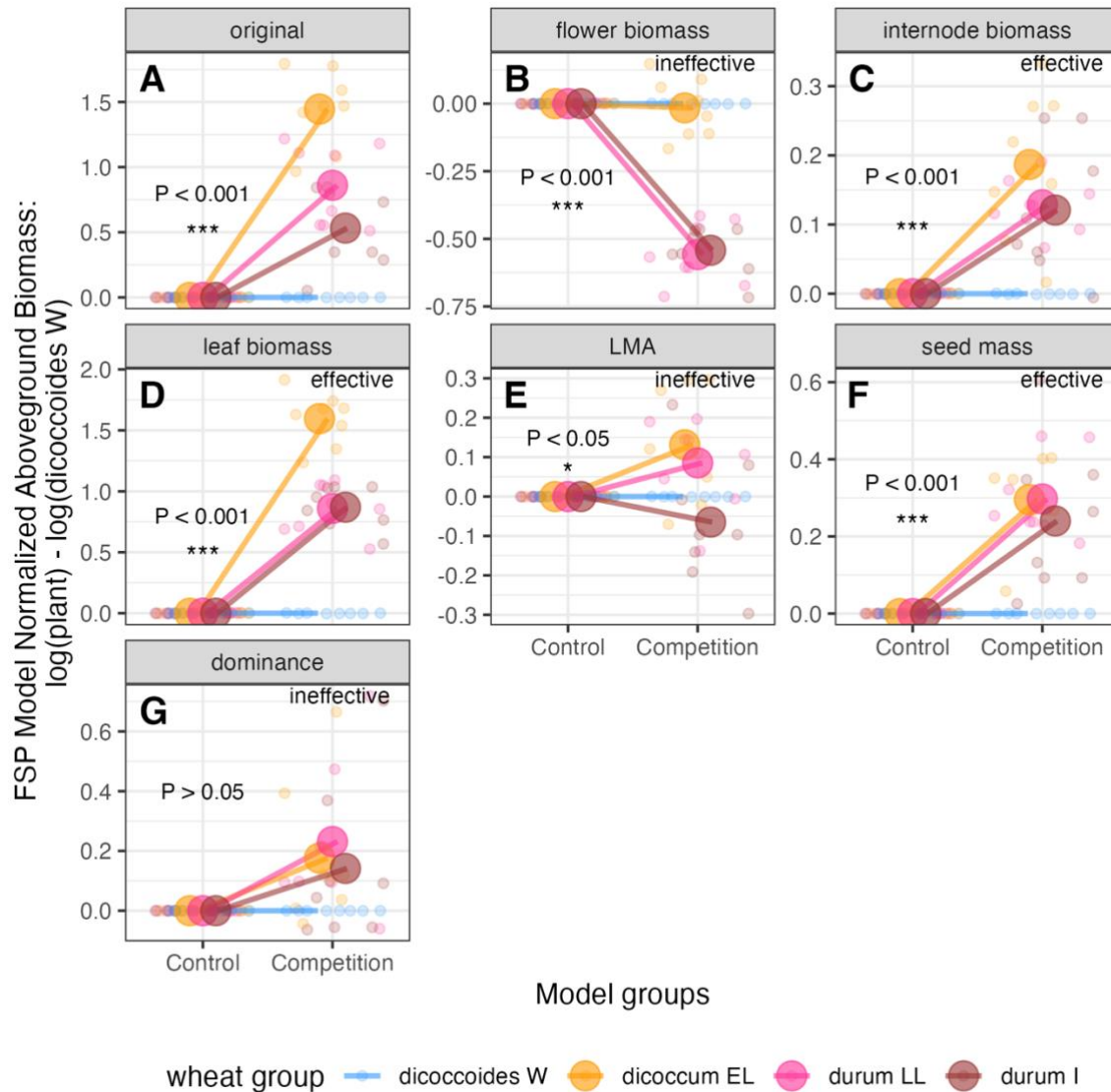
**Figure 1: Normalized differences between early diverging landraces and wild wheats in response to increased neighbour densities. a, aboveground biomass. b, plant height. c, tiller number.** The abbreviation “W” represents wild and “EL” early diverging domesticated landraces. In each case, values were first normalized relative to the values for plants growing with no neighbours. We then compared the normalized values for EL and W as  $\log(\text{EL}) - \log(\text{W})$ , such that increasing values indicate stronger competitive ability in EL compared to W. The panels (left to right) show comparisons between *T. timopheevii* EL vs *T. araraticum* W (Timopheev’s wheat), *T. monococcum* EL vs *T. boeoticum* W (einkorn wheat) and *T. dicoccum* EL – *T. dicoccoides* W (emmer wheat) respectively ( $n = 3$  for each panel is used to calculate average values). Linear models were fitted to the data, with p-values showing the significance of model fits. See also Figure S2.



**Figure 2: Model simulations to test which trait changes were responsible for differences in competitiveness among types in the interspecific experiment.** All panels show model simulations of the differences in trait values between early diverging landraces (EL) and wild wheat (W) in response to increased neighbour densities. In the sensitivity analysis, we switched values of the trait of interest between W and EL, holding all other parameters at the appropriate W or EL values. The columns (left to right) show comparisons between *T. timopheevii* EL - *T. araraticum* W (Timopheev's wheat), *T. monococcum* EL - *T. boeoticum* W (einkorn wheat) and *T. dicoccum* EL - *T. dicoccoides* W (emmer wheat) respectively (n = 5 for each panel). The labels "loss" indicates that switching the parameter values makes the EL competitive advantage disappear and return to the same level as W. However, "reversal" indicates that exchanging the trait made EL a weaker competitor than W, reversing the original outcome. Rows each show the outcome for a different trait of interest. Linear models were fitted to the data, with p-values showing the significance of model fits. See also Figure S3.



**Figure 3: Wheat performance in the face of weed competition at different stages of domestication.** a, aboveground biomass. b, total plant biomass. c, relative growth rate (RGR). d, leaf mass per area (LMA). e, leaf mass fraction (LMF). f, stem mass fraction (SMF). Key to names: T. *dicoccoides* W (wild emmer), T. *dicoccum* EL (early diverging landraces of emmer), T. *durum* LL (late diverging landraces of durum), T. *durum* I (improved elite cultivars of durum). In each case, values were first normalized relative to the values for plants growing with no neighbours. We then compared the normalized values for each domesticated form (i.e. “plant”, EL, LL or I) with those of W, using  $\log(\text{plant}) - \log(W)$ . Linear models were fitted to the data, with  $p$ -values showing whether there is a significant difference among slopes. See also Figure S4.



