# Increasing plant group productivity through latent genetic variation for cooperation

Samuel E. Wuest[1,2,3*], Nuno D. Pires[1], Shan Luo[4], Francois Vasseur[5,6], Julie Messier[5,7], Ueli Grossniklaus[1], and Pascal A. Niklaus[2]

1) Department of Plant and Microbial Biology & Zurich-Basel Plant Science Center, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland

2) Department of Evolutionary Biology and Environmental Studies & Zurich-Basel Plant Science Center, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

3) Group Breeding Research, Division Plant Breeding, Agroscope, Müller-Thurgau-Strasse 8, CH-8820 Wädenswil, Switzerland

4) Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, United Kingdom

5) CEFE, CNRS, Univ Montpellier, Univ Paul Valéry Montpellier 3, EPHE, IRD, F-34090 Montpellier, France

6) Laboratoire d'Ecophysiologie des Plantes sous Stress Environnementaux (LEPSE), INRA, Montpellier SupAgro, UMR759, F-34060 Montpellier, France

7) Department of Biology, University of Waterloo, 200 University Avenue West, Waterloo N2L 3G1, Canada

*correspondence to: Samuel E Wuest (samuel.wuest@agroscope.admin.ch)

## Abstract

Technologies for crop breeding have become increasingly sophisticated, yet it remains unclear whether these advances are sufficient to meet future demands. A major challenge with current crop selection regimes is that they are often based on individual performance. This tends to select for plants with "selfish" traits, which leads to a yield loss when they compete in high-density stands. In traditional breeding, this well-known "tragedy of the commons" has been addressed by anticipating ideotypes with presumably preferential characteristics. However, this approach is limited to obvious architectural and physiological traits, and it depends on a mechanistic understanding of how these modulate growth and competition. Here, we developed a general and simple method for the discovery of alleles promoting cooperation of plants in stands; it is based on the game-theoretical premise that alleles increasing cooperation incur a cost to the individual but benefit the monoculture group. Testing the approach using the model plant *Arabidopsis thaliana,* we found a single major effect locus where the rarer allele was associated with increased levels of cooperation and superior monoculture productivity. We show that the allele likely affects a pleiotropic regulator of growth and defense, since it is also associated with reduced root competition but higher race-specific resistance against a specialized parasite. Even though cooperation is considered evolutionarily unstable, conflicting selective forces acting on a pleiotropic gene might thus maintain latent genetic variation for it in nature. Such variation, once identified in a crop, could be rapidly leveraged in modern breeding programs and provide efficient routes to increase yields.

# Main Text

## Introduction

Crop breeding is currently undergoing fundamental transformations. Speed breeding and genomic prediction can shorten generation times and increase effective population sizes, leveraging rates of phenotypic change to unprecedented levels (*1*, *2*). At the same time, large-scale, high-throughput phenotyping platforms have become available and allow for the simultaneous quantification of multiple traits in ever larger greenhouse and field trials (*3*). Yet, it remains unclear whether current rates of yield increase are sufficient to meet the increasing demands driven by human population growth, in particular in combination with the concomitant demand for more feed (*4*, *5*).

Historically, the highest rates in yield increase were achieved in the middle of the 20th century, at the beginning of the "Green Revolution". Combining breeding with improved management, yield potentials of major crops, such as wheat and tropical rice, approximately doubled within only a few plant generations (*6*, *7*). In retrospect, these gains in yield potential appear unusual in several respects. In contrast to most classical breeding that operates through selection on polygenic variation, they were largely realized by capitalizing on single genes, notably the introgression of discrete but pleiotropic dwarfing alleles with major effects on plant form and function (*8*, *9*). This resulted in smaller and less bushy individuals, which diverted less resources to competition. In other words, breeding of these more "communal" genotypes allowed increasing crop yield per unit land area rather than per individual by exploiting a trade-off between individual fitness and group-level performance (*10–14*).

The importance of avoiding excessive allocation to competition, i.e. fostering a form of cooperation between plants, had been recognized by breeders and led to the anticipation of ideotypes with a suite of presumably desirable traits for a given environment, e.g. short stature, vertical leaf angles, and a compact root system for a high-density stand (*11*, *12*, *15*). However, a practical difficulty with ideotype breeding is that relevant variation in traits and growth strategies may remain enigmatic to the human observer. In addition, the nature of cooperation in plants, and how and under which environmental conditions it evolves, are currently not well

understood (*16*). Interestingly, animal breeding has focused to a much larger extent on cooperation and social strategies (*17*), not least because these are often based on behavioral traits and, thus, more easily recognized by the human observer.

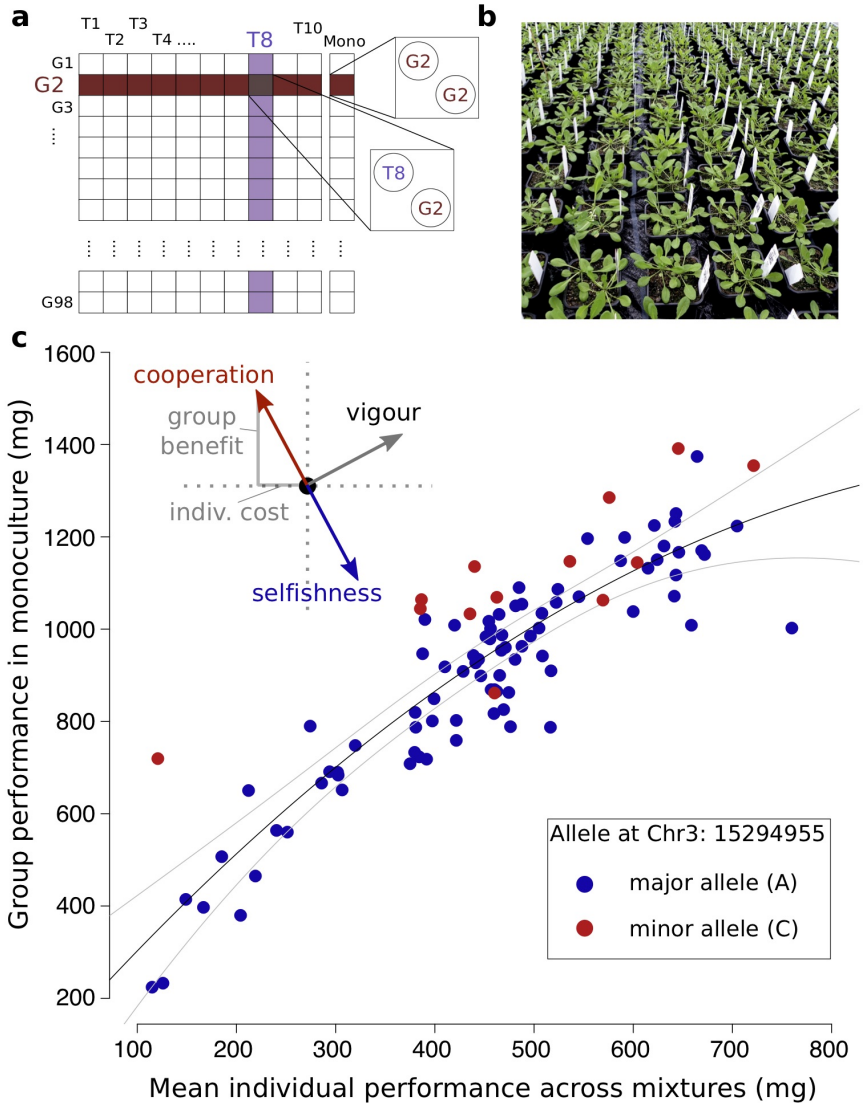
Cooperation is not generally an evolutionary stable strategy in nature because individual-level selection will favor alleles that promote the allocation of resources to competition and increase the fitness of non-cooperators relative to cooperators. Therefore, it is expected that a population of cooperators can rapidly be invaded by non-cooperators (*18*), and that cooperation only evolves under special circumstances (*16*). In breeding, selection at the group level was proposed to address this problem (*19*, *20*), but in practice such selection regimes are difficult to implement.

