Effects of genomic and functional diversity on stand-level productivity and performance of non-native Arabidopsis

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Abstract

Biodiversity can affect the properties of groups of organisms, such as ecosystem function and the persistence of colonizing populations. Genomic data offer a newly available window to diversity, complementary to other measures like taxonomic or phenotypic diversity. We tested whether native genetic diversity in field experimental stands of *Arabidopsis thaliana* affected their aboveground biomass and fecundity in their colonized range. We found no relationship between genetic diversity and stand total biomass. Increasing stand genetic diversity did increase fecundity in high resource conditions. Polyculture (multiple genotypes) stands consistently yielded less biomass than expected based on the yields of component genotypes in monoculture. This under-yielding was strongest in stands with late-flowering and high biomass genotypes, potentially due to interference competition by these genotypes. Using a new implementation of association mapping, we identified genetic loci whose diversity was associated with stand-level yield, revealing a major flowering time locus associated with under-yielding of polycultures. Our field experiment supports community ecology studies that find a range of diversity-function relationships in the field. Nevertheless, our results suggest diversity in colonizing propagule pools can enhance population fitness. Furthermore, interference competition among genotypes differing in flowering time might limit the advantages of polyculture.

INTRODUCTION

The characteristics of groups of organisms, such as their genetic diversity, can affect their persistence and collective functions. The emergent properties of groups of organisms are major topics in fields such as agriculture and ecology [1–3]. The mechanisms underlying the benefits of diversity for group-level performance can be divided into at least two major categories [4]. First, greater diversity can reduce the negative effects associated with high density populations or communities. This can occur via diversity in resource use that reduces competition, diversity in susceptibility to enemies that reduces “apparent” competition, or facilitation among diverse individuals. Second, diversity can increase group-level performance via a sampling effect: greater diversity increases the chance that high-performing individuals will be present. By contrast, diversity can also lead to reduced group-level performance. This can occur when more diverse groups tend to have lower performing individuals (e.g. when diversity is driven by immigration of maladapted individuals) [5,6] or when diversity results in interference competition among different types [7]. While diversity effects on ecosystem functions (EF) can act at both population and community levels, they have been mostly studied at the community level (considering species and higher levels of diversity) [8,9]. However, *intraspecific* diversity can have major impacts on EF, potentially surpassing interspecific effects when a few species dominate biomass [10].

Largely independent of the work on EF, invasion biologists have studied how genetic diversity affects the probability that a population establishes in a new location. Though an independent line of research, diversity can affect establishment via many of the same mechanisms described above. Invasion biology has long investigated how the number of individuals in a founding group affects colonization success [11,12]. Evidence from many studies suggests that increased genetic diversity, rather than increased numbers of individuals *per se*, causes improved establishment [13], growth rate [13–15], biomass production [2,16,17], and persistence of colonizing populations, and decreases vulnerability to environmental changes (reviewed in [18]). The effects of diversity on group-level performance (e.g. average fitness) and EF are likely to be conditional on the environment. For example, positive facilitative interactions may dominate in extremely harsh environments, leading to stronger positive diversity effects [19,20], or novel environments might be more limited by diversity due to a rarity of high-functioning individuals. Empirical studies of genetic diversity in an invasion context have found it favorable under some conditions but not others [2,21] and theoretical predictions also conflict [17,22].

Diversity effects on the performance of a group of organisms arise fundamentally due to the effects of phenotypic diversity [23]. However, the phenotypes that affect group-level performance are often unknown. Instead, genetic, taxonomic, or phylogenetic diversity can be useful proxies. Genetic markers can measure diversity and it is now feasible to characterize whole genome diversity in many non-model systems. However, past studies of intraspecific diversity and EF have used either genotypes of unknown relatedness [16,17], or have used a small number of markers having unclear connections to functional variation [2,24,25]. Genetic diversity effects may be most strongly associated with loci that underly complex phenotypes associated with resource economics. Genetic variation in complex traits corresponding to life history and resource use likely involves changes in many loci [26,27], necessitating a genome-wide perspective. Furthermore, genetic mapping approaches to identify genetic loci controlling phenotypic variation may be useful for identifying loci controlling diversity effects on EF [20,28].

Here we investigate how intraspecific diversity influences productivity and fecundity for the model plant *Arabidopsis thaliana* across environmental conditions in a field experiment outside of the native range of this species. Arabidopsis is useful for our questions: it is a model for ecological genomics [29], diverse germplasm with resquenced genomes is available [30], and it exhibits variation in resource strategies and life history [31,32] suggesting that diversity may impact EF. Our study builds upon previous work by studying Arabidopsis in ecologically realistic and relevant field experimental conditions, including a low nutrient well-drained soil treatment, and studying stands with up to 20 genotypes. Because Arabidopsis is largely selfing and we studied a single generation, we set aside the effects of diversity on population performance due to sexual reproduction, such as heterosis.

Experimental studies of biodiversity effects typically use randomly assembled groups of genotypes or species, despite existing prior knowledge of potential drivers of compositional and diversity effects on EF. Here, in addition to randomly assembled groups, we used knowledge of our system to develop *a priori* predicted groups of genotypes that we hypothesized would exhibit particularly strong differences in ecosystem function, and groups of genotypes we predicted would be particularly well-suited for the experimental site. We used information indicative of local adaptation to the climate at our site as well as information on genetic diversity in an ecologically important plant trait (flowering time) to design collections of genotypes predicted to differ in performance or to perform well.

METHODS

Plant material

We studied 60 diverse Arabidopsis genotypes from the native Eurasian range of Arabidopsis, mainly from the Mediterranean, central Asia, the UK and central Europe (Figure S1). All genotypes are representatives of natural inbred lines that had their genomes resequenced [30]. We selected these genotypes based on diversity and seed availability from a common seed production environment used in previous experiments.

Experimental design

To assess the impact of different levels of genetic diversity in experimentally assembled non-native populations of Arabidopsis, we measured performance of Arabidopsis stands in a field common garden at a site (40.8106º N, 77.8472º W) in the non-native range near other established non-native populations (within ~10 km) but with none at this site (within ~1km). Thus our experimental stands were likely not influenced by density-associated processes driven by wild individuals nearby. To assess the environmental context dependency of diversity effects, we replicated all stand genotype compositions in two soil types: a putatively benign high-resource potting mixture, and a lower resource sandy soil (described below). Each of the 60 genotypes were grown in monoculture in three replicate stands for each of the two soil environments, for a total of 360 monoculture stands (Figure S2).

Prediction stands

We began by constructing polycultures using *a priori* hypotheses about factors likely to affect productivity. We used five different criteria to generate these 'prediction stands': (1) genomic diversity among accessions, (2) climate similarity of collection location to our field site, combined with genomic diversity, (3) early flowering genotypes, (4) late flowering genotypes, (5) climate similarity of collection location to our study site, combined with flowering time diversity. Details on the algorithms we used to assemble these stands are found in the Online Supplement. Two stand compositions were chosen for each of the five prediction scenarios at each diversity level (2, 10, 20), for a total of ten prediction stand compositions for each diversity level. Each of the prediction stands were planted into both of the two soil environments, for a total of 60 prediction stands.

Randomly assembled stands

After genotypes were assigned to prediction stands, we also generated random stand compositions. In assembling these stands we sought to limit similarity of stands within a

treatment and within increasing diversity levels [16,33]. We generated polycultures of either 2, 10, or 20 different randomly selected genotypes, with ten stand replications per diversity level, for a total of 30 different randomly generated polycultures. All genotypes were included within the 10 stand replications, randomly assigned to each replication such that each replication had a different assortment of genotypes but had the same diversity level. Each of these polycultures were planted into both soil environment treatments with 10 replications of diversity level each for a total of 60 randomly assigned polyculture stands. Further methods on assigning these stand compositions are found in the Supplement

Field experimental conditions

All seeds were stratified on April 30, 2018 in tap water for 4 days and planted on May 3-4, 2018 in square 10.16 x 10.16 x 8.89 cm cow manure pots (CowPots, East Canaan, CT), each of which contained a 20-plant stand. Assigned genotypes for each stand were randomly planted into a gridded location within the stand (4 rows of 5 plants each) and were planted approximately 1.5 cm apart. Stands designated as a low resource treatment were filled with 50% medium commercial grade sand and 50% potting mix (Premier pro-mix PGX), whereas stands representing a high resource treatment contained 100% potting mix. All potting components were autoclaved prior to filling pots.

After each stand was planted, it was placed into darkness at 4°C for at least 24 hours. Once all stands were planted, stands were placed into a growth room at 20-25°C with a 20 hour photoperiod with light levels between 100-200 PAR, and covered until germination. Once cotyledons were expanded, plants were thinned to one plant per position in stand (giving 20 plants), and trays of pots were rotated every other day between the growth room and a Percival growth chamber (Model PGC-40L2, Percival Scientific, Inc., Perry, IA) set to 600-620 PAR and daily temperature cycles from 15 to 26°C, to acclimate plants to higher light levels and cooler night temperatures. After thinning and eight days prior to transplanting into the field, the germination rate for each planting position within stands was 92%.

Pots were transplanted to the 850 m^2 ploughed field site on May 24, 2018. The site was located at 314 m asl in a meadow on flat topography at the bottom of a slope, with soils that were high in clay (Hagerstown silty clay loam, USDA Web Soil Survey https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx). Pot locations in the field were randomly assigned and pots were buried into the soil so that the pot soil was at the same level as the field soil. All monoculture, polyculture, and prediction pots (stands) across both treatments were randomly assigned locations within the field plot (Figure S2). Stands were

organized into four blocks, each block containing 120 stands (4 x 30 stands). There was a 15.24 cm buffer between stands within a block, and a 91.44 cm buffer between blocks and between blocks and the edge of the ploughed site. The field site was completely fenced in and was weeded for non-Arabidopsis plants twice weekly. Initial plant number per stand was assessed by counting the surviving seedlings five days after transplanting stands into the field, totaling 8384 plants across the 480 stands (averaging 17.5 plants/stand on May 29).