**Figure 4: Model simulations to test which trait changes were responsible for differences in competitiveness among types in the intraspecific experiment.** All panels show model simulations of the differences in trait values among species in response to control or competition treatments. In the original simulations, the target traits were tuned to fit experimental observations. In the other simulations, values of each named target trait were assigned to represent species differences in the model, while holding the other traits at the average value across all wheat types. In each case, values were first normalized relative to the values for plants growing with no neighbours. We then compared the normalized values for each domesticated form (i.e. “plant”, EL, LL or I) with those of W, using  $\log(\text{plant}) - \log(W)$ . The note ‘effective’ indicates that the trait had positive effects on competitiveness and it is consistent with the competitiveness ranking of (a), while “ineffective” indicates that the trait had inconsistent or negative effects on competitiveness. The lines and points are offset horizontally by a small amount so that the individual lines representing each type can be distinguished. A linear model was fitted to the data, with p-values showing whether there is a significant difference among slopes.

## STAR Methods

### EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We carried out two real competition experiments and ran simulations of each experiment using a functional-structural plant (FSP) model. The experimental designs are shown in Figure S1. First, an interspecific experiment investigated competitiveness across three independent domestication events in wheat (emmer, einkorn and Timopheev's wheat), comparing wild accessions with landraces in each case. Secondly, an intraspecific experiment investigated how competitive ability changed during emmer wheat evolution, comparing multiple accessions of wild emmer, emmer and durum landraces, and elite durum wheats.

#### Interspecific experiment

##### Plant materials and growth

The interspecific experiment was carried out in spring 2023. We compared three domestication events across three pairs of wheat species: *T. araraticum* W vs *T. timopheevii* EL, *T. boeoticum* W vs *T. monococcum* EL, *T. dicoccoides* W vs *T. dicoccum* EL (Figure S1 and Table S1). For each species, we used data from a previous screening experiment<sup>52</sup> to select a single accession with biomass values closest to the average for the phenotypic diversity within the species. All the seeds were derived from the harvest of this previous experiment. Seeds were first stored at 4°C for 24 h, and then germinated on moist filter paper in a closed petri dish<sup>53</sup>. Germination was carried out in an incubator (versatile environmental test chamber, Panasonic, UK) at 12 h dark, 12 h light, 20 °C, photosynthetic photon flux density (PPFD) 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 60% relative humidity (RH).

Germinated seeds were transplanted (one plant per cell) into trays (4×6 cells) containing high nutrient compost (M3, Levington Horticulture Ltd., Ipswich, UK), supplemented with perlite to facilitate good drainage (Sinclair Nursery Stock Propagation, Levington Horticulture Ltd., Ipswich, UK) in a 3:1 ratio. These pots were labelled and moved into a new controlled-environment growth cabinet (Convion BDW 40, Convion, Winnipeg, Manitoba, Canada). This controlled environment, designed for vernalizing winter wheats, was: 12 h dark, 12 h light, 4 °C, PPFD 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 60% RH.

After an eight-week vernalization period, seedlings were moved into pots (15×15×20 cm, 3.5 L, LBS Horticulture, UK) containing high nutrient compost (M3, Levington Horticulture Ltd., Ipswich, UK), supplemented with perlite to facilitate good drainage (Sinclair Nursery Stock Propagation, Levington Horticulture Ltd., Ipswich, UK) in the same 3:1 ratio as above, growing in a controlled environment greenhouse. Here, the environmental settings were 16 h light (PPFD from sunlight supplemented using lamps so that it was at least 300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at 20 °C, and 8 h dark at 15 °C, with constant 70% RH. At this point, the plants were 7-17 cm in height and had 2-4 leaves and 1-2 tillers. They were arranged using the experimental design outlined in Figure S1.

### Experimental design

We applied a gradient neighbor density design (Figure S1) as described by Goldberg & Landa (ref. <sup>54</sup>). There were five pots in each replicate block. Each pot contained one focal plant of one species in the centre, surrounded by neighbours comprising the other species, i.e. when the central plant was wild wheat, the neighboring plants were its domesticated relatives, whereas if the central plant was a landrace, the neighboring plants were its wild progenitor. The focal central plant was used to observe growth responses to competition, while the neighboring

plants provided a competitive environment. Densities of the neighbors varied from low to high (0, 1, 4, 9 and 21 individuals per pot), which corresponded to field densities of 0, 44, 178, 400 and 933 plants/m<sup>2</sup>. A sowing density of 200-400 plants/m<sup>2</sup> is typical for wheat in an intensive agricultural system.

## **Intraspecific experiment**

### *Plant materials and growth*

The intraspecific experiment was conducted in spring 2018. We selected 32 accessions to sample the domestication and diversification history of durum wheat. Specifically, these included eight accessions of wild emmer wheat (*T. dicoccoides*), eight accessions of early diverging landraces (domesticated emmer, *T. dicoccum*), eight accessions of late landraces (domesticated durum, *T. durum*) and eight accessions of modern wheat (*T. durum*). Seeds were obtained from INRA-CRB (Small grain cereals Biological Resources Centre, France; see Table S3 for accession identifiers and seed donors). We individually weighed 24-35 seeds per accession using a microbalance (1µg precision; Mettler Toledo MX5, Columbus OH, USA) and planted each of them on peat-filled flats. After approximately two weeks, 24 seedlings per accession were transplanted into square pots (15 x 15 x 20 cm, 3.6 L), applying the experimental design outlined below. Pots contained washed sand and a slow-release fertilizer (5 g L<sup>-1</sup> Basacote Plus 6M; Compo, Barcelona, Spain). The amount of fertilizer was set to grow plants under high nutrient availability conditions. All pots were randomly placed along two benches in a greenhouse at the Universidad Rey Juan Carlos (Madrid, Spain). Pots were periodically watered to ensure adequate water supply. Air temperature (T) and relative humidity (RH) in the glasshouse were recorded hourly (mean T ± SD = 16.1 ± 8.1°C, mean