The research we present here is based on the premise that there likely remains untapped potential for yield increase through breeding for cooperation in plants (*21*). We therefore developed a practical framework within which the recent advances in technology – including genome-wide association studies (GWAS) and large-scale phenotyping – can effectively be harnessed to identify alleles and traits that promote cooperation. We further aimed for such a framework to be as general and unbiased as possible, in order to detect yield gains that emerge from any type of cooperation, including for resources unknown to and through specific strategies unrecognized by the experimenter. We thus designed competition experiments and analytical methods that allowed us to rank plant genotypes on a scale ranging from competitive and "selfish" to communal and "cooperative". Finally, we applied these methods in a proof-of-concept experiment with a population of *A. thaliana* genotypes and produced a genetic map of a group vs. individual (G-I) performance trade-off to identify genomic regions associated with increased levels of cooperation.

## Results and Discussion

We tested the potential of our method using an association panel of 98 natural *A. thaliana* accessions – a subset of the RegMap population (*22*). Aboveground dry matter production served as measure of performance. However, the approach we developed can in principle be applied to other species, in particular crops, and to other target characteristics such as agricultural yield. Each of the 98 focal genotypes was grown in a pot that contained two congenotypic individuals (monoculture), and

additionally as individuals in ten further pots with one individual from each of ten tester genotypes (Fig. 1a,b). These tester genotypes were a subset of the original population of genotypes chosen to span a wide range of competitive abilities (Fig. 1a,b; Supplemental Fig. 1b). However, this is not a methodological requirement and tester genotypes that are not part of the original panel would have worked equally well. This design was replicated in two blocks. As expected, competitive interactions among individuals were strong, with large negative effects of average tester size (average across all pots) on the shoot biomass of the focal genotypes (ANOVA $F_{1,960} = 88.23$; $P < 0.001$). To evaluate a group vs. individual (G-I) performance trade-off of genotypes, we related the mean individual shoot biomass of the target genotypes' in monoculture (group performance) to its average biomass when grown in competition with a tester genotype (individual performance; Fig. 1c). Not surprisingly, across genotypes, group and individual performance were highly positively associated, with more vigorous genotypes producing more biomass both in monoculture groups and as individuals subject to competition with testers. This relationship was slightly non-linear (second degree polynomial $F_{1,95}=8.4$, $P=0.005$), a pattern that might originate from predictable ecological interactions (*23*) or increasing effects of space limitations with increasing plant sizes. Irrespective of the nature of this effect, we treated this overall relation as heuristic, and used the distance from this empirical relationship to locate each genotype on an orthogonal axis that quantified the G-I trade-off (Methods and Fig 1c). In other words, this procedure transformed the separate values for group performance in monoculture and mean individual performance in mixtures into two metrics: the position along the general relationship reflects general genotypic vigor (e.g. increased productivity due to better adaptation to the specific growth conditions); and the position perpendicular to the general relationship reflects a G-I trade-off value that characterizes the communal properties of the focal genotype (inset Fig 1c). For example, the G-I value is positive for more cooperative genotypes, which are expected to have relatively lower individual performances in mixtures (non-cooperative environment) and higher performance in monocultures (cooperative environment).




147 **Figure 1: A general framework for the genetic dissection of the G-I trade-off. a**.
148 Experimental design of the competition experiment. G1, G2, … G98: focal genotypes 1-98;
149 natural *A. thaliana* accessions sampled from the RegMap panel. T1, T2, … T10: one of ten
150 tester genotypes, chosen to represent different plant sizes to capture a large portion of the
151 genetic variation present within *A. thaliana*. **b.** Experimental setup **c.** Relationship between a
152 genotype's mean performance as an individual across all mixtures with tester genotypes and
153 its group performance in monoculture. The inset outlines three genetic effects a hypothetical
154 allele could have on a genotype's strategy. Red and blue dots show genotypes carrying
155 different alleles at position 15'294'955 on chromosome 3 (see below).
156
157 Next we performed genome-wide association tests for the genotypic G-I trade-off
158 value. Genome-wide polymorphism data of our population were available through

the RegMap panel (*22*) and single nucleotide polymorphism (SNP) information was available for 214,000 sites. The G-I trade-off value was significantly associated with a major effect locus on chromosome three (Fig. 2a,b). The rarer allele was found in 18% of the RegMap population and was associated with lower individual/higher group performance, i.e. with increased cooperation (Fig. 1c). The SNP with the strongest association resides in the center of a transposon-rich region and explained approximately 25% of the variation in the genotypic G-I trade-off values (Fig. 2c). Direct mapping of untransformed data, i.e. of variation in either individual or monoculture group biomass alone, did not reveal any significant associations (Supplemental Fig. 2a,b) because this fails to separate general vigor from the trade-off value that measures group suitability. A more detailed genomic analysis based on a subset of 68 genotypes and genome-wide re-sequencing data (*24*) revealed association signals across many polymorphisms in a region of approximately 150 kb around the identified RegMap SNP, all in high linkage disequilibrium (LD) (Fig. 2b).