Phenotypes

Specific leaf area (SLA) were measured for all monoculture stands when the first plant in the entire experiment was ready to measure fecundity (June 21, defined as plants with more than 50% browning or yellowing fruits). One representative, healthy leaf was selected from one plant in the stand for both SLA. Leaf area (including the petiole) was measured on leaves selected for SLA using Easy Leaf Area [34] on an Android device, which analyzes pixel RGB to distinguish between the leaf and background within digital images, using a red 4 cm^2 square reference to calculate leaf area. Dry leaf weight (including the petiole) was measured using a Sartorius analytical micro balance (Model CP2P, Goettingen, Germany). Canopy area was similarly measured for each stand just prior to the first harvested plant using Easy Leaf Area [34].

Flowering status was recorded twice per week starting May 29, decreasing to once per week due to slower rate of flowering starting on July 6. Each stand was scored for five stages of flowering, based on percentage of plants that flowered: (1) when at least one plant flowered, but less than 25% of plants flowered, (2) when 25% of plants flowered, but less than 50% of plants flowered, (3) when 50% of plants flowered, but less than 75% of plants flowered, (4) when 75% of plants flowered, but less than 100% of plants flowered, and (5) when 100% of plants flowered. Flowering was defined as at least one open flower on a plant.

Harvest

Once a plant reached maturity, defined as when more than 50% of siliques were brown/yellow, it was harvested. We chose this phenological criterion for harvest to avoid loss of senescing plants and dehiscing fruits from wind and water. In our experience these genotypes at this stage produce very little additional biomass and fruits. When harvesting plants, we recorded the total silique number on the plant, and the length of one representative central silique was measured and recorded. The plant's aboveground parts (excluding the root) were cleaned of soil, placed into the corresponding stand envelope and dried for at least 24 hours in a drying oven at 200 °C prior to obtaining biomass.

Total above-ground biomass was measured for the remaining plants that did not produce mature fruits by July 18. These remaining plants were harvested on July 18-20. These dates were chosen for final biomass harvest because many plants that had not flowered started to senesce and would thus be challenging to collect at a later date, and no plant had initiated flowering in the prior 10 days. Plants that were in flower at this time were aborting nearly every fruit likely due to high temperatures. Each stand had a corresponding envelope in which all plants within the stand were stored and dried after harvest. Total number of plants harvested for each stand was recorded, and after each day of harvest, all plants were dried as above. We were unable to harvest 50 stands that were destroyed by intruding dogs, escaped livestock, or flooding.

Measures of stand composition and diversity

To estimate genomic diversity of stands, we used published SNPs from resequencing data [30]. We calculated the genetic distance matrix using the R package SNPRelate [35] and then calculated the mean genetic distance among plants sown in a stand (including zero distance for individuals of the same genotype). We also estimated phenotypic variation, based on our new SLA data and published flowering time data [30]. For SLA, we took breeding values of log(SLA) measured on plants here in monoculture and calculated mean for individual plants in all stands. Flowering time composition and diversity were respectively estimated using individuals' breeding value averages of the 10ºC and 16ºC published flowering time experiments [30].

Statistical analyses

To gain general insight into the sources of variation in phenotypic, fecundity and biomass production, we tested for treatment effects, estimated broad-sense heritability, and estimated the genomic signature of performance in monocultures. To test for treatment effects on trait plasticity in monocultures, we implemented linear mixed models using the R package 'VCA' [36] and included genotype and block as random effects and soil treatments as fixed effects. We estimated broad sense heritability of stand-level traits and performance for monocultures using linear models in R where genotypes were fixed effects, taking R^2 of these as broad-sense heritability. We tested for a genomic signature in fecundity and biomass production using genomic selection models, where traits are a function of genotype-specific random effects that are correlated according to the genome-wide similarity matrix, using the R package 'rrBLUP' [37]. We used out-of-sample prediction and ten-fold cross validation to get an estimate of the predictive ability of genome-wide similarity.

To address our primary research questions, we then tested whether multiple measures of diversity affected stand level performance, assessed by fecundity, aboveground biomass, and leaf canopy area. In our analyses, we controlled for variation among stands in the number of plants surviving transplant or germinating late, with a minimum of 11 was required for inclusion in analysis. We used two different counts of plants surviving transplant, on May 29 and June 12, and took the maximum, but we found results were similar when using the count on either date.

We used linear regression models to test diversity effects on stand-level yield while accounting for additional sources of error. The covariates were each tested in models including an interaction with the resource-limitation treatment. Covariates tested in separate models included diversity treatment level (1, 2, 10, or 20 genotypes), genomic similarity (mean genetic distance among plants in a stand), stand-level average of mean flowering time for each genotype, a measure of the stand-mean climate distance from the field site, and stand-mean SLA breeding value. We similarly tested for stand diversity and composition effects on fecundity (mean estimated total silique length per fruiting plant in stand).

We calculated the difference between the observed polyculture biomass yields and that expected based on yields of monocultures and their proportional representation in the polyculture. This difference is a commonly studied metric in community diversity-ecosystem function studies [4], and we refer to this quantity as the deviation from monoculture expectation (DME, note this is referred to the net diversity effect by [4]). We tested how the measures of diversity and composition described above were related to DME, using linear models with a parallel structure to those used for aboveground biomass and fecundity (described above).

To determine whether our prediction stands were successful at explaining variation in fecundity and biomass production, we compared different stand types in an ANOVA. Different prediction criteria were each coded as a factor level as were randomly assembled stands. Two-way ANOVA showed no significant treatment-stand type interaction, thus we focused on stand type effects in a two-way ANOVA without interactions. We compared each pair of stand types with post-hoc Tukey's tests with FDR control. Because only two stands predicted to be later flowering produced any fruit, we removed this plot type from our analysis of fecundity in prediction plots.

To map loci across the Arabidopsis genome where allele frequency and variance were related to stand biomass and DME, we used an approach inspired by genome wide association mapping. Specifically, we tested how both stand level per plant biomass and DME were associated with allele frequency and variance (the latter a measure of diversity for a biallelic

locus) in each stand, for each SNP. We used SNPs from published whole genome resequencing [30]. We excluded SNPs segregating at <0.05 minor allele frequency in our panel of 60 genotypes, leading to a total of ~1.9M SNPs. Because background variation in small effect mutations across the genome can contribute to phenotypic variation, we controlled for genome-wide similarity among stands. To control for the genomic background effect, we used an estimated kinship matrix calculated as the similarity among stands in either allele frequency or variance at all SNPs [38]. This builds off the traditional mixed-model approach in genome-wide associations for phenotypes. For each SNP's allele frequency or variance, we used a linear mixed model to test for association with total yield or DME, including a random effect that was correlated among stands according to the estimated kinship matrix using EMMA [38].

RESULTS

Plastic changes in traits and performance in monoculture stands

Comparing phenotypes for monoculture stands, SLA did not change significantly across treatments (linear mixed-effects models with genotype random effects, log SLA high - low resource = -0.1035 log(cm^2/mg), p = 0.0626). First flowering date was not significantly affected by treatment (high - low resource = -0.36 days, p=0.7667 when not including 'did not flower'; high - low resource = -1.36 days, p = 0.1078 when including 'did not flower'). Both average plant fecundity (high - low resource = 19.3 mm total silique length, p = 0.0444) and total stand fecundity (high - low resource = 343.9 mm, p= 0.0245) were on average greater under high than low resource treatments in monocultures. Biomass per plant in monocultures was slightly but non-significantly greater in the high resource treatment (high - low resource = 0.0026 g, p = 0.0713).

We found moderate to high broad-sense heritability in many traits. Date of first flowering was highly heritable (despite not being monitored daily), with the date of first flowering individual in each stand having heritability of 0.88 in high and 0.79 in low resource treatments (excluding stands where no individual flowered) and 0.87 in high and 0.91 in low resource treatments (assigning non-flowering stands a date 2 days past the harvest date). log(SLA) was fairly heritable, with broad sense heritability being 0.42 in high resource and 0.52 in low resource stands. Heritability of stand total fecundity was 0.37 in high and 0.57 in low resource and for mean flowering plant fecundity 0.38 in high and 0.66 in low resource. Biomass was slightly less heritable, being 0.38 in high and 0.37 in low resource.

Genomic signature of performance variation

There was a strong effect of genome-wide similarity among genotypes on biomass production in monoculture in the low resource treatment. Genomic prediction of per plant biomass in monoculture (square root transformed) based on genome-wide similarity among genotypes with ten-fold cross validation was correlated with actual breeding values for biomass in monoculture in high resource (r = 0.05) and low resource (r = 0.38) treatments. For example, in the low resource treatment a group of closely related ecotypes from the Caucasus region (Azerbaijan and Georgia) were among the most productive, while other clusters of related genotypes from central Europe and Spain had low productivity. We found a similar pattern for mean per plant fecundity in monocultures (genomic prediction accuracy: high resource r = -0.01, low resource r = 0.33).