408 RH  $\pm$  SD = 68  $\pm$  22.6%).

409

#### 410 Experimental design

411 During transplanting, half of the seedlings per accession were assigned to a control treatment  
412 as individual focal plants were grown in isolation, and half to a competition treatment. The  
413 competition treatment consisted of surrounding a focal wheat plant by three individuals of the  
414 grass *Lolium multiflorum* L. (Poaceae) that had been sown and transplanted at the same time.  
415 *Lolium multiflorum* is a strong competitor<sup>55</sup>, and an important weed that occurs in rich  
416 agricultural/grassland soils, adversely impacting emmer/durum wheat growth and seed  
417 production<sup>56</sup>. Within each treatment, six replicates of each accession were grown until the end  
418 of the life cycle (i.e. until fruiting) for non-destructive trait measurements (monitoring plants)  
419 and six other replicates were harvested at regular intervals for dissection, scanning, and  
420 weighing (calibration plants), following previous work<sup>57</sup>.

421

## 422 **METHOD DETAILS**

### 423 **Interspecific experiment**

#### 424 Trait measurements

425 We ended the experiment when most of the central wheat plants had transitioned from  
426 vegetative to reproductive growth (i.e. spikes had fully emerged on the main stem), but before  
427 reproductive maturity. At this time, we measured plant height and tiller number. After that, we  
428 harvested the aboveground parts of each central plant from the soil, dividing plant organs into

spikes, leaf blades and stems (including leaf sheaths). These samples were oven-dried at 45 °C for one week and weighed to obtain dry mass.

We harvested the experiment during the transition to flowering, since we expected competition to occur during the vegetative phase. Fitness in annual plants is usually related to biomass, and wheat follows this relationship. We have replotted data for 142 wheat accessions representing the diversity of wild and domesticated forms published in ref. <sup>52</sup>. This shows a relationship of seed number at maturity to aboveground biomass during the transition to flowering (Figure S5A). The relationship applies whether or not a correction is applied to account for seed losses due to predation or dispersal (data not shown). The aboveground biomass at flowering used to evaluate differences in competitive ability is therefore a good proxy for fitness.

#### FSP model simulations

The model we used is based on the principles of functional-structural plant (FSP) modelling<sup>17</sup>. FSP models simulate plant growth and development in 3D space. Plant growth is driven by light and temperature, and competition between plants for light is an emergent property of mutual shading depending on plant developmental status, population density and organ sizes. Our model has been described previously<sup>58</sup>. In brief, organ appearance (leaves, internodes) is driven by thermal time. Organ growth is simulated mechanistically based on assimilate production through photosynthesis by green tissues, and assimilate allocation following the relative sink strength principle. The model was implemented in the GroIMP modelling platform<sup>59</sup>. We used the FSP model to represent the interspecific experiment *in silico*. Model parameters were fitted for *T. araraticum* W, *T. timopheevii* EL, *T. boeoticum* W, *T. monococcum* EL, *T. dicoccoides* W and *T. dicoccum* EL using data from a previous

experiment<sup>52</sup>. Species differences in the model were defined by six key traits defining plant morphology and development (Table S2). In the simulations, we replicated the design of the competition experiment, setting one target plant of each species in the centre of a plot, with its corresponding wild/domesticated relatives as neighbours. We simulated their densities and growth as in the experiment.

Next, we used the FSP model to test which trait changes were responsible for species differences in competitiveness. For each trait in turn, we exchanged the values of model parameters in wild and domesticated species, respectively, and kept all other parameter values unchanged. This sensitivity test allowed us to evaluate the extent to which competition depended on each parameter. We also added planting densities to the gradient used in the experiment to simulate ten densities, in order to better fit linear models to the responses.

## **Intraspecific experiment**

### *Trait measurements*

For monitoring plants, the following traits were measured non-destructively: plant height, canopy diameter, number of tillers, number of leaves and leaf length every 3 to 8 days during the whole period of growth. In addition, the following phenological stages were recorded: germination (cotyledon visible), early vegetative stage (first tiller visible), late vegetative stage (several tillers), flowering stage (first no-grain spikes visible), and fruiting stage (first grain spikes visible). At the end of the experiment, when most of the focal plants were at the fruiting stage, we also counted the number of spikes and collected them. Spikes were dried at 60°C for at least 3 d and weighed on a precision balance (1µg precision; Mettler-Toledo) for dry mass

quantification. Seed number at maturity was also related to aboveground biomass in these plants (Figure S5B).

For calibration plants, six to nine destructive harvests were conducted during the vegetative growth period. At each harvest, one plant per accession and competition treatment was harvested after measuring the non-destructive traits. Harvested plants were washed and divided into stems, leaves, roots, leaf litter and reproductive fraction (buds, flowers and fruits; when available). We scanned all leaf laminae at a 400-dpi resolution and measured the total leaf area per plant using image analysis software (Photoshop CS6, Adobe Systems Inc., San Jose CA, USA). Each plant fraction was dried at 60°C for at least 3 d and weighed. Total mass (g) per plant was computed as the sum of all mass fractions at each harvest date.

#### FSP model simulations

We also used the FSP model to represent the intraspecific experiment *in silico*. Model parameters were fitted using morphological data from the experiment, focusing on six parameters shown in Table S4. We also calculated the average parameter values across all four wheat species and used this parameterisation to represent the *Lolium* weeds in the experiment (Table S4). Simulations were used to compare the aboveground biomass of wheat in the presence and absence of weed competition. We also applied modelling to understand which parameters were responsible for competitive outcomes. First, we set all six of the parameters that distinguished wheat accessions in the model to the average value across all accessions. Next, we sequentially selected each parameter and set it to its corresponding species-specific value. This means the selected parameter exhibits species specificity, while the other five parameters remain the same across all species. Then, we reran the competition experiment

simulation. Based on the outcome of competition, we were able to determine whether each trait had positive, inconsistent or negative effects on competitiveness.

## QUANTIFICATION AND STATISTICAL ANALYSIS

All the measured biomass, height and tiller number data were transformed into size-standardized values, by normalizing them with respect to the reference value of plants without neighbours. The transformed data were analysed using a multivariable linear regression model with interaction effects (domestication and neighbours) in R version 4.2.3 (<https://www.r-project.org/>). Figures show means, fitted linear models and the underlying raw data distributions.