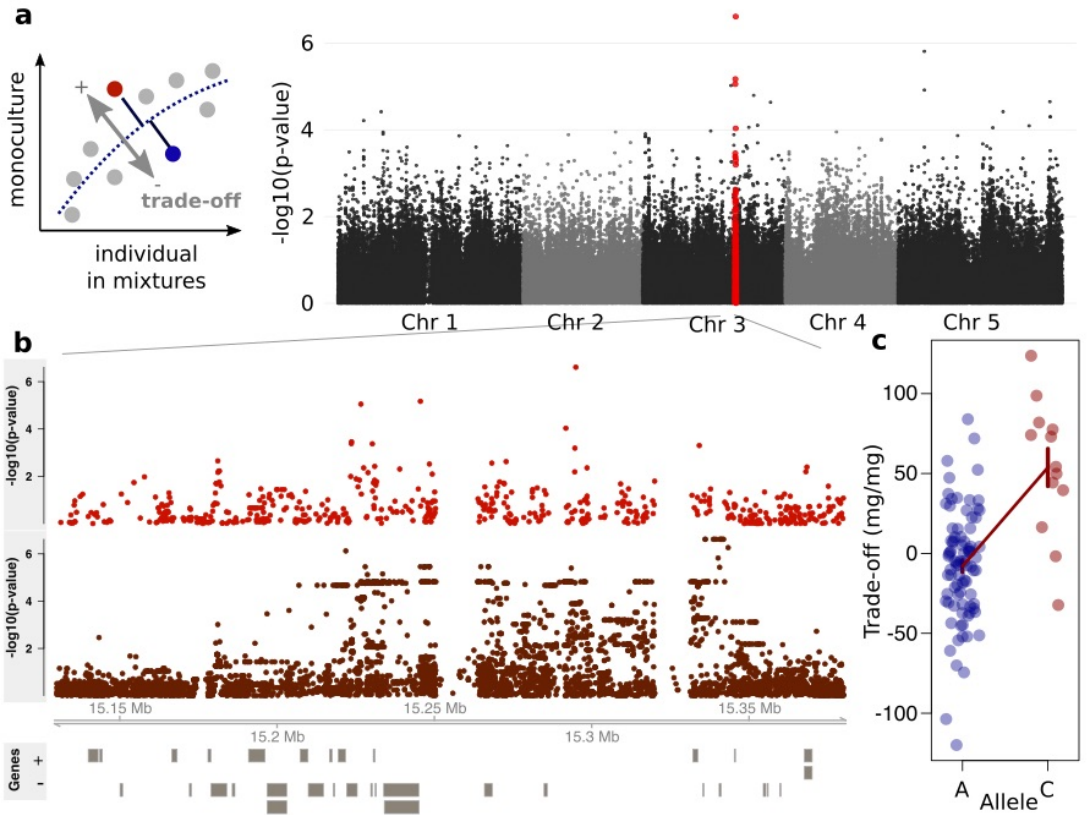
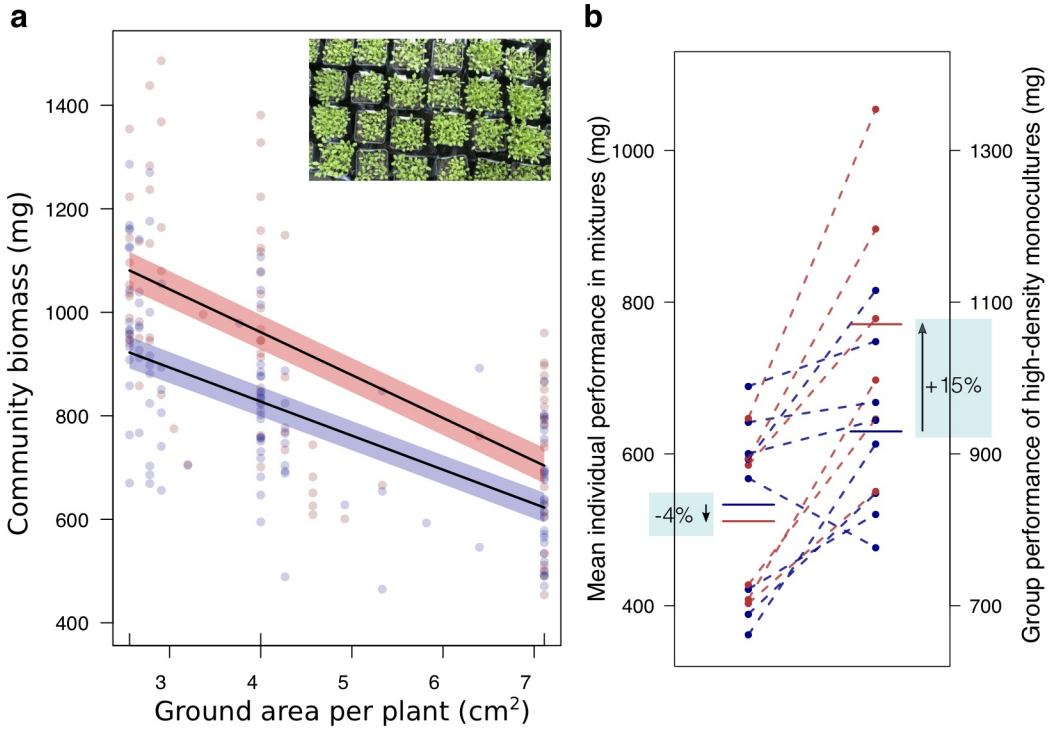



**Figure 2: Allelic variation at a major effect locus affects the G-I trade-off in *A. thaliana*. a.** Manhattan plots of genome-wide association tests for variation in the G-I trade-off, based on the 250k SNP chip data. The genotypic G-I trade-off value is the distance from

the overall trend between group and individual performance in monoculture and mixtures, respectively (inset). **b.** Zoom in on a segment of chromosome 3, showing Manhattan plots of either an association analysis using SNP chip polymorphisms (top), or, for a subset of 68 genotypes, genome-wide re-sequencing polymorphisms (bottom). Models of protein-coding genes are drawn as boxes below, on either + (upper) or – (lower) strand. **c.** Association of variation at SNP 15'294'955 and the G-I trade-off. Error bars denote means ± s.e.m.

High LD impedes the identification of the causal genetic variant(s) but might become relevant to test evolutionary hypotheses about selective pressures affecting genetic variation at this locus. However, since we were primarily interested in the usefulness of our molecular-ecological framework for predicting plant group properties, we next tested the hypothesis that the benefit of cooperation increases with increasing inter-individual competition, e.g. along a planting density gradient (*14*, *25*). For this, we performed a stratified sampling of genotypes differing in size and carrying different alleles at the identified locus. We then assessed the productivity of these genotypes in monocultures sown at different individual densities. Despite slightly lower individual performances across mixtures in the competition experiment, genotypes carrying the cooperation-associated allele exhibited superior productivity (+15% biomass at the highest sown density, average across all genotypes; Figure 3a,b; ANOVA $F_{1,10.6}$=7.5 , P=0.02). As anticipated, they also showed a lower degree of self-inhibition along the density gradient, i.e. gains were more pronounced at higher but less pronounced at lower densities (Figure 3a; ANOVA $F_{1,14.9}$ = 7.0, P = 0.019 for allele × ground area per individual). These results demonstrate that the molecular framework presented here is able to predict group-level features that cannot be deduced from individual-level properties, and that these allow improving monoculture stand productivity.




204 **Figure 3: Genotypes carrying the cooperator-associated allele exhibit superior**
205 **monoculture performances in high-density groups**. **a.** Monoculture biomass changes of
206 genotypes carrying either the cooperation-associated allele (red) or the alternative allele
207 (blue) across a realized planting density gradient. Lines show linear regression estimates ±
208 s.e.m. Uppward x-axis ticks show per plant areas at the sown target densities. **b.** Comparison
209 of genotype's mean individual shoot biomass in mixtures versus monoculture biomass at
210 densities of 25 plants per pot. Horizontal lines: mean values across all genotypes carrying
211 either allele. Red and blue: cooperation-associated and alternative allele at SNP Chr 3
212 15'294'955. Note the different scales of the left and the right y-axes.
213
214 To study different functional traits that may have enhanced cooperation in our
215 experiments, we quantified two traits that characterize growth and competitive
216 strategies of genotypes in our experiment. We chose rosette diameter as indicator of
217 investment into aboveground competition, and monoculture root-to-shoot ratio as
218 indicator of relative investment into root competition (Methods). On top of that, we
219 further included two publicly available phenotypic traits into our analysis (*26*),
220 namely flowering time in the field and vegetative growth rate. Genotypes that carried
221 the cooperation-associated allele did not differ from the other genotypes in rosette