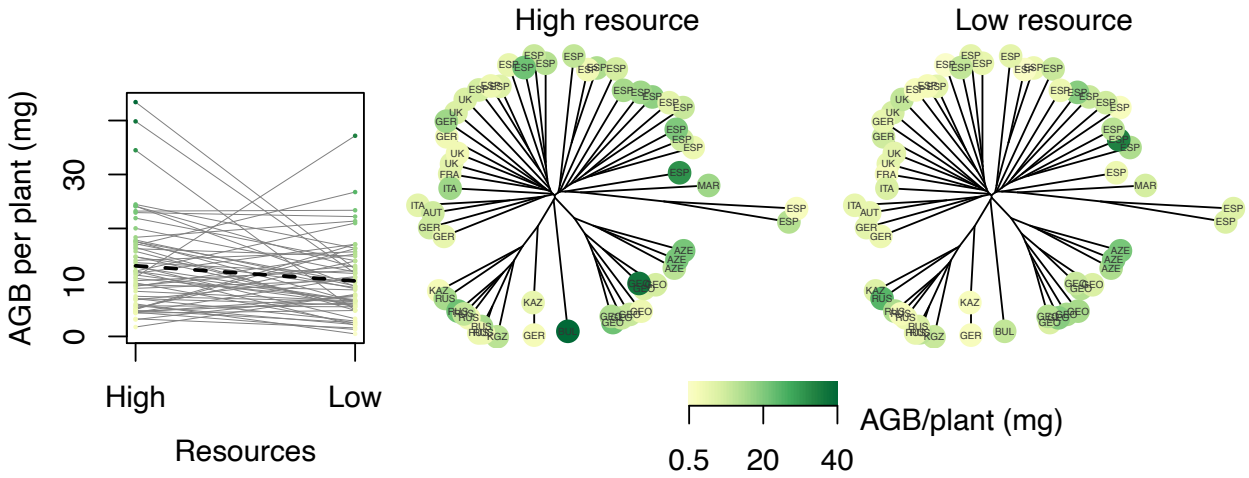

Figure 1. Reaction norms for AGB (left) and neighbor-joining trees (based on pairwise genetic distance), where higher yielding genotypes are colored in green. Three letter ISO country codes indicate the origin of each natural genotype. Two genotypes with poor germination are not shown.

How did composition and diversity of stands impact stand fecundity and productivity?

Among all stands (including monocultures and polycultures), the low resource soil treatment significantly reduced stand fecundity, canopy coverage, and biomass production, as tested in separate linear models of each response variable (Figure 2, Tables 1-2 & S1). We found that a greater number of genotypes in a stand significantly increased the stand level fecundity in the high resource treatment (Table 1) but not the low resource treatment, while other measures of composition and diversity were unrelated with stand fecundity. We found that higher average breeding values for flowering time were associated with significantly greater stand biomass in

both treatments, while lower breeding values for SLA was associated with greater stand biomass only in the high resource treatment. None of the several diversity measures we tested were significantly associated with biomass production.

We also tested if prediction stands had distinct stand level fecundity or biomass from randomly assembled stands (Figure S5). After controlling for multiple comparisons, we did not find a significant effect of stand type in a two-way ANOVA for either plot level fecundity or biomass.

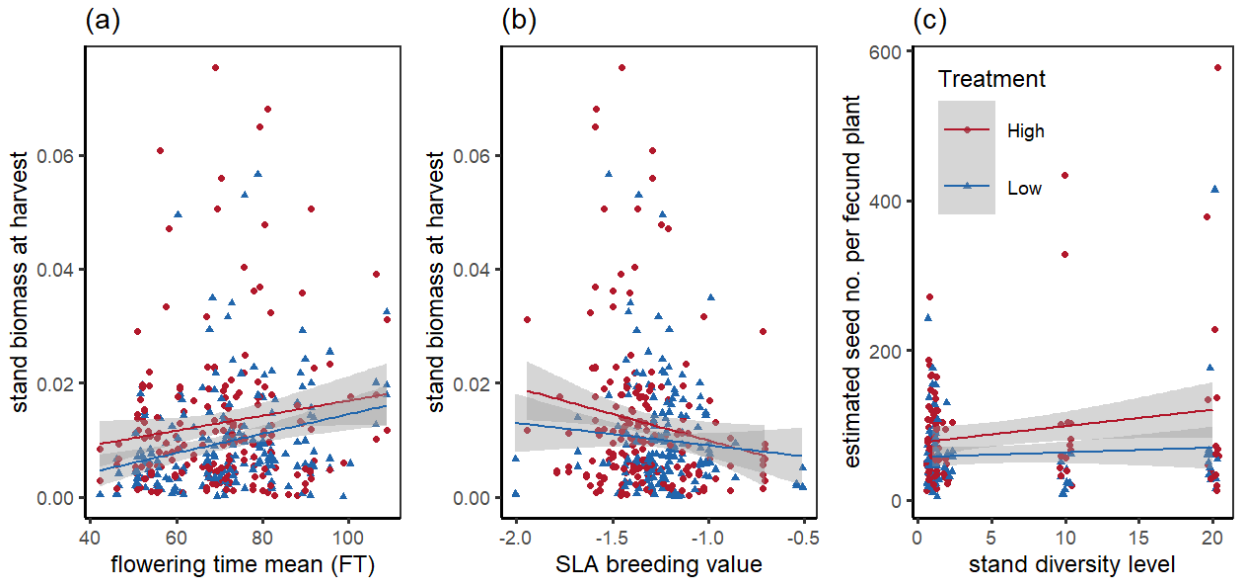

Figure 2. Biomass and fecundity performance in experimental stands of *Arabidopsis thaliana.* Points represent mean value for each stand; red circles indicate stand in the high resource treatment, blue triangles indicate stands in the low resource treatment. Treatment had a significant effect on both biomass and fecundity (Table 1, 2). Shaded areas represent standard error. (a) Later mean breeding values for flowering time from published experiments [30] significantly increased stand biomass at harvest. (b) log(SLA) breeding value had a significant effect on stand biomass at harvest in the high resource treatment. (c) Experimental stand diversity level (1, 2, 10, 20 genotypes) significantly increased estimated seed number produced per fecund plant in the high resource treatment.

How did polyculture productivity deviate from monoculture expectation?

We found that in both treatments, the yield of polyculture stands was not closely correlated with the expectation based on the yield of their component genotypes in monoculture (high resource, $r = 0.051$, $p = 0.7138$; low resource, $r = 0.007$, $p = 0.9585$). Specifically, polycultures tended to yield less than expected based on the yield of their component genotypes in monoculture. The deviation from monoculture expectation (DME) was significantly less than zero in the high resource stands (median = -61.01 mg, wilcoxon test $p = 0.0025$) and in the low resource stands

(median = -57.13 mg, wilcoxon test $p = 0.0158$). These results were unchanged (both $p < 0.02$) when we generated randomly assembled polycultures to match the number of plants surviving transplant using genotype-specific transplant survival in monoculture.

To evaluate potential causes of negative DME, we tested correlations between DME and explanatory factors. One of our hypotheses was that negative DME could result from competitive inhibition of many smaller plants by late flowering plants whose rosettes grew to overtop the earlier flowering smaller plants. We found that in the high resource treatment, stands with greater average expected flowering time or with the presence of plants with greater flowering time had more negative DME either when considering mean (linear model, flowering time in high resource slope = -0.0064 g/day, $p = 0.0167$, in low resource slope = -0.0012 g/day, $p = 0.6532$) or 90th percentile of flowering time (high resource slope = -0.0051 g/day, $p = 0.0170$, in low resource slope = -0.0006 g/day, $p = 0.7883$, Table S2). We also found (perhaps unsurprisingly) that biomass in monoculture of component genotypes was negative associated with DME in polyculture: stands with greater median or 90th percentile of genotypes' biomass in monoculture showed significantly bigger reductions in polyculture yield in both high and low resource treatments (Table S2). We also tested whether DME might be due to genomic similarity, number of genotypes, or climate of origin of genotypes. We found no strong effects on DME of mean kinship, total tree diversity, number of genotypes, mean SLA, or mean distance to climate of origin along the first five PCs (Table S2).

We also tested if prediction plots had distinct deviations from monoculture expectation (DME). We found that there were significant differences in DME among prediction plot criteria (two-way ANOVA with treatment and stand prediction criteria, including randomly assembled stands: treatment $p = 0.8675$, prediction $p = 0.0433$, only including prediction stands: treatment $p = 0.8258$, prediction $p = 0.0328$). Consistent with the regression of DME on flowering time on all plots, the differences among our prediction plots were largely driven by differences between the predicted early (positive diversity effect) and late flowering (negative diversity effects) stands (Tukey HSD comparison of means, including randomly assembled stands, only significant difference after multiple comparisons correction is: early flowering - late flowering predicted stands DME = 0.27 g, FDR adjusted $p = 0.02920$).