### Interspecific experiment

The sample size of the experiment was 720 plants: 2 domestication statuses (wild and early landrace)  $\times$  3 domestication events (*T. araraticum* W – *T. timopheevii* EL, *T. boeoticum* W – *T. monococcum* EL and *T. dicoccoides* W – *T. dicoccum* EL)  $\times$  40 plants (35 neighbour plants (0+1+4+9+21) + 5 focal plants)  $\times$  3 replicates.

We log-transformed the wild and domesticated wheat trait values and then subtracted the wild wheat trait values ( $\log(W)$ ) from the domesticated / early landrace ( $\log(EL)$ ) wheat trait values to obtain their difference. The zero baseline in this case was the performance of W plants under competition, and was used as a reference line in plots. A difference ( $\log(EL) - \log(W)$ ) greater than zero means the domesticated wheat is more competitive than the wild wheat for that trait value comparison. Conversely, if the difference is lower than zero, wild wheat is more

competitive than domesticated forms. We used a general linear model with ANOVA to test if the slopes of the lines had significant differences or not. The two predictors in the linear model for the interspecific experiment were neighbour number ( $\log(\text{neighbor} + 1)$ ) and wheat species (“W” vs “EL”). The predictors in the linear model for the intraspecific model were experimental treatment (“Control” vs “Competition”) and wheat species (“W”, “EL”, “LL” and “I”).

### **Intraspecific experiment**

The sample size of the experiment was 768 plants: 32 accessions  $\times$  2 treatments (control and competition)  $\times$  2 plant types (calibration and monitoring)  $\times$  6 replicates.

Five statistical models were evaluated to predict total dry mass, leaf dry mass, stem dry mass, root dry mass and leaf area with mixed linear regression (LMM), using the non-destructive traits as predictors. These models were tested on the calibration plants for which we had both destructive and non-destructive measurements. Models were fitted separately for each competition treatment, with accession identity as a random effect over the intercept. To allow the relationship between the response variable and predictors to vary across accessions, we included a random slope effect over the non-destructive trait measurements. We used cross-validation to assess the prediction accuracy of our models by calculating the coefficient of correlation ( $r^2$ ) between the measured and predicted variables. We could explain on average > 99% of the variance in the response variables, similarly to a previous paper using the same approach<sup>57</sup>. We used the predictive models to estimate dry masses and leaf area during the whole growth period on monitoring plants.

541 Using *T. dicoccoides* W as a reference, we also compared intraspecific variation in  
542 aboveground and total biomass among the eight different accessions from both EL and LL  
543 landraces. In the statistical analysis, these accessions were treated as random effects. Models  
544 with and without accessions as random effects were fitted, and the two models were compared  
545 using a likelihood ratio test. All models were run with the lmer function of the lme4 R package<sup>60</sup>  
546 with the Maximum Likelihood (ML) estimation.