diameter, flowering time in the field, or vegetative growth rate (Fig. 4a; Supplemental Fig. 3), but they showed significantly lower root-to-shoot ratios (ANOVA $F_{1,95}$=5.13, $P$=0.026). Also, the measured G-I trade-off value was not statistically significantly associated with rosette diameter, flowering time in the field, or vegetative growth rate (not shown), but exhibited a statistically significant negative relationship with root-to-shoot ratio (ANOVA $F_{1,95}$=18.4, $P$<0.001; Fig. 4a). We confirmed this pattern of higher root mass fraction in less cooperative genotypes in a separate, independent experiment for trait measurements, in both monocultures and isolated individual plants and on a different soil type (Fig. 4c, and Supplementary Fig. 3). Overall, our analyses therefore indicate that altered root allocation is part of a genetically fixed strategy associated with enhanced cooperation. Model analyses and field experiments in two of the globally most important crops, soybean and wheat, are in line with our findings: despite a long breeding history, soybean and wheat plants divert amounts of resources to root (and shoot) competition that are detrimental to agricultural yield. In soybean, a G-I trade-off was observed in both an elegant experimental manipulation of belowground competition (*27*) and a field-scale experimental reduction of leaf area (*28*), both of which affected yield. For wheat, the analysis of breeding records indicates that yield improvements of the past decades were associated with reduced root allocation (*25*, *29*, *30*) suggesting that a reduction in belowground competition resulted from inadvertent selection for higher yields over the last decades.

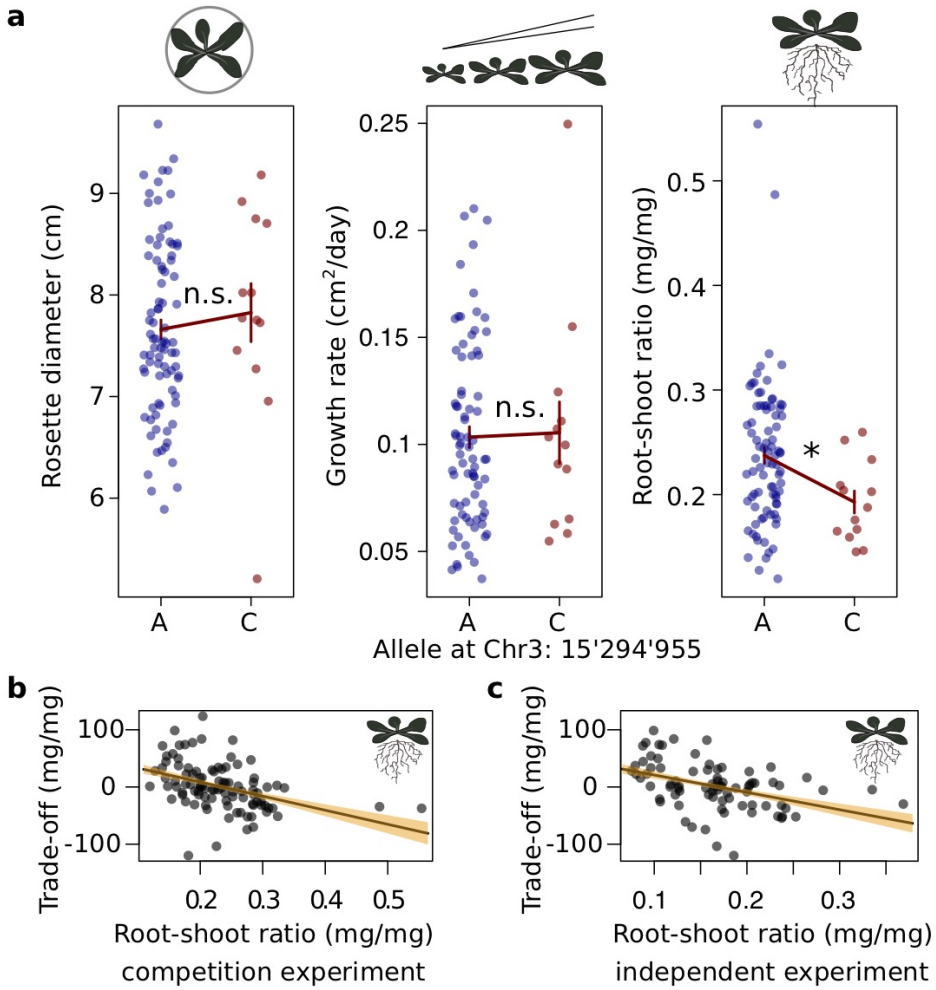



**Figure 4: Altered allocation to roots but not growth or life history is associated with increased levels of cooperation. a** Association of allelic variation at SNP Chr3:15'294'955 with variation in traits related to different plant strategies. **b. and c.** Relationship between the individual-vs-group performance trade-off and plant root-to-shoot ratio in monocultures of the competition experiment (**b**) or monocultures of an independent experiment (**c**; Methods and Suppl. Fig. S3). Bars and regression lines show means ± s.e.m. * ANOVA $P < 0.05$; n.s.: not significant.

Evolutionary theory predicts that an allele which promotes cooperation will be selected against in a natural population, except under special circumstances (*18*). We were thus surprised that the cooperation-associated allele we identified is found over a wide geographic range and at a rather remarkably high frequency (Fig. 5a). Since genes often have multiple functions, we reasoned that conflicting selective forces acting on such pleiotropic genes (or genes in tight linkage) might underlie the

259 persistence of alleles underlying cooperation in natural populations (*31*). Examining
260 genes in the identified genomic region, we found *AtMIN7*, a documented regulator of
261 both growth and defense. The AtMIN7 protein targets pathogen effectors that
262 suppress the plant immune response (*32*); furthermore, mutants are affected in auxin
263 transport pathways (*33*) and growth (*34*). Importantly, variation at the *AtMIN7* gene
264 has been associated with race-specific resistance against *Hyalonperonospora*
265 *arabidopsidis*, an obligate pathogen of *A. thaliana* (*35*). Plants homozygous for the
266 loss-of-function allele *min7-2* exhibited a more compact morphology with a lower
267 root-to-shoot ratio than co-segregants (Supplemental Fig. 4a); however, these
268 mutants were much less productive and did not exhibit significant differences in self-
269 inhibition along the plant density gradient described above (Supplemental Fig. 4b).
270 Therefore, it appears unlikely that the natural accessions we tested exhibit a
271 substantial reduction of *AtMIN7* function. However, analyzing published data on *A.*
272 *thaliana* resistance against *H. arabidopsidis* (*35*), we detected a statistically
273 significant relation of the cooperation-associated allele with partial or full resistance
274 against strain Noco2 (Figure 5b, Fisher's exact test; $P < 0.001$). Additionally, the
275 resistance level against Noco2 explained significant amounts of variation in the G-I
276 trade-off value of our genotypes (ANOVA $F_{2,79}=3.57$, $p=0.03$, Figure 5c). Therefore,
277 we refer to this naturally occurring genetic variation as latent variation for
278 cooperation, since contributions to pathogen resistance rather than cooperation might
279 have maintained the minor allele in the population.
280