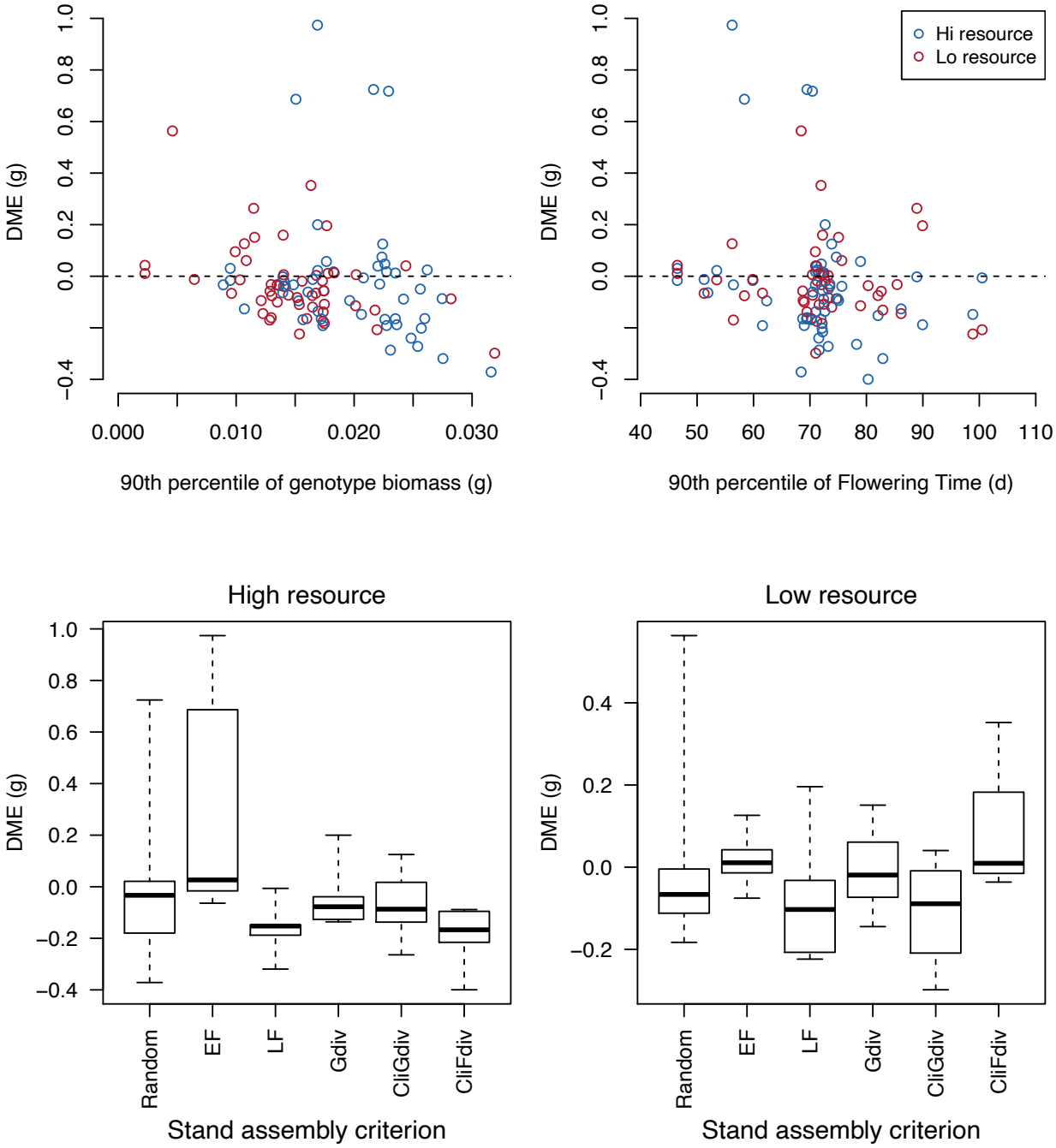

Figure 3. Polyculture deviations from monoculture expectation (DME) in comparison with measures of stand composition (top panels) or stand assembly criteria (bottom panels). (Top panels) Stands with large biomass genotypes, or late flowering genotypes (90th percentiles) also tend to show lower DME (under-yielding), even more so than when measured via mean monoculture biomass or flowering time (Table S2). (Bottom panels) Stands assembled via different criteria show different DME. In particular, stands with genotypes predicted to be more early flowering (EF) had higher DME (over-yielding) compared to late flowering (LF) stands (Tukey HSD, FDR adjusted p = 0.0292).

399

400 *Genome mapping of diversity effects*

401 We tested whether per plant biomass or DME in each treatment were associated with allele
402 frequency or diversity at particular SNPs across the genome. We found that overall, there were
403 few loci with dramatically stronger (outlier) associations with biomass and DME, but rather
404 patterns suggest that the genetic basis of variation in biomass and DME were polygenic.
405 Nevertheless, we found that, in concordance with the association of late-flowering genotypes
406 with under-yielding polycultures, the top SNP (chr. 2, 9584630 bp, TAIR10) associated with
407 DME in the control treatment (both allele frequency and variance association scans) was closest
408 to SHORT VEGETATIVE PHASE (SVP, also known as AGL-22, AT2G22540), a MADS-box
409 transcription factor, one of the top loci associated with natural variation in Arabidopsis flowering
410 time in [30] (Figure 4). Indeed, the minor allele of this SNP that we identified here as having
411 more positive yields in polycultures compared to expected was also associated with earlier
412 flowering at 16C among the 60 genotypes we used from [30] (t-test, $t= -2.6687$, $p = 0.0279$). As
413 the frequency of this early-flowering minor allele increased and the stand variance at this locus
414 increased, DME also became more positive (Figure 4).

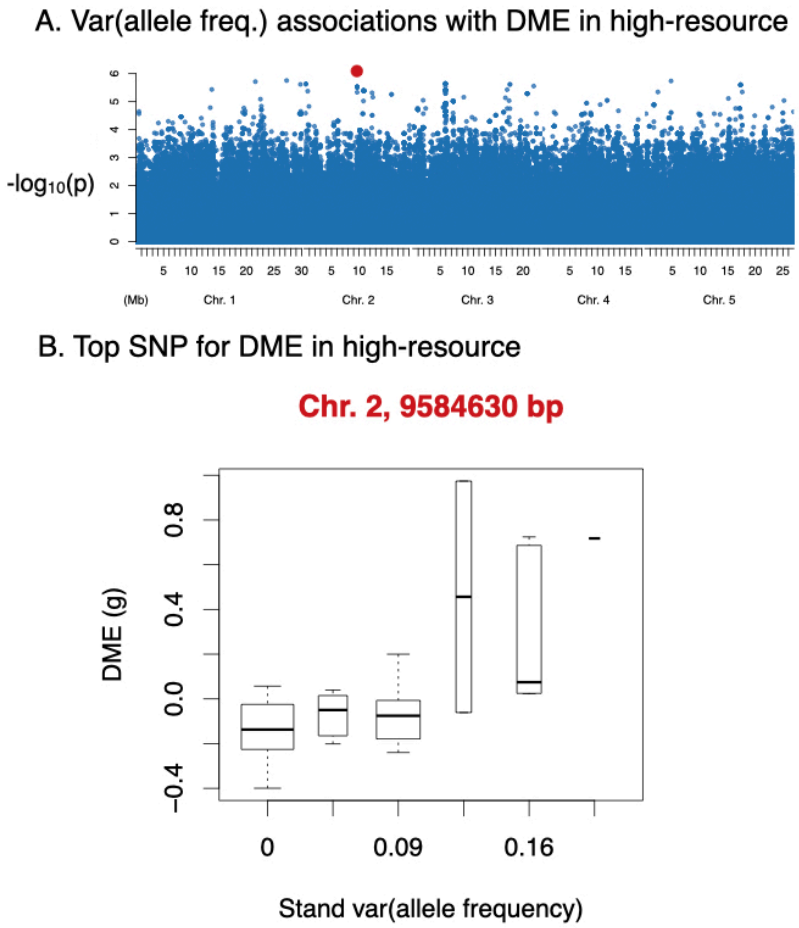

Figure 4: Manhattan plot (panel A) for linear mixed model genome-wide association with 1.9M SNPs allele frequency variance versus deviation from monoculture expectation (DME) in high resource environments. The top SNP is highlighted in red and panel B (this was also the top SNP for allele frequency associations with DME). Boxplot (panel B) shows variance in allele frequency within polycultures (x-axis) at the top SNP (red SNP in panel A, chromosome 2, 9584630 bp) associated with DME of biomass (panel B y-axis) in the high resource environment.

DISCUSSION

Diversity can affect the group-level properties of organisms, including ecosystem functions like carbon and nutrient cycling and population trajectories. These effects of diversity have been often studied via observation of natural, uncontrolled systems that vary in species or genetic diversity and testing whether diversity covaries with group properties [25,39]. In particular, species and higher levels of diversity have been demonstrated to have a range of effects on ecosystem function via multiple mechanisms [8,40]. Here we built on this research to test how

433 intraspecific variation in trait and genomic composition and diversity affect the productivity and
434 fecundity of an established non-native plant in the field. We found generally that the diversity of
435 genotypes did not increase biomass production, but rather polycultures showed lower biomass
436 production than expected, suggesting interference competition among genotypes. This was
437 associated with particularly low polyculture yield of stands containing late-flowering genotypes
438 that had high productivity in monoculture. We identified genetic variation in known flowering time
439 loci associated with these effects. We also found a weak but significant increase in fecundity
440 with the number of genotypes in a treatment, due to unclear mechanisms.
441
442 *Conceptual links between diversity effects on ecosystem function and fecundity*
443 Community ecologists have often hypothesized that more diversity increases ecosystem
444 functions [41,42] while invasion biologists have hypothesized that greater diversity increase the
445 population growth rates of colonizing species [13–15]. These two research programs have not
446 been synthesized but they share much in common. Both of these hypotheses are based on the
447 same underlying biological processes: 1) sampling effects, whereby greater diversity increases
448 the chance a group will contain high functioning/performing individuals, 2) insurance effects (a
449 type of sampling effect), whereby greater diversity increases the chance that a group will
450 contain an individual that is high functioning under some potential new environment, or 3)
451 complementarity effects, whereby diversity relieves negative density effects. Here we sought to
452 connect these ideas and test these hypotheses in *Arabidopsis thaliana*, which is non-native at
453 our research site but suited to the regional environment (as judged by the presence of
454 established populations in the region). We hope that future research will further connect
455 subfields of evolution and ecology that study how diversity effects on group properties arise
456 from the same underlying processes.
457
458 *Diversity effects on average individual fecundity*
459 Because of logistical and (in the case of invasive species) bioethical constraints, many studies
460 of the effect of diversity on population performance focus on the impact on biomass production
461 and may not assess fecundity directly (see [2,16,17]). While none of the diversity metrics we
462 tested had an effect on biomass production, we did find a small but significant effect of genotype
463 number of plot level fecundity in the high resource environment (Fig 2c). The mechanism
464 underlying this effect is unclear, given the lack of an effect on biomass. This may be due to
465 sampling effects, specifically where greater diversity increases the chance a group will contain
466 early flowering and more fecund genotypes. Alternately, interference competition may trigger