547

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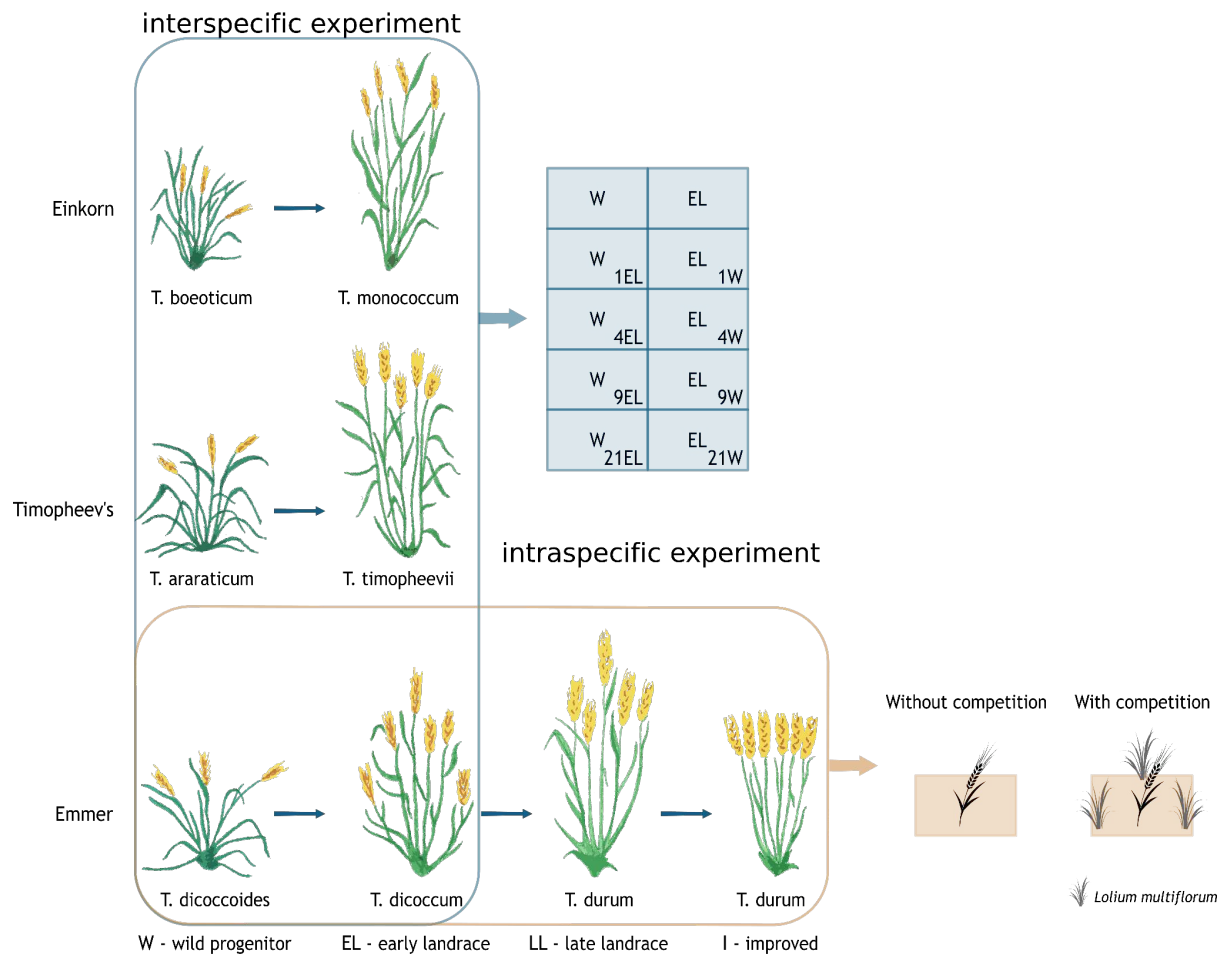
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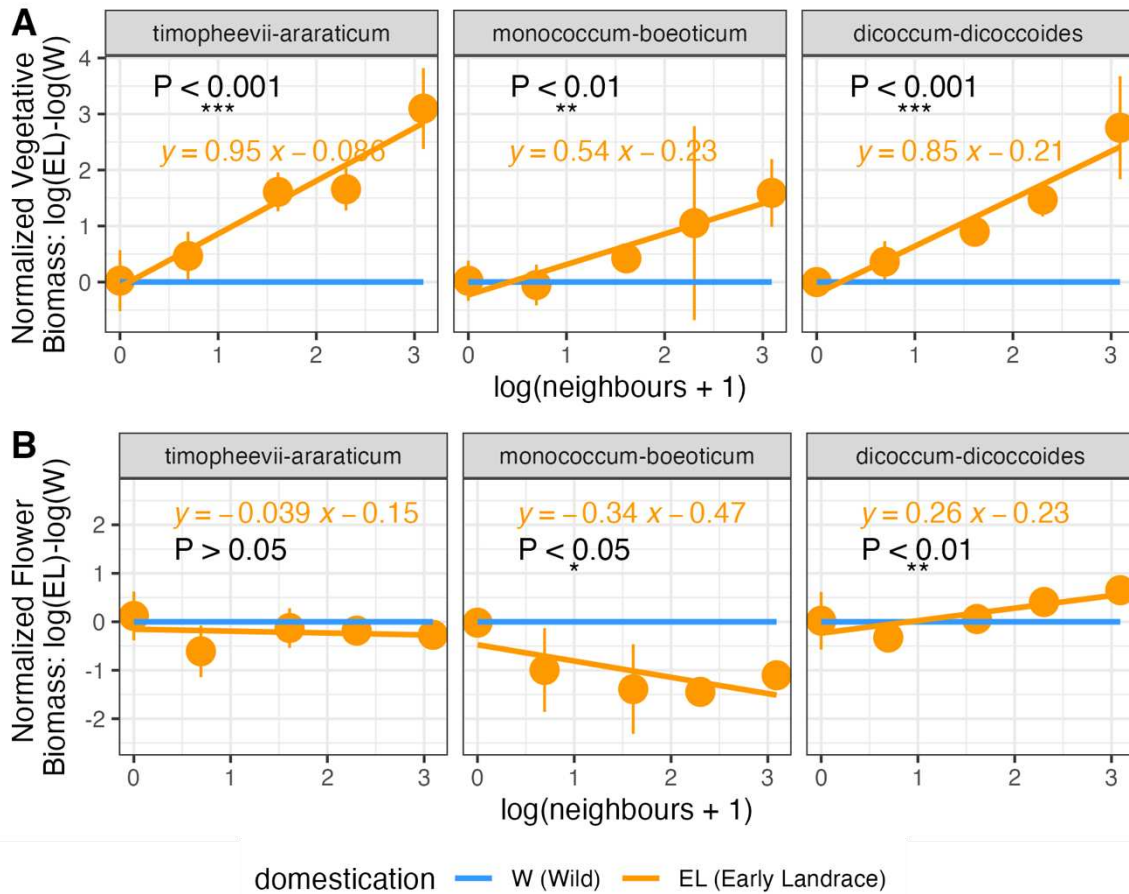
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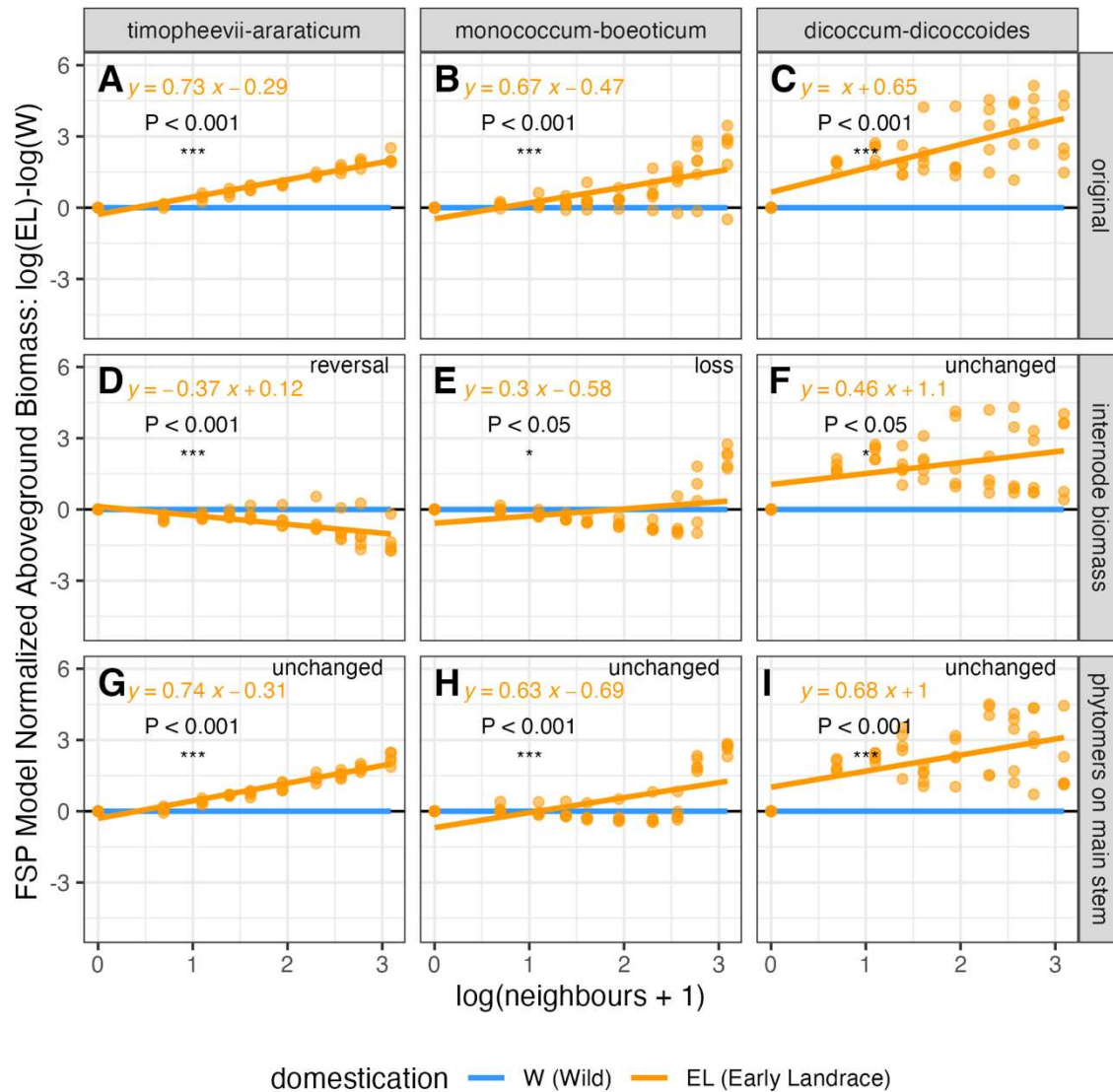
**Figure S1. Conceptualisation and experimental design, related to Star Methods.**