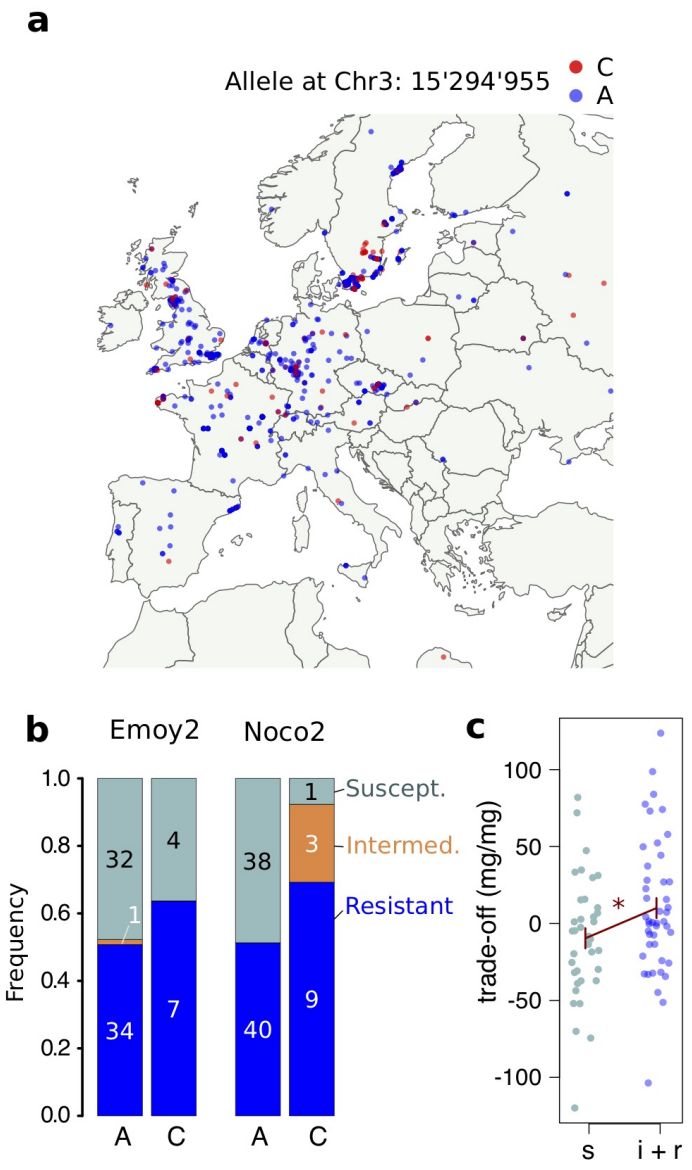



**Figure 5: The cooperation-associated allele exhibits a wide geographic distribution and is correlated with increased race-specific pathogen resistance. a.** Occurrence of natural *A. thaliana* accessions carrying the cooperation-associated allele (red) or the alternative allele (blue) across sampling sites in Europe. **b.** Association of Chr 3 SNP 15'294'955 with resistance against two strains of *H. arabidopsidis*, Emoy2 and Noco2, based on published data (*34*). Numbers indicate genotype counts. **c.** Association of Noco2 resistance levels with the G-I trade-off. s = susceptible, i+r = intermediately and fully resistant.

Yield advances attained through traditional breeding are currently slowing (*4*, *7*), shifting hopes to novel approaches that might help avert future crop shortages. In the

long term, biotechnological improvements of basic cellular functions including photosynthesis might pave the way to large productivity gains (*36*), but it is still unclear when and how such endeavors will materialize in improved yields of major crops (but see (*37*, *38*)). Others have proposed to re-evaluate whether breeding strategies of the Green Revolution, in particular the exploitation of G-I trade-offs, could be adopted for crops other than the graminoids wheat, rice, and barley, which so far have received most attention (*21*, *23*, *39*). There may also be less evident trade-offs that have not found their way into common ideotypes. The framework we developed here appears particularly well suited to support this goal. It is general and simple and integrates genome-wide association and trait-based approaches. It could be used in combination with genomic prediction on breeding populations, or alternatively to identify highly cooperative genotypes that can be used in pre-breeding. As a particular advantage, our method is unbiased by mechanistic expectations. In our model study, it led to the discovery of a cooperation-associated allele that had substantial consequences on productivity in monoculture groups. It is thus conceivable that a larger-scale systematic search will reveal alleles with comparable effects in crops. Once identified, such latent variation in cooperation could rapidly be co-opted in marker-assisted breeding programs. At a more fundamental level, the finding that large-effect genetic variants for cooperation are maintained in a natural population leads to the intriguing thought that social traits can arise as evolutionary exaptations, i.e. by co-option of an existing trait unrelated to cooperation (*40*).

## Materials and Methods

### Plant material

The natural *A. thaliana* accessions used (Supplementary Dataset S1) are a subset of the RegMap population(*22*) for which a comprehensive list of traits has been collected (*26*). The *AtMIN7* loss-of-function allele was represented by the T-DNA insertion present in line SALK_013761 (i.e. the *min7-2* allele, obtained from the Nottingham Arabidopsis Stock Center; N513761). In this line, the wild type allele was confirmed by PCR using primers min7-2 LP = 5'-TGGAAAGTGAAATTGGTGAGC-3' and min7-2 RP = 5'-CAAGGATTCTTCTCTGCATGG-3', and the mutant allele using primer min7-2 LP and SALK_LB = 5'-CTTTGACGTTGGAGTCCAC-3'. A co-segregant line confirmed to be homozygous for the wild-type allele was used in comparison with the *min7-2* loss-of-function mutant.

### Experimental Design

Competition experiment: Pairs of individual plants were grown in small pots in a factorial design in which the 97 genotypes of the panel were each grown together with one of ten tester genotypes, the latter of which were a subset of the panel. Each genotype was further grown in a monoculture of two individuals. Each genotype composition was replicated twice, in separate blocks. In the second block, however, insufficient seeds for one line (LP-2-6) were available, and this accession was replaced in the second block by Kn-0, effectively resulting in 98 genotypes grown across the ten tester accessions. This resulted in 2134 pots containing two plants each. Each tester line was also grown as individual plant, once per block. Pots containing single plants (including pots in which one plant died at the seedling stage) were, however, removed from subsequent analyses.

Density gradient: In order to test for decreased self-inhibition of genotypes along a plant density gradient, six genotypes (Bor-4, Est-1, Mt-0, Ra-0, Sav-0, Wa-1) that varied in their average individual performances across mixtures, but carried all the cooperation-associated allele, were paired with seven genotypes (An-1, Br-0, Can-0, Kondara, Nfa-10, Shahdara, St-0) of similar average individual performances but carrying the alternative allele. In addition, the co-segregant (Col-0 background) wild-

type and the *min7-2* loss-of-function lines were used. This genotype selection controlled for size-dependency of the self-inhibition effect, i.e. enabled a meaningful comparison of larger (e.g. co-segregant) and smaller (e.g. *min7-2*) genotypes.