467 flowering and fruit production earlier in small (especially early flowering) genotypes to a greater
468 degree than large (especially late flowering) genotypes, leading to positive diversity fecundity
469 associations.
470
471 *Diversity effects on stand-level biomass*
472 We generally found no evidence that increased genetic diversity led to greater stand-level
473 aboveground biomass production of Arabidopsis in the field. Our findings may be explained by a
474 lack of such genetic diversity effects in such Arabidopsis populations in general, or by
475 technical/logistical constraints that led us to overlook such effects. First, raw diversity effects
476 might not have been observed if potential positive effects of diversity (complementarity of
477 resource use or pathogen susceptibility) were opposed by negative effects (interference
478 competition) [7] or if diversity effects did not exist. Our finding of negative reduced polyculture
479 yield compared to expectation from monoculture (DME) suggests this as one potential
480 explanation. Second, diversity effects might have been overlooked if they occurred along
481 dimensions of performance or function that were not measured, such as seed survival or
482 nutrient use [23]. Diversity effects might also have been overlooked if they are strongest across
483 environmental fluctuations unobserved in our single year study [43,44].
484 By contrast, we found consistent under-yielding of polycultures of genotypes compared
485 to the expectations from their biomass in monoculture and relative representation in the
486 polycultures (deviation from monoculture expectation, DME, known in community ecology
487 literature as “diversity effects”) [4,7]. Generally, negative DMEs are thought to arise from
488 processes related to interference competition [7]. More specifically, interference competition can
489 be observed by genotypes being limited more by different genotypes than clonal individuals of
490 the same genotype, as we observed here. This process could play out in our experiment as
491 follows: when grown with genotypes having different trait values, individuals exhibit reduced
492 performance compared to in monoculture with genetically identical individuals, and apparently
493 without much benefit to the performance of the higher performing genotypes. For example, [45]
494 found that *Pseudomonas flourescens* genotypic diversity lead to reduced ecosystem function
495 (host plant protection) due to antagonistic interference (mutual poisoning) among genotypes.
496 These patterns are similar to those that have been interpreted as evidence of plant kin
497 selection, where individuals have higher performance among similar genotypes while reduced
498 performance among different genotypes [21,46,47]. For example, [21] found reduced variance
499 in biomass among individuals and higher individual fecundity of *Plantago lanceolata* when
500 grown among related individuals, which he interpreted as being due to reduced interference

501 competition in high relatedness stands (though the term “interference competition” was not
502 used). This might occur if higher performing genotypes reduce access to resources of lower
503 performing genotypes to a greater degree than those high performing genotypes benefit by
504 being surrounded by fewer of their own type. We found that polyculture plots containing later
505 flowering and larger biomass (in monoculture) genotypes were those that had the strongest
506 negative DME possibly due to shading of different and early flowering smaller neighbors. This
507 explanation for such findings seems more likely than plants’ ability to recognize kin *per se* and
508 reduce interference with neighbors (cf. [47]).
509 We demonstrated how genomic data on individuals in experimental stands can be used
510 to identify genetic loci that are the putative cause of group-level performance. Specifically, the
511 combined performance of groups of individuals can be related to their genetic composition and
512 diversity across the genome. Recent studies using Arabidopsis grown in pots, combined with
513 linkage [20] or association mapping [28] have demonstrated complementary approaches using
514 a smaller number of genotypes and individuals per stand (two genotypes and three-four
515 individuals/pot). Controlled experiments like these and our present study combined with group-
516 level performance and genetic data could be applied to nearly any system. It is not clear
517 whether such approaches could detect genetic loci operating in natural uncontrolled systems,
518 where uncontrolled environmental variation plays an important but often unmeasured role in
519 driving spatial variation in group-level performance. Here, we implemented a study of
520 association of stand level performance with both allele frequency and variance in stands.
521 However, note that to distinguish between effects of variance (diversity *per se*) versus frequency
522 (composition) at a biallelic SNP, a given SNP would need to span a wide range of allele
523 frequencies among stands. This condition is not likely met for most SNPs given they have low
524 minor allele frequency, thus allele frequency and variance show a large degree of covariation,
525 limiting our ability to distinguish the effects at a given locus’s diversity versus allelic composition.
526
527 *Phenotypes and genotypes associated with stand-level performance*
528 We found evidence that stand composition in measured phenotypes was associated with stand-
529 level performance. Specifically, monoculture productivity was associated with certain closely
530 related genotypes under the low-resource environment, and mono- and polyculture productivity
531 was associated with late-flowering genotypes. Late flowering genotypes invest greater
532 proportions of resources and time in vegetative growth before transitioning to reproduction. For
533 this reason late-flowering genotypes may be more productive in terms of biomass and similarly
534 they may often possess traits useful for biomass production crops [48]. Here, the late-flowering

genotypes we studied were associated with polycultures in the high resource environment that had less biomass than expected based on monocultures of component genotypes. This suggests that late-flowering genotypes may have been more likely to be involved in interference competition when resources were abundant, perhaps because these larger individual plants limited their competitors from resource capture (e.g. by shading) more than they benefited, reducing the overall summed biomass [21]. Evidence suggests that size asymmetries leading to shading [49] as well as allelopathy against competitors or other trophic levels [50] can also lead to such interference competition.

Comparison with previous studies on Arabidopsis

Previous studies in the laboratory have shown some evidence that certain combinations of Arabidopsis genotypes may result in higher stand level performance. In greenhouse populations of Arabidopsis, both additive and non-additive benefits of up to eight genotypes per stand (from a pool of 23) were found to increase emergence, biomass, flowering duration, and fecundity [16]. [20] used an Arabidopsis biparental mapping population to identify a single locus causing overyielding when grown in diversity in pots. Additionally, [28] used pairwise pot experiments and association mapping on individual genotype's association with over- versus under-yielding when grown with another genotype. Our study represents the first field experiment on diversity effects on stand performance in the model plant. However, it is noteworthy that [51] found that natural stands in Germany with a single genotype were on average smaller (in terms of number of individuals) than stands with multiple genotypes, suggesting potential positive diversity effects in the native range of Arabidopsis.

A priori prediction of stand-level performance

Ecology has been criticized for not being a predictive science. Here we sought to test our knowledge of the system with *a priori* sets of stands predicted to have divergent performance. Overall we found that our predictions were most closely associated with stand-level yield driven by flowering time differences among genotypes. As discussed earlier, it is no accident that we chose flowering time as the one trait to include in our prediction criteria. Flowering time has been well-documented to be associated with a major axis of life history and physiological variation [32,52], and is so intensely studied partly for agronomic interest. While the stands we predicted to differ in productivity did not show strong differences from randomly assembled stands, we believe the use of phenotyped and genotyped individuals in such experiments are a

way forward for developing greater predictive approaches in studies of group performance and diversity.

Conclusions

Biodiversity can affect the properties of groups of organisms and may be important understanding the performance and persistence of both natural and introduced populations and communities. Though here we did not identify strong effects of genetic diversity *per se* on the performance of stands of non-native Arabidopsis populations, we nevertheless did identify a pattern of higher biomass yield when genetic composition was shifted to late-flowering stands., We also identified that in polyculture this composition led to lower-than expected yield, possibly due to interference competition. Genomic data offer a window to complement phenotypic measures of diversity that can now be applied in non-model systems. Our research here on diversity effects on performance in the field for the model plant Arabidopsis suggest a way forward to understanding the importance of such effects in nature.

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590 **Table 1**. Linear models of plot-level fecundity of Arabidopsis stands measured in the field
591 common garden.

Covariate	**Treatment**	**Estimate**	p	$R^2_{adjusted}$
Diversity metrics				
Diversity Level	High	2.20762	0.0289*	0.046
Diversity Level	Low	0.63101	0.5733	
Mean genetic distance	High	26.37127	0.0944	0.035
Mean genetic distance	Low	-2.10719	0.9026	
Composition metrics				
Distance in PCs 1-5 (mean)	High	1.52930	0.5467	0.023
Distance in PCs 1-5 (mean)	Low	0.16076	0.9483	
SLA breeding value (mean)	High	-30.27388	0.3107	0.017
SLA breeding value (mean)	Low	-3.20336	0.9215	
FT (mean)	High	-0.05192	0.9461	0.038
FT (mean)	Low	1.43961	0.0625	

592 Plot level fecundity measured as estimated mean seed number (described in text). Asterisk
593 indicates significance of covariate in linear models at P <0.05.
594
595
596

Table 2. linear models of per plant biomass of Arabidopsis stands measured in the field common garden.

Covariate	**Treatment**	**Estimate**	p	$R^2_{adjusted}$
Diversity metrics				
Diversity Level	High	-0.00004	0.7958	0.015
Diversity Level	Low	-0.00011	0.4743	
Mean genetic distance	High	-0.00161	0.4251	0.017
Mean genetic distance	Low	-0.00192	0.3577	
Composition metrics				
Distance in PCs 1-5 (mean)	High	-0.00049	0.1298	0.022
Distance in PCs 1-5 (mean)	Low	-0.00031	0.3325	
SLA breeding value (mean)	High	-0.00926	0.0095*	0.029
SLA breeding value (mean)	Low	-0.00392	0.3388	
FT (mean)	High	0.00013	0.0204*	0.050
FT (mean)	Low	0.00017	0.0024*	

Plot level biomass measured as aboveground dry weight at harvest (described in text). Asterisk indicates significance of covariate in linear models at $P < 0.05$.