The blue circle circumscribes the three independent comparisons made in the interspecific experiment. The blue table shows the design of this experiment, such that a target plant in each pot is grown with varying densities of neighbours, in a reciprocal design (“W” wild wheats, “EL” early diverging landraces).

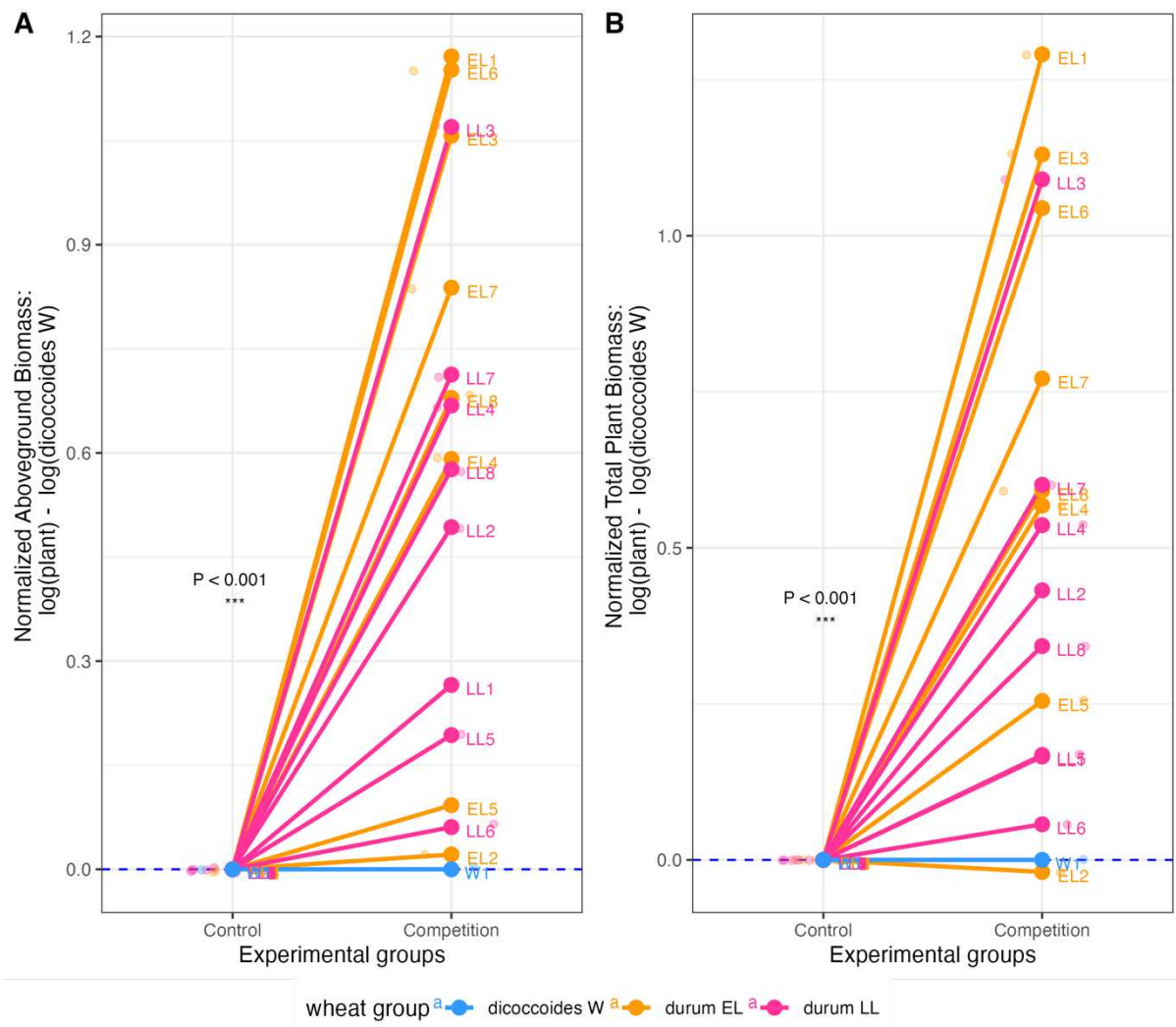
The orange circle circumscribes the comparisons made in the intraspecific experiment, and the diagram in the lower right corner shows its design. Here, the control treatment is plants grown alone, while the experimental treatment is exposure to three *Lolium multiflorum* L. competitors (“LL” late diverging landraces, “I” improved elite modern varieties).