Plants and growth conditions

Competition experiment: Seeds of all accessions were sown directly onto soil (four parts Einheitserde ED73, Gebrüder Patzer, Germany; one part quartz sand) in February 2016. Pots of a given block were randomly placed into trays covered with plastic lids for germination. In order to ensure the growth of two plants per pot, multiple seeds were sown (approx. 5-20 seeds) per position in a pot, and the two genotypes (and all monocultures) were sown at a distance of approximately 3-4 cm apart. Once seeds had germinated, surplus seedlings were removed, such that only one (two for monocultures) healthy seedling remained per genotype per pot. Block 1 was sown on February 17$^{th}$ and block 2 on February 18$^{th}$ 2016, and pots were placed in trays in a greenhouse compartment. Additional light was provided if necessary, achieving a photoperiod of 14 hours. Day-time and night-time temperatures were maintained around 20–25 °C and 16–20 °C, respectively. Seedlings were thinned continuously until a single, healthy seedling remained per position. Trays were randomly re-arranged within the greenhouse every 3-5 days. After 5-5.5 weeks, pots were transferred from trays onto three tables with automated watering and randomly re-arranged every week. Flowering shoots of individual plants were tied to wooden sticks as they grew taller than approx. 10 cm. All plants were harvested on April 14th (Block 1) and April 15$^{th}$ (Block 2) 2016, i.e. approx. eight weeks after sowing. Each plant was cut below the rosette and individually dried at 65°C for 4-5 days and then stored at room temperature until weighing. Roots from a pot were isolated by thoroughly rinsing off the soil through a metal sieve, and total root mass determined after drying at 65°C for four days. Flowering time during the experiment was determined every 2–3 days by scoring all individuals that had a flowering bolt of >0.5 cm.

Density gradient: Monocultures were sown in pots of 9×9×10 cm (inner pot diameter ~ 8×8 cm) at densities of either 9, 16 or 25 plants per pot, on the same soil and under the same conditions as used above and for 54 days. Because some seedling

379 mortality was observed early in the experiment, realized planting density was re-
380 evaluated using photographs taken 27 days after sowing, i.e. at a time where only
381 limited competition was apparent. Above-ground biomass was then harvested, dried,
382 and weighed as described.
383 Independent biomass allocation measurements: For an independent assessment of
384 root-to-shoot biomass ratios in the studied natural accessions, 80 genotypes that were
385 used in the main competition experiment were grown for 43 days either as single
386 plants or as monoculture (consisting of four plants per pot) and in pots of 7×7×8cm
387 size on a mixture of one part ED73 and four parts quartz sand. The measurements
388 were performed as described above. Measurements of root-to-shoot ratios of *AtMIN7*
389 co-segregants and *min7-2* loss-of-function mutants were performed independently,
390 under the same conditions and at 50 days after sowing.
391
392 Statistical analyses
393 All statistical analyses were performed using the statistical software R version
394 3.4.1 (*41*). Average individual performance of genotypes across mixtures or
395 monocultures were estimated using least square means from a model including just
396 block and genotype. Monoculture biomass per individual (i.e. total average
397 monoculture biomass divided by two) was then fitted as function of linear and
398 quadratic forms of individual biomass, using the R-function lm. The G-I trade-off
399 value was determined as orthogonal distance by determining the point in the
400 quadratic heuristic that was closest to the respective point by non-linear minimization
401 using the R-function nlm. The GWAS analyses were performed with easyGWAS
402 (https://easygwas.ethz.ch) (*42*), using the EMMAX algorithm (*43*) and using SNPs
403 from the 250k SNP chip (http://bergelson.uchicago.edu/) or the 1001 genomes
404 project (http://1001genomes.org/). SNPs with a minor allele frequency below 5%
405 were removed. For the density gradient experiment, productivity was modelled in
406 dependence of the fixed terms area_per_individual, allele, plus their interaction. The
407 corresponding random terms were accession, and the interaction between accession
408 and area_per_individual. The realized densities deviated from sown densities
409 because of a relatively high initial mortality. Therefore, we instead used densities
410 determined from photographs of each pot that were made mid-way through the

411 experiment. Two pots were removed from the analysis because realized densities
412 were much higher than planted densities, probably because they accidentally had not
413 been thinned to the intended densities.
414

415 **Acknowledgements**
416

417 We thank Bernhard Schmid (UZH) and Andrea Patocchi (Agroscope) for support
418 and helpful discussions, Cyrille Violle (CEFE) for helpful comments on the
419 manuscript, Matthias Philipp, Daniel Trujillo and Mariela Soto Araya for help with
420 sowing and harvesting the competition experiment, and Matthias Furler for technical
421 support in the greenhouse. This work was supported by the University of Zurich,
422 Agroscope, an Advanced Grant of the European Research Council (to UG), and an
423 Ambizione Fellowship (PZ00P3_148223) of the Swiss National Science Foundation
424 (to SEW). FV acknowledges funding from the French Agency for Research (ANR
425 grant ANR-17-CE02-0018-01, 'AraBreed'), and the Agreenskills fellowship
426 programme (grant agreement n° 3215), which has received funding from the EU's
427 Seventh Framework Programme under the agreement N° FP7-609398.
428

429 **Author contributions:**
430

431 SEW, NDP and PAN designed the research, SEW performed the experiments
432 with help from NDP and SL. SEW and PAN performed the analyses and wrote the
433 manuscript with input from JM, FV, and UG. NDP, JM, FV, and UG also
434 contributed technical resources and data. All authors revised and approved the final
435 version of the manuscript.
436

437 **Data availability**

438 The datasets described and a basic analysis script are available through the
439 Zenodo data repository (DOI:10.5281/zenodo.2659735). More extensive analysis
440 scripts are available from the authors upon request.
441

442 **Competing interests**

443 The authors declare no competing financial interests.

444

445 **References**

446

447 1. A. Watson *et al.*, Speed breeding is a powerful tool to accelerate crop research
448 and breeding. *Nat. Plants*. **4**, 23–29 (2018).

449 2. J. Crossa *et al.*, Genomic Selection in Plant Breeding: Methods, Models, and
450 Perspectives. *Trends Plant Sci.* **22**, 961–975 (2017).

451 3. R. T. Furbank, M. Tester, Phenomics - technologies to relieve the phenotyping
452 bottleneck. *Trends Plant Sci.* **16**, 635–644 (2011).

453 4. D. K. Ray, N. Ramankutty, N. D. Mueller, P. C. West, J. A. Foley, Recent
454 patterns of crop yield growth and stagnation. *Nat. Commun.* **3** (2012),
455 doi:10.1038/ncomms2296.

456 5. D. K. Ray, N. D. Mueller, P. C. West, J. A. Foley, Yield Trends Are
457 Insufficient to Double Global Crop Production by 2050. *PLoS One*. **8**, e66428
458 (2013).

459 6. N. E. Borlaug, in *Third International Wheat Genetics Symposium* (1968), pp 1–
460 36.

461 7. G. S. Kush, Green revolution: the way forward. *Nat. Rev. Genet.* **2**, 815–821
462 (2001).

463 8. P. Hedden, The genes of the Green Revolution. *Trends Genet.* **19**, 5–9 (2003).

464 9. W. Spielmeyer, M. H. Ellis, P. M. Chandler, *Semidwarf* (*sd-1*), "green
465 revolution" rice, contains a defective gibberellin 20-oxidase gene. *Proc. Natl.*
466 *Acad. Sci.* **99**, 9043–9048 (2002).

467 10. C. M. Donald, in *Wheat Science - Today and Tomorrow*, L. T. Evans, W. J.
468 Peacock, Eds. (Cambridge University Press, 1981), pp. 223–247.

469 11. C. M. Donald, The breeding of crop ideotypes. *Euphytica*. **17**, 385–403 (1968).

470 12. P. R. Jennings, Plant Type as a Rice Breeding Objective. *Crop Sci.* **4**, 13–15
471 (1964).