603 **References**

604 1. Denison RF. 2012 *Darwinian Agriculture: How Understanding Evolution Can Improve*
605 *Agriculture*. Princeton University Press.

606 2. Hughes AR, Stachowicz JJ. 2004 Genetic diversity enhances the resistance of a seagrass
607 ecosystem to disturbance. *Proc. Natl. Acad. Sci. U. S. A.* **101**, 8998–9002.
608 (doi:10.1073/pnas.0402642101)

609 3. Loreau M. 2010 *From populations to ecosystems: theoretical foundations for a new*
610 *ecological synthesis*. Princeton University Press. See
611 http://books.google.com/books?id=qIxM7eNj9sUC.

612 4. Loreau M, Hector A. 2001 Partitioning selection and complementarity in biodiversity
613 experiments. *Nature* **412**, 72–76. (doi:10.1038/35083573)

614 5. Lasky JR. 2019 Eco-evolutionary community turnover following environmental change. *Evol.*
615 *Appl.* **12**, 1434–1448. (doi:10.1111/eva.12776)

616 6. Mouquet N, Loreau M. 2003 Community Patterns in Source-Sink Metacommunities. *Am.*
617 *Nat.* **162**, 544–557.

618 7. Loreau M. 1998 Separating Sampling and Other Effects in Biodiversity Experiments. *Oikos*
619 **82**, 600–602. (doi:10.2307/3546381)

620 8. Cadotte MW. 2013 Experimental evidence that evolutionarily diverse assemblages result in
621 higher productivity. *Proc. Natl. Acad. Sci.* (doi:10.1073/pnas.1301685110)

622 9. Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotchnick N. 2012
623 Phylogenetic diversity and the functioning of ecosystems. *Ecol. Lett.* **15**, 637–648.
624 (doi:10.1111/j.1461-0248.2012.01795.x)

625 10. Reynolds LK, Chan KM, Huynh E, Williams SL, Stachowicz JJ. 2018 Plant genotype identity
626 and diversity interact with mesograzer species diversity to influence detrital consumption in
627 eelgrass meadows. *Oikos* **127**, 327–336. (doi:10.1111/oik.04471)

628 11. Simberloff D. 2009 The role of propagule pressure in biological invasions. *Annu. Rev. Ecol.*
629 *Evol. Syst.* **40**, 81–152.

630 12. Vahsen ML, Shea K, Hovis CL, Teller BJ, Hufbauer RA. 2018 Prior adaptation, diversity,
631 and introduction frequency mediate the positive relationship between propagule pressure
632 and the initial success of founding populations. *Biol. Invasions* **20**, 2451–2459.
633 (doi:10.1007/s10530-018-1713-4)

634 13. Szűcs M, Vahsen ML, Melbourne BA, Hoover C, Weiss-Lehman C, Hufbauer RA. 2017
635 Rapid adaptive evolution in novel environments acts as an architect of population range
636 expansion. *Proc. Natl. Acad. Sci.* **114**, 13501–13506. (doi:10.1073/pnas.1712934114)

637 14. Hufbauer RA, Rutschmann A, Serrate B, Conchard HV de, Facon B. 2013 Role of
638 propagule pressure in colonization success: disentangling the relative importance of

demographic, genetic and habitat effects. *J. Evol. Biol.* **26**, 1691–1699. (doi:10.1111/jeb.12167)

15. Szűcs M, Melbourne BA, Tuff T, Hufbauer RA. 2014 The roles of demography and genetics in the early stages of colonization. *Proc. R. Soc. B Biol. Sci.* **281**, 20141073. (doi:10.1098/rspb.2014.1073)

16. Crawford KM, Whitney KD. 2010 Population genetic diversity influences colonization success. *Mol. Ecol.* **19**, 1253–1263. (doi:10.1111/j.1365-294X.2010.04550.x)

17. Drummond EBM, Vellend M. 2012 Genotypic Diversity Effects on the Performance of Taraxacum officinale Populations Increase with Time and Environmental Favorability. *PLoS ONE* **7**. (doi:10.1371/journal.pone.0030314)

18. Forsman A, Wennersten L. 2016 Inter-individual variation promotes ecological success of populations and species: evidence from experimental and comparative studies. *Ecography* **39**, 630–648. (doi:10.1111/ecog.01357)

19. Bertness MD, Callaway R. 1994 Positive interactions in communities. *Trends Ecol. Evol.* **9**, 191–193. (doi:10.1016/0169-5347(94)90088-4)

20. Wuest SE, Niklaus PA. 2018 A plant biodiversity effect resolved to a single chromosomal region. *Nat. Ecol. Evol.* **2**, 1933–1939. (doi:10.1038/s41559-018-0708-y)

21. Tonsor SJ. 1989 Relatedness and Intraspecific Competition in Plantago lanceolata. *Am. Nat.* **134**, 897–906. (doi:10.1086/285020)

22. Hedge LH, Leung B, O'Connor WA, Johnston EL. 2014 The interacting effects of diversity and propagule pressure on early colonization and population size. *J. Anim. Ecol.* **83**, 168–175. (doi:10.1111/1365-2656.12125)

23. Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S. 2011 Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology* **92**, 1573–1581. (doi:10.1890/10-1245.1)

24. Fischer DG *et al.* 2017 Tree genetics strongly affect forest productivity, but intraspecific diversity–productivity relationships do not. *Funct. Ecol.* **31**, 520–529. (doi:10.1111/1365-2435.12733)

25. Madritch MD, Kingdon Clayton C., Singh Aditya, Mock Karen E., Lindroth Richard L., Townsend Philip A. 2014 Imaging spectroscopy links aspen genotype with below-ground processes at landscape scales. *Philos. Trans. R. Soc. B Biol. Sci.* **369**, 20130194. (doi:10.1098/rstb.2013.0194)

26. Lasky JR *et al.* 2015 Genome-environment associations in sorghum landraces predict adaptive traits. *Sci. Adv.* **1**, e1400218. (doi:10.1126/sciadv.1400218)

27. Reynolds M, Tuberosa R. 2008 Translational research impacting on crop productivity in drought-prone environments. *Genome Stud. Mol. Genet. Ed. Juliette Meaux Maarten Koornneef Plant Biotechnol. Ed. Andy Greenl. Jan Leach* **11**, 171–179. (doi:10.1016/j.pbi.2008.02.005)

677 28. Wuest SE, Pires ND, Luo S, Vasseur F, Messier J, Grossniklaus U, Niklaus PA. 2019
678 Increasing plant group productivity through latent genetic variation for cooperation. *bioRxiv* ,
679 641449. (doi:10.1101/641449)

680 29. Mitchell-Olds T, Schmitt J. 2006 Genetic mechanisms and evolutionary significance of
681 natural variation in Arabidopsis. *Nature* **441**, 947–952. (doi:10.1038/nature04878)

682 30. Alonso-Blanco C *et al.* 2016 1,135 Genomes Reveal the Global Pattern of Polymorphism in
683 Arabidopsis thaliana. *Cell* **166**, 481–491. (doi:10.1016/j.cell.2016.05.063)

684 31. Vasseur F, Sartori K, Baron E, Fort F, Kazakou E, Segrestin J, Garnier E, Vile D, Violle C.
685 2018 Climate as a driver of adaptive variations in ecological strategies in Arabidopsis
686 thaliana. *Ann. Bot.* **122**, 935–945. (doi:10.1093/aob/mcy165)

687 32. Lovell JT *et al.* 2013 Pleiotropy of FRIGIDA enhances the potential for multivariate
688 adaptation. *Proc. R. Soc. B Biol. Sci.* **280**, 20131043. (doi:10.1098/rspb.2013.1043)

689 33. Huston MA, McBride AC. 2002 Evaluating the relative strengths of biotic versus abiotic
690 controls on ecosystem processes. *Biodivers. Ecosyst. Funct. Synth. Perspect. Oxf. Univ.*
691 *Press Oxf.* , 47–60.

692 34. Easlon HM, Bloom AJ. 2014 Easy Leaf Area: Automated digital image analysis for rapid and
693 accurate measurement of leaf area1. *Appl. Plant Sci.* **2**. (doi:10.3732/apps.1400033)

694 35. Zheng X, Levine D, Shen J, Gogarten SM, Laurie C, Weir BS. 2012 A high-performance
695 computing toolset for relatedness and principal component analysis of SNP data.
696 *Bioinforma Oxf Engl* **28**. (doi:10.1093/bioinformatics/bts606)

697 36. Schuetzenmeister A, Dufey F. 2018 *VCA: Variance Component Analysis*. See
698 https://CRAN.R-project.org/package=VCA.

699 37. Endelman JB. 2011 Ridge Regression and Other Kernels for Genomic Selection with R
700 Package rrBLUP. *Plant Gen* **4**, 250–255.

701 38. Kang HM, Zaitlen NA, Wade CM, Kirby A, Heckerman D, Daly MJ, Eskin E. 2008 Efficient
702 Control of Population Structure in Model Organism Association Mapping. *Genetics* **178**,
703 1709–1723. (doi:10.1534/genetics.107.080101)

704 39. Zhang Y, Chen HYH, Reich PB. 2012 Forest productivity increases with evenness, species
705 richness and trait variation: a global meta-analysis. *J. Ecol.* **100**, 742–749.
706 (doi:10.1111/j.1365-2745.2011.01944.x)

707 40. Hooper DU *et al.* 2012 A global synthesis reveals biodiversity loss as a major driver of
708 ecosystem change. *Nature* **486**, 105–108. (doi:10.1038/nature11118)

709 41. Loreau M. 1998 Biodiversity and ecosystem functioning: A mechanistic model. *Proc. Natl.*
710 *Acad. Sci.* **95**, 5632–5636.