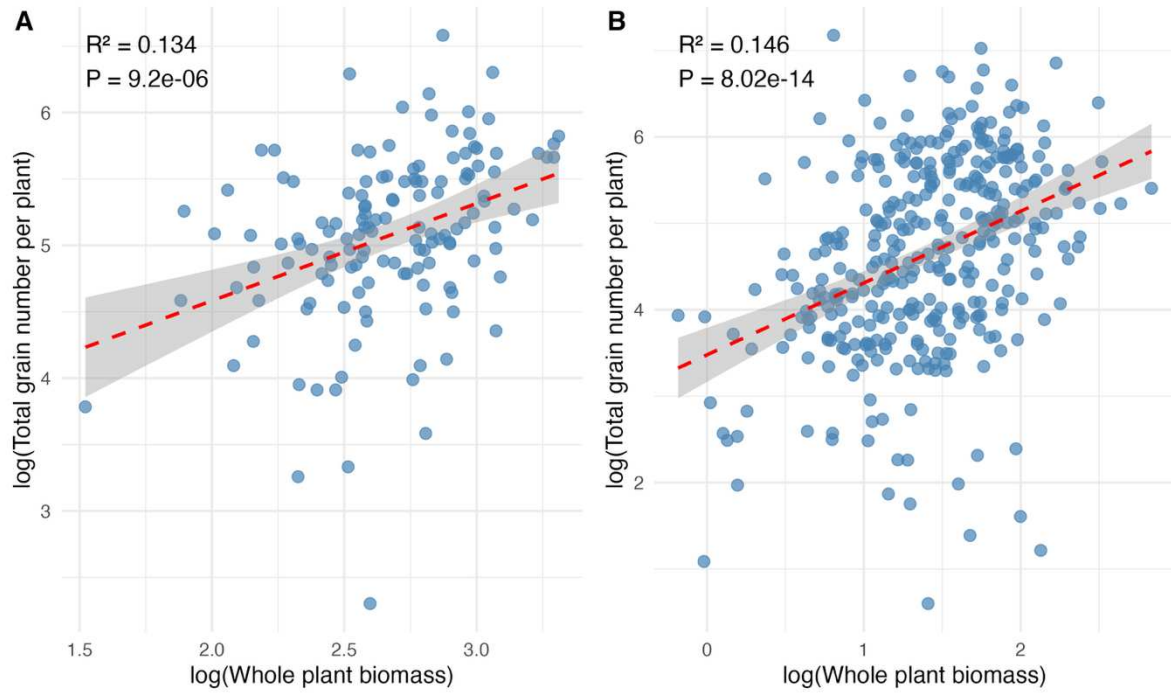
**Figure S2: Normalized differences between early diverging landraces and wild wheats in response to increased neighbour densities, related to Figure 1. a, vegetative biomass. b, flower biomass.** The abbreviation “W” represents wild and “EL” early diverging domesticated landraces. In each case, values were first normalized relative to the values for plants growing with no neighbours. We then compared the normalized values for EL and W as  $\log(\text{EL}) - \log(\text{W})$ . The panels (left to right) show comparisons between *T. timopheevii* EL vs *T. araraticum* W (Timopheev’s wheat), *T. monococcum* EL vs *T. boeoticum* W (einkorn wheat) and *T. dicoccum* EL – *T. dicoccoides* W (emmer wheat) respectively (n = 3 for each panel is used to calculate average values). Linear models were fitted to the data, with p-values showing the significance of model fits.



**Figure S3: Model sensitivity analysis showing traits making minor contributions to differences in competitiveness between species in the interspecific experiment, related to Figure 2.** All panels show FSP model simulations of the differences in trait values between early diverging landrace (EL) and wild wheat (W) in response to increased neighbour densities. In the sensitivity analysis, we switched values of the trait of interest between W and EL, holding all other parameters at the appropriate W or EL values. The columns (left to right) show comparisons between *T. timopheevii* EL - *T. araraticum* W (Timopheev's wheat), *T. monococcum* EL - *T. boeoticum* W (einkorn wheat) and *T. dicoccum* EL - *T. dicoccoides* W (emmer wheat), respectively (n = 5 for each panel). The labels "loss" indicates that switching the parameter values makes the EL competitive advantage disappear and return to the same level as W. However, "reversal" indicates that exchanging the trait made EL a weaker competitor than W, reversing the original outcome. Rows each show the outcome for a different trait of interest. Linear models were fitted to the data, with p-values showing the significance of model fits.



**Figure S4: Diversity in competitiveness among landrace accessions in comparison with wild relatives, related to Figure 3a, aboveground biomass. b, total plant biomass.** Key to names: *T. dicoccoides* W (wild emmer), *T. dicoccum* EL (early diverging landraces of emmer), *T. durum* LL (late diverging landraces of durum). In each case, values were first normalized relative to the values for plants growing with no neighbours. We then compared the normalized values for each domesticated form (i.e. “plant”, EL or LL) with those of W, using log(plant)-log(W). The numerical codes corresponding to EL, and LL represent different accessions within the species. When performing statistical analysis, the accession is treated as a random effect, and the likelihood ratio between the two models with and without the addition of accession is compared, with p-values showing whether there is a significant difference among slopes.



**Figure S5: Relationships between fitness and biomass, relating to the Star Methods.** Plots show: (A) Total seed number at maturity against biomass at anthesis across 142 accessions of wild and domesticated wheat, including landraces and elite varieties; and B) Total seed number at maturity against biomass at maturity for wild and domesticated accessions of emmer and durum wheat in the intraspecific experiment. For A, the plants were grown in a common garden and the data are from ref. <sup>S1</sup>.