472 13. P. R. Jennings, J. J. De Jesus, Studies on competition in rice I. Competition in
473 mixtures of varieties. *Evolution.* **22**, 119–124 (1968).

14. D. N. Duvick, J. S. C. Smith, M. Cooper, in *Plant Breeding Reviews. Part 2. Long Term Selection: Crops, Animals and Bacteria, Vol. 24*, J. Janick, Ed. (JohnWiley & Sons, New York, 2004), pp. 109–151.

15. S. Peng, G. S. Khush, P. Virk, Q. Tang, Y. Zou, Progress in ideotype breeding to increase rice yield potential. *F. Crop. Res.* **108**, 32–38 (2008).

16. S. A. Dudley, Plant cooperation. *AoB Plants*. **7**, plv113 (2015).

17. W. M. Muir, Group selection for adaptation to multiple-hen cages: Selection program and direct responses. *Poult. Sci.* **75**, 447–458 (1996).

18. M. A. Nowak, Five rules for the evolution of cooperation. *Science.* **314**, 1560–1563 (2006).

19. M. J. Wade, P. Bijma, E. D. Ellen, W. Muir, Group selection and social evolution in domesticated animals. *Evol. Appl.* **3**, 453–465 (2010).

20. C. Goodnight, The influence of environmental variation on group and individual selection in a cress. *Evolution.* **39**, 545–558 (1985).

21. R. F. Denison, *Darwinian Agriculture* (Princeton Univ. Press, Princeton, NJ, 2012).

22. M. W. Horton *et al.*, Genome-wide patterns of genetic variation in worldwide *Arabidopsis thaliana* accessions from the RegMap panel. *Nat. Genet.* **44**, 212–216 (2012).

23. J. Weiner, Y. L. Du, C. Zhang, X. L. Qin, F. M. Li, Evolutionary agroecology: individual fitness and population yield in wheat (*Triticum aestivum*). *Ecology*. **98**, 2261–2266 (2017).

24. C. Alonso-Blanco *et al.*, 1,135 genomes reveal the global pattern of polymorphism in *Arabidopsis thaliana*. *Cell*. **166**, 481–491 (2016).

25. Y. H. Zhu, J. Weiner, M. X. Yu, F. M. Li, Evolutionary agroecology: Trends in root architecture during wheat breeding. *Evol. Appl.* **00**, 1–11 (2018).

26. S. Atwell *et al.*, Genome-wide association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. *Nature*. **465**, 627–631 (2010).

27. M. Gersani, J. S. Brown, E. E. O'Brien, G. M. Maina, Z. Abramsky, Tragedy of the commons as a result of root competition. *J. Ecol.* **89**, 660–669 (2001).

28. V. Srinivasan, P. Kumar, S. P. Long, Decreasing, not increasing, leaf area will raise crop yields under global atmospheric change. *Glob. Chang. Biol.* **23**, 1626–163 (2017).

29. J. G. Waines, B. Ehdaie, Domestication and crop physiology: Roots of green-revolution wheat. *Ann. Bot.* **100**, 991–998 (2007).

30. A. Roucou *et al.*, Shifts in plant functional strategies over the course of wheat domestication. *J. Appl. Ecol.* **55**, 25–37 (2018).

31. M. Todesco *et al.*, Natural allelic variation underlying a major fitness trade-off in *Arabidopsis thaliana*. *Nature*. **465**, 632–636 (2010).

32. K. Nomura *et al.*, A bacterial virulence protein suppresses host innate immunity to cause plant disease. *Science.* **313**, 220–223 (2006).

33. H. Tanaka *et al.*, Cell Polarity and Patterning by PIN Trafficking through Early Endosomal Compartments in *Arabidopsis thaliana*. *PLoS Genet.* **9**, e100354 (2013).

34. H. Tanaka, S. Kitakura, R. De Rycke, R. De Groodt, J. Friml, Fluorescence Imaging-Based Screen Identifies ARF GEF Component of Early Endosomal Trafficking. *Curr. Biol.* **19**, 391–7 (2009).

35. A. Nemri *et al.*, Genome-wide survey of *Arabidopsis* natural variation in downy mildew resistance using combined association and linkage mapping. *Proc. Natl. Acad. Sci.* **107**, 10302–10307 (2010).

36. C. H. Foyer, A. V. Ruban, P. J. Nixon, Photosynthesis solutions to enhance productivity. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160374 (2017).

37. P. F. South, A. P. Cavanagh, H. W. Liu, D. R. Ort, Synthetic glycolate metabolism pathways stimulate crop growth and productivity in the field. *Science.* **363**, eaat9077 (2019).

38. J. Kromdijk *et al.*, Improving photosynthesis and crop productivity by accelerating recovery from photoprotection. *Science (80-. ).* **354**, 857–861 (2016).

39. R. F. Denison, E. T. Kiers, S. A. West, Darwinian Agriculture: When Can Humans Find Solutions Beyond The Reach of Natural Selection? *Q. Rev. Biol.* **78**, 145–168 (2003).

40. S. J. Gould, E. S. Vrba, Exaptation—a Missing Term in the Science of Form. *Paleobiology*. **8**, 4–15 (1982).

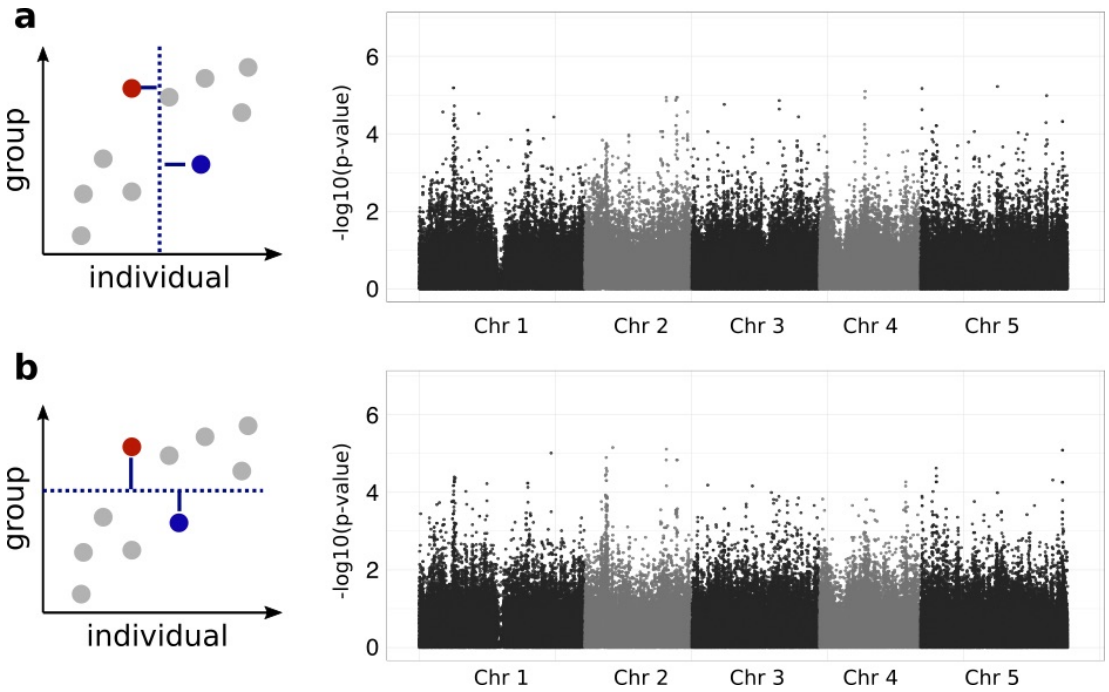
41. R Core Team, R: A Language and Environment for Statistical Computing. *R Found. Stat. Comput. Vienna, Austria* (2017), p. ISBN 3-900051-07-0, , doi:http://www.R-project.org/.