711 42. Naeem S, Li S. 1997 Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509.
712 (doi:10.1038/37348)

43. Isbell F *et al.* 2015 Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**, 574–577.

44. Lasky JR, Uriarte M, Boukili VK, Erickson DL, John Kress W, Chazdon RL. 2014 The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecol. Lett.* **17**, 1158–1167. (doi:10.1111/ele.12322)

45. In press. Increasing antagonistic interactions cause bacterial communities to collapse at high diversity - Becker - 2012 - Ecology Letters - Wiley Online Library. See https://onlinelibrary.wiley.com/doi/full/10.1111/j.1461-0248.2012.01759.x (accessed on 19 November 2019).

46. Donohue K. 2003 The Influence of Neighbor Relatedness on Multilevel Selection in the Great Lakes Sea Rocket. *Am. Nat.* **162**, 77–92. (doi:10.1086/375299)

47. Dudley SA, File AL. 2007 Kin recognition in an annual plant. *Biol. Lett.* **3**, 435–438. (doi:10.1098/rsbl.2007.0232)

48. Rooney WL, Blumenthal J, Bean B, Mullet JE. 2007 Designing sorghum as a dedicated bioenergy feedstock. *Biofuels Bioprod. Biorefining* **1**, 147–157. (doi:10.1002/bbb.15)

49. Weiner J, Thomas SC. 1986 Size Variability and Competition in Plant Monocultures. *Oikos* **47**, 211–222. (doi:10.2307/3566048)

50. Wardle DA, Nilsson M-C, Gallet C, Zackrisson O. 1998 An ecosystem-level perspective of allelopathy. *Biol. Rev.* **73**, 305–319. (doi:10.1017/S0006323198005192)

51. Bomblies K, Yant L, Laitinen RA, Kim S-T, Hollister JD, Warthmann N, Fitz J, Weigel D. 2010 Local-Scale Patterns of Genetic Variability, Outcrossing, and Spatial Structure in Natural Stands of Arabidopsis thaliana. *PLOS Genet.* **6**, e1000890. (doi:10.1371/journal.pgen.1000890)

52. Mitchell-Olds T. 1996 Genetic Constraints on Life-History Evolution: Quantitative-Trait Loci Influencing Growth and Flowering in Arabidopsis Thaliana. *Evolution* **50**, 140–145. (doi:10.1111/j.1558-5646.1996.tb04480.x)

53. Pisupati R *et al.* 2017 Verification of Arabidopsis stock collections using SNPmatch, a tool for genotyping high-plexed samples. *Sci. Data* **4**, 170184. (doi:10.1038/sdata.2017.184)

54. Ågren J, Schemske DW. 2012 Reciprocal transplants demonstrate strong adaptive differentiation of the model organism Arabidopsis thaliana in its native range. *New Phytol.* **194**, 1112–1122. (doi:10.1111/j.1469-8137.2012.04112.x)

55. Burghardt LT, Metcalf CJE, Wilczek AM, Schmitt Johanna, Donohue K. 2015 Modeling the Influence of Genetic and Environmental Variation on the Expression of Plant Life Cycles across Landscapes. *Am. Nat.* **185**, 212–227. (doi:10.1086/679439)

56. DeLeo VL, Menge DNL, Hanks EM, Juenger TE, Lasky JR. 2019 Effects of two centuries of global environmental variation on phenology and physiology of Arabidopsis thaliana. *Glob. Change Biol.* **0**. (doi:10.1111/gcb.14880)

57. Gienapp P, Fior S, Guillaume F, Lasky JR, Sork VL, Csilléry K. 2017 Genomic quantitative genetics to study evolution in the wild. *Trends Ecol. Evol.*

58. Lasky JR, Des Marais DL, Lowry DB, Povolotskaya I, McKay JK, Richards JH, Keitt TH, Juenger TE. 2014 Natural variation in abiotic stress responsive gene expression and local adaptation to climate in Arabidopsis thaliana. *Mol. Biol. Evol.* **31**, 2283–2296. (doi:10.1093/molbev/msu170)

59. Lasky JR, Des Marais DL, McKay JK, Richards JH, Juenger TE, Keitt TH. 2012 Characterizing genomic variation of Arabidopsis thaliana: the roles of geography and climate. *Mol. Ecol.* **21**, 5512–5529. (doi:10.1111/j.1365-294X.2012.05709.x)

60. Lasky JR, Forester BR, Reimherr M. 2018 Coherent synthesis of genomic associations with phenotypes and home environments. *Mol. Ecol. Resour.* **18**, 91–106. (doi:10.1101/051110)

61. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005 Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978.

62. Kalnay E *et al.* 1996 The NCEP/NCAR 40-Year Reanalysis Project. *Bull. Am. Meteorol. Soc.* **77**, 437–471. (doi:10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2)

63. Zomer RJ, Trabucco A, Bossio DA, Verchot LV. 2008 Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agric. Ecosyst. Environ.* **126**, 67–80. (doi:10.1016/j.agee.2008.01.014)

772 **Online supplement**

773

774 *Seeds used in experiments*

775 We excluded any genotypes that were reported as contaminants by the supplying lab [53].
776 Seeds were obtained from the Arabidopsis Biological Resource Center and were bulked
777 November 2016 through June 2017 in a growth room at a constant temperature between 20-25
778 °C, under 90-120 PAR with a 16-hour photoperiod.

779

780 *Assembly of prediction stands*

781 We used five different criteria to generate these 'prediction stands': (1) genomic diversity among
782 accessions, (2) climate similarity of collection location to study site combined with genomic
783 diversity, (3) early flowering genotypes, (4) late flowering genotypes, (5) climate similarity of
784 collection location to our study site, combined with flowering time diversity. For (1) and (2), we
785 sought to maximize genome-wide diversity. We began with a random genotype and then
786 followed adding genotypes based on lowest average kinship with already selected genotypes
787 (kinship matrix calculated by [30], based on whole genome resequencing data). For (2), we
788 conducted the same exercise except that we began with the ecotype closest in climate space to
789 the study site (see below) and then selected a subset of ecotypes closest in climate space to
790 the study site. From this subset we then chose the least closely related genotype (lowest kinship
791 coefficient) and then followed adding genotypes based on the combined ranks of a) low average
792 kinship with already chosen genotypes and b) low climate distance from the experimental site.

793 For (2) and (3), we calculated principal components of climate for the 60 ecotype
794 locations of origin combined with our experimental site, using variables potentially important in
795 local adaptation in Arabidopsis [54–60]: mean April temperature, mean diurnal temperature
796 range, minimum temperature of coldest month, mean monthly minimum and mean monthly
797 maximum temperatures during the growing season, growing season precipitation relative to
798 potential evapotranspiration, inter-annual coefficient of variation in growing season precipitation,
799 growing season length, coefficient of variation in monthly precipitation across the years, and
800 coefficient of variation in monthly precipitation during the growing season [59,61–63]. The first
801 five PCs accounted for 93% of the total climate variation. The first PC largely corresponded to
802 an axis of temperature variation among sites. The second PC largely corresponded to high
803 precipitation variability, high maximum growing season temperatures, a large diurnal
804 temperature range, and dry growing seasons at one extreme. We then calculated each

ecotype's Manhattan distance from the experimental site in the space of the first five principal components.

For (3-5) we calculated average flowering time for these genotypes grown at 10ºC and 16ºC in growth chambers, using published data [30]. For (3) early flowering stands, we selected the lower tail of flowering times (tail size depending on number of genotypes in stand: 0.1, 0.3, or 0.5) and then randomly selected genotypes within that tail. For (4) the late flowering stands we used the same method with similarly sized upper tails of the flowering time distribution. For (5), we again began with a genotype from similar climate to the study site and then selected a subset of genotypes closest in climate space to the study site. From this subset we chose the genotype with the most different flowering time and then followed adding genotypes based on combined ranks of low flowering time similarity with already chosen genotypes and low climate distance from the experimental site.

Randomly assembled stands

Pairwise comparisons were made for all stand compositions (including prediction stands) to minimize redundancy across stands. If a potential random stand genotype composition overlapped by more than the allowed number of genotypes with a prediction stand or a previously accepted random stand (no repeat lines allowed among 2-genotype stands, 4 repeat lines allowed among 10-genotype stands, 9 repeat lines allowed among 20-genotype stands), that stand composition was rejected and a new one randomly generated. In the resulting final stand compositions (including predicted and random stands), each 2-genotype stand was unique; each pair of 10-genotype stands shared 0.795 genotypes on average; and each pair of 20-genotype stands shared 1.725 genotypes on average. The average genotype was represented in 0.67 (SD=0.46) 2-genotype stands, 3.33 (SD=2.08) 10-genotype stands, and 6.67 (SD=2.26) 20-genotype stands.

836 **Table S1**. Linear models of per plant canopy area of Arabidopsis stands measured in the field
837 common garden.