| Common name                     | Botanical name                                          | Domestication status | Species label  |
|---------------------------------|---------------------------------------------------------|----------------------|----------------|
| <i>Interspecific experiment</i> |                                                         |                      |                |
| Emmer wheat                     | <i>Triticum dicoccoides</i> (Asch. & Graebn.) Schweinf. | Wild                 | dicoccoides W  |
|                                 | <i>Triticum dicoccum</i> (Schränk ex Schübl.)           | Domesticated         | dicoccum EL    |
| Einkorn wheat                   | <i>Triticum boeoticum</i> Desf.                         | Wild                 | boeoticum W    |
|                                 | <i>Triticum monococcum</i> Desf.                        | Domesticated         | monococcum EL  |
| Timopheev's wheat               | <i>Triticum araraticum</i> Jakubz.                      | Wild                 | araraticum W   |
|                                 | <i>Triticum timopheevii</i> Zhuk.                       | Domesticated         | timopheevii EL |
| <i>Intraspecific experiment</i> |                                                         |                      |                |
| Emmer wheat                     | <i>Triticum dicoccoides</i> (Asch. & Graebn.) Schweinf. | Wild                 | dicoccoides W  |
|                                 | <i>Triticum dicoccum</i> (Schränk ex Schübl.)           | Domesticated (EL)    | dicoccum EL    |
|                                 | <i>Triticum durum</i> Desf.                             | Domesticated (LL)    | durum LL       |
|                                 | <i>Triticum durum</i> Desf.                             | Domesticated (I)     | durum I        |

**Table S1: Species used in the experiments, related to the Star Methods**

| Domestication event | Species                            | finalPhytNum | wmaxInt | wmaxLeaf | specificInternodeLength | dominance | leafAngle |
|---------------------|------------------------------------|--------------|---------|----------|-------------------------|-----------|-----------|
| Timopheev's wheat   | wild <i>T. araraticum</i>          | 10           | 274     | 140      | 0.80                    | 4.9       | 60.5      |
|                     | domesticated <i>T. timopheevii</i> | 10           | 396     | 100      | 0.88                    | 4.7       | 47.1      |
| Einkorn wheat       | wild <i>T. boeoticum</i>           | 9            | 324     | 70       | 0.95                    | 2.8       | 42.5      |
|                     | domesticated <i>T. monococcum</i>  | 10           | 360     | 130      | 0.77                    | 4.5       | 28.6      |
| Emmer wheat         | wild <i>T. dicoccoides</i>         | 9            | 417     | 150      | 0.76                    | 4.0       | 50.3      |
|                     | domesticated <i>T. dicoccum</i>    | 10           | 445     | 240      | 0.59                    | 5.5       | 35.3      |

**Table S2: FSP model parameters used to differentiate the wheat species in simulations of the interspecific experiment, related to the Star Methods.** All other parameters were fixed at constant values. finalPhytNum (final phytomer number on the main stem), wmaxInt (maximum potential internode biomass, mg), wmaxLeaf (maximum potential leaf biomass, mg), specificInternodeLength (ratio of internode length to mass, mm/mg), dominance (parameter determining main stem dominance, which suppresses tillering), leafAngle (insertion angle of leaves into stem, degrees, where 90° = horizontal).

| Botanical name                                          | Dom. status     | Accession identifier | Accession country |
|---------------------------------------------------------|-----------------|----------------------|-------------------|
| <i>Triticum dicoccoides</i> (Asch. & Graebn.) Schweinf. | Wild progenitor | 27004                | Israel            |
|                                                         |                 | 27020                | Israel            |
|                                                         |                 | 27021                | Israel            |
|                                                         |                 | 27023                | Syria             |
|                                                         |                 | 27024                | Iraq              |
|                                                         |                 | 27025                | Iraq              |
|                                                         |                 | 33774                | Turkey            |
|                                                         |                 | 33776                | Israel            |
| <i>Triticum dicoccum</i> (Schränk) Schübl               | Early landrace  | 26894                | Algeria           |
|                                                         |                 | 33756                | Turkey            |
|                                                         |                 | 33757                | Iraq              |
|                                                         |                 | 33759                | Iran              |
|                                                         |                 | 33760                | Italy             |
|                                                         |                 | 33761                | Russia            |
|                                                         |                 | 33762                | Slovakia          |
|                                                         |                 | 33764                | Germany           |
| <i>Triticum durum</i> Desf.                             | Late landrace   | 26899                | Algeria           |
|                                                         |                 | 26931                | Pakistan          |
|                                                         |                 | 26966                | Egypt             |
|                                                         |                 | 26970                | Palestine         |
|                                                         |                 | 26974                | Russia            |
|                                                         |                 | 26982                | Spain             |
|                                                         |                 | 33799                | Turkey            |
|                                                         |                 | 33800                | Turkey            |
| <i>Triticum durum</i> Desf.                             | Improved        | 14060                | France            |
|                                                         |                 | 14063                | France            |
|                                                         |                 | 27246                | France            |
|                                                         |                 | 27288                | France            |
|                                                         |                 | 30727                | France            |
|                                                         |                 | 31269                | France            |
|                                                         |                 | 33801                | France            |
|                                                         |                 | 33802                | France            |

**Table S3. Botanical name, domestication status and geographical origin for each accession included in the intraspecific experiment, related to the Star Methods.** Accession identifier refers to the code assigned by the germplasm center INRA – CRB (Small grain cereals Biological Resources Centre, France). Dom. status refers to domestication status.

| species    | dicoccoides | dicoccum | durum  | durum  | average |
|------------|-------------|----------|--------|--------|---------|
| stage      | W           | EL       | LL     | I      |         |
| wmaxFlower | 520.58      | 557.90   | 896.22 | 944.90 | 729.90  |
| wmaxInt    | 56.18       | 161.64   | 68.55  | 68.12  | 88.62   |
| wmaxLeaf   | 42.44       | 57.94    | 47.16  | 47.11  | 48.66   |
| LMA        | 2.88        | 2.78     | 2.76   | 2.95   | 2.84    |
| seedMass   | 42.83       | 49.47    | 53.55  | 48.09  | 48.48   |
| dominance  | 5.00        | 5.95     | 5.96   | 5.97   | 5.72    |

**Table S4: FSP model calibration for the intraspecific comparison experiment, related to the Star Methods.** All other parameters were fixed at constant values. wmaxFlower (maximum potential inflorescence biomass, mg), wmaxInt (maximum potential internode biomass, mg), wmaxLeaf (maximum potential leaf biomass, mg), LMA (leaf mass per unit area, g cm<sup>-2</sup>), seedMass (seed mass, mg), dominance (parameter determining main stem dominance, which suppresses tillering).

## Supplemental Reference

- S1 Shan, Y., and Osborne, C.P. (2024). Diversification of quantitative morphological traits in wheat. *Annals of Botany* 133, 413–426. <https://doi.org/10.1093/aob/mcad202>.