42. D. G. Grimm *et al.*, easyGWAS: A Cloud-Based Platform for Comparing the Results of Genome-Wide Association Studies. *Plant Cell*. **29**, 5–19 (2016).

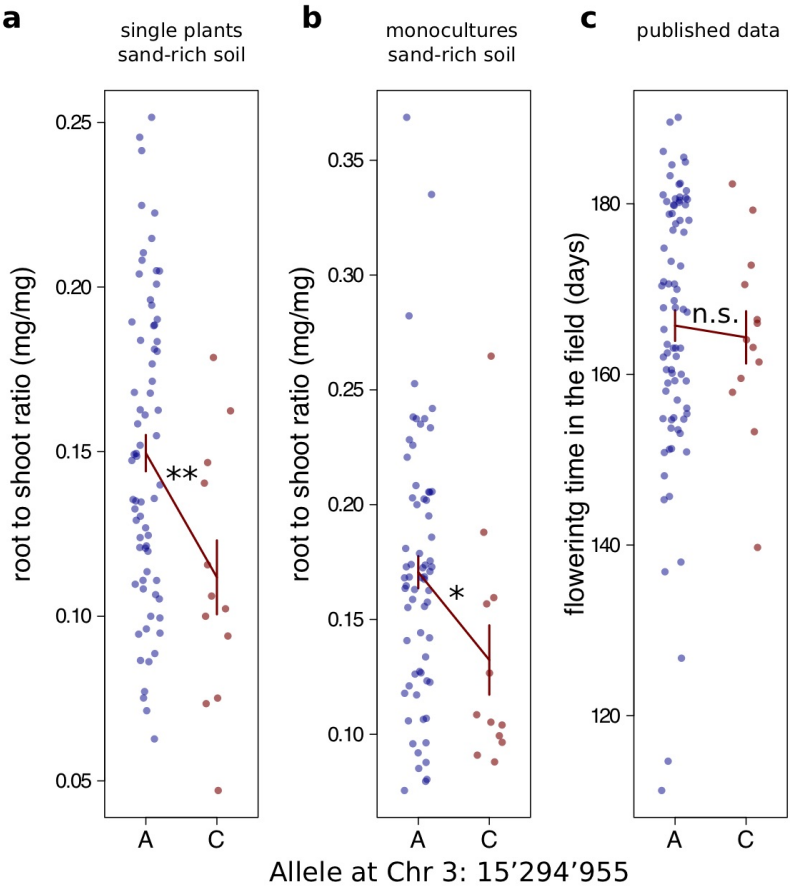
43. H. M. Kang *et al.*, Variance component model to account for sample structure in genome-wide association studies. *Nat. Genet.* **42**, 348–354 (2010).

# Supplemental Material

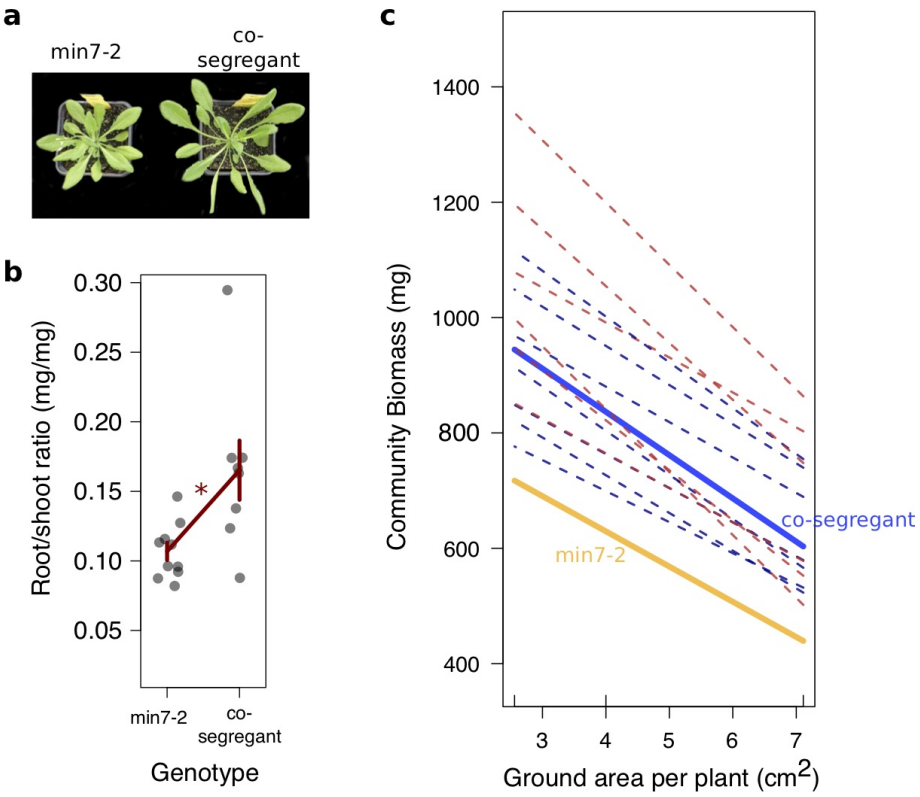

**Supplemental Figure S1: Experimental setup of the competition experiment**. **a. - c.** Photos show the experiment at sowing (**a**), midway through the experiment (**b**) and at harvest day (**c**).




**Supplemental Figure S2. Association tests for variation in average individual performance across mixtures (a) or average monoculture performance (b).**




556 **Supplemental Figure S3. Associations of SNP Chr3:15'294'955 with**
557 **phenotypic variation in traits related to plant strategies. a.** and **b.** Shoot-to-root
558 ratios for genotypes grown in monocultures (**a**) or as individual plants (**b**) in an
559 independent experiment and on sand-rich soil are shown, as well as published data of
560 genotypic means in flowering time in the field (*26*) (**c**). Bars show mean ± s.e. ** =
561 ANOVA $p < 0.01$; * = ANOVA $p < 0.05$; n.s. not significant.
562




564 **Supplemental Figure S4: Altered growth and root-allocation in *min7-2***
565 **mutant plants, but no difference in self-inhibition along a planting density**
566 **gradient. a.** and **b.** Differences in rosette habit (**a**) and shoot-to-root ratio (**b**) in
567 *min7-2* homozygous and wild-type co-segregant lines. * = ANOVA P-value < 0.05 **c.**
568 Decrease of self-inhibition of different genotypes along a planting density gradient.
569 Red/blue dashed lines represent reaction norms or genotypes carrying different
570 alleles at Chr 3 SNP 15'294'955, the yellow solid line represents the reaction norm
571 of the *min7-2* loss-of-function mutant, and the blue solid line the reaction norm of the
572 co-segregant (Col-0 background) genotype.
573
574
575 **Supplemental Dataset S1:** List of *A. thaliana* accessions used in the study, their
576 estimated productivities across mixtures and monocultures, and measured trait
577 values.