Covariate	**Treatment**	**Estimate**	p	$R^2_{adjusted}$
Diversity metrics				
Diversity Level	High	-0.00121	0.7710	0.201
Diversity Level	Low	0.00009	0.9831	
Mean genetic distance	High	-0.02716	0.6574	0.202
Mean genetic distance	Low	-0.02649	0.6648	
Composition metrics				
Distance in PCs 1-5 (mean)	High	-0.00051	0.9572	0.201
Distance in PCs 1-5 (mean)	Low	-0.00053	0.9539	
SLA breeding value (mean)	High	-0.02102	0.8549	0.205
SLA breeding value (mean)	Low	-0.03843	0.7463	
FT (mean)	High	-0.00075	0.6662	0.202
FT (mean)	Low	-0.00026	0.8782	

838
839

840 **Table S2.** Linear model statistics for associations with DME (deviation from monoculture
841 expectation)

Covariate	Treatment	Estimate	p	$R^2_{adjusted}$
Diversity metrics				
Mean genome-wide similarity	High	-0.04639	0.7244	<0
Mean genome-wide similarity	Low	0.02015	0.8821	
NJ tree branch length	High	0.00108	0.6369	<0
NJ tree branch length	Low	-0.00028	0.9063	
N genotypes	High	0.00330	0.3896	<0
N genotypes	Low	-0.00024	0.9526	
Composition metrics				
FT (90th percentile)	High	-0.00514	0.0170	0.0275
FT (90th percentile)	Low	-0.00060	0.7883	
FT (mean)	High	-0.00643	0.0167	0.0290
FT (mean)	Low	-0.00121	0.6532	
AGB (90th percentile)	High	-11.62425	0.0030	0.0954
AGB (90th percentile)	Low	-11.58907	0.0309	
AGB (median)	High	-14.68487	0.0133	0.0812
AGB (median)	Low	-18.78808	0.0167	
SLA (mean)	High	0.70971	0.3544	<0
SLA (mean)	Low	0.47972	0.3066	
Distance in PCs 1-5 env (mean)	High	0.03969	0.0485	0.0096
Distance in PCs 1-5 env (mean)	Low	0.00313	0.8785	

842
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847

Figure S1. Map of location of origin of each of the 60 native-range genotypes used in this study (blue circles).

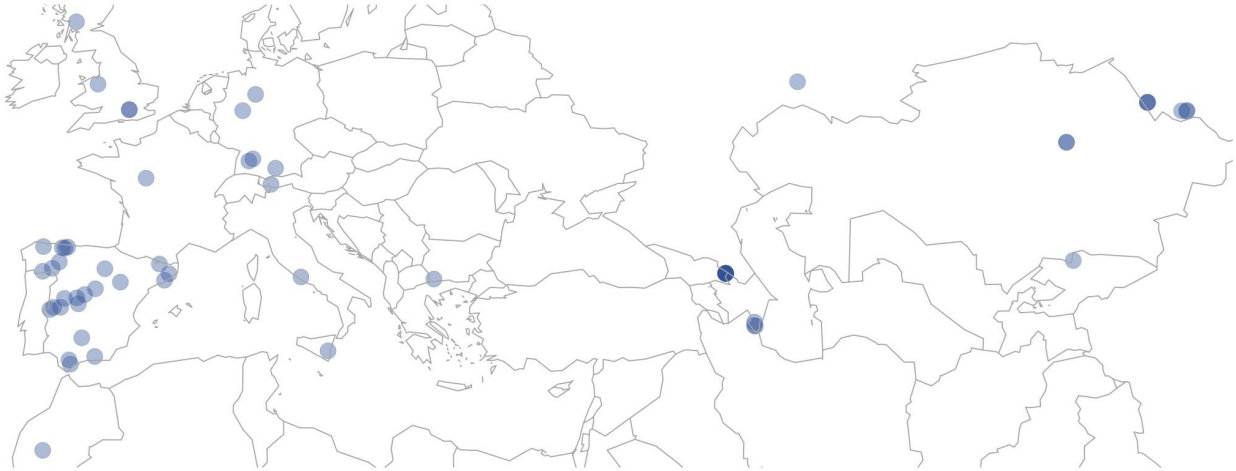

Figure S2. Field plot design with four blocks. Each square represents a stand. Total plot area was 85 square meters (10 x 8.5 meters).

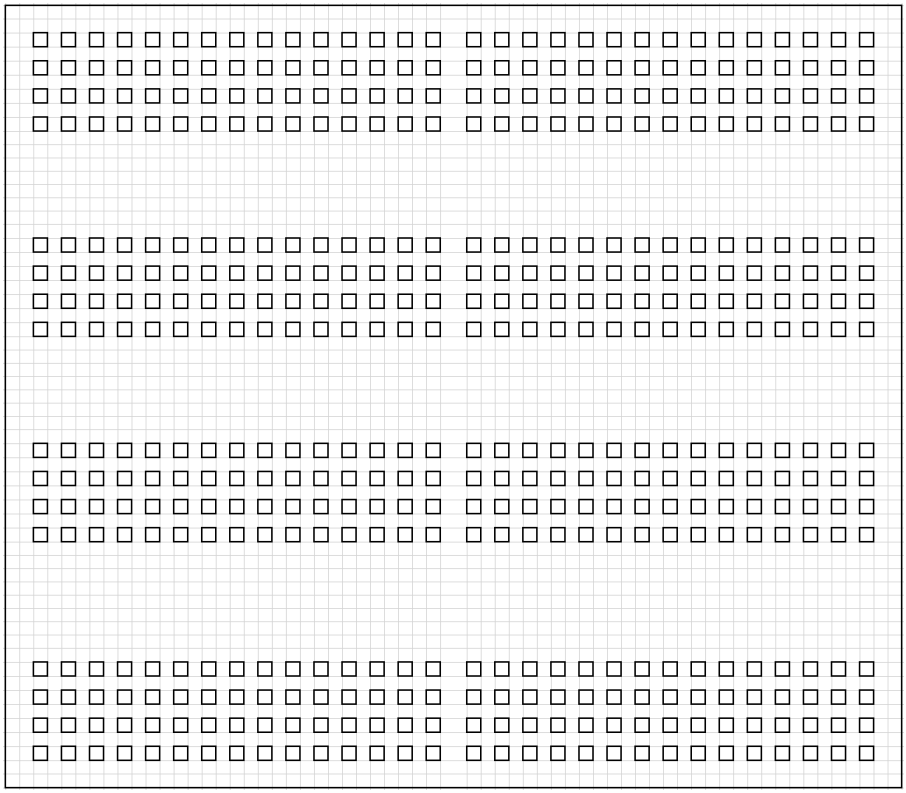

Figure S3. Percent volumetric water content (VWC%) for each treatment in addition to the surrounding high clay soil was monitored each week within each block using EM-50 dataloggers and EC-5 probes (METER Group Inc., Pullman, WA). At the beginning of the experiment (June 8, 2018), mean VWC for the high resource stands was 13.85%, 9.9% for the low resource stands, and 29.25% for the surrounding field soil (which had high clay content). Toward the end of the experiment (July 12, 2018), VWC for the high resource stands was 11.95%, 5.38% for the low resource stands, and 26.78% for the surrounding field soil.

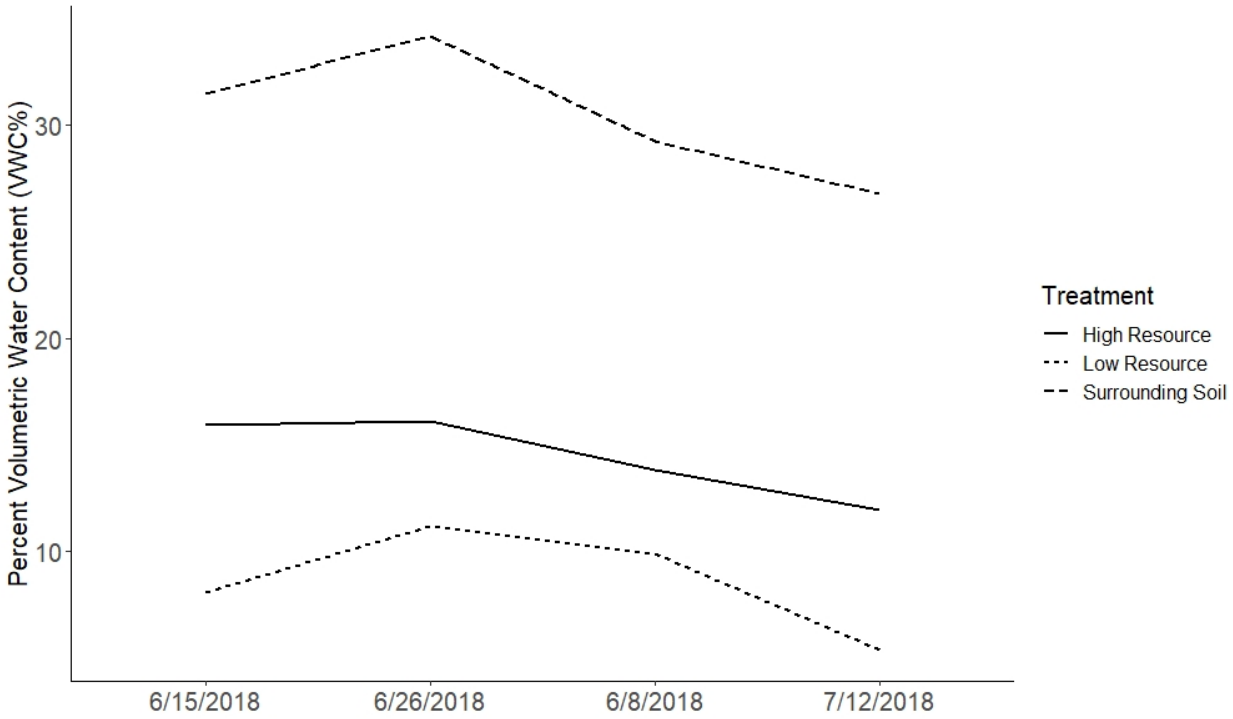

Figure S4. Genome-wide associations between stand biomass or DME and allele frequency within stands, or variance among individuals within stands. y-axes show -$\log_{10}$ p-values of association, the five chromosomes of Arabidopsis are arrayed on the x-axes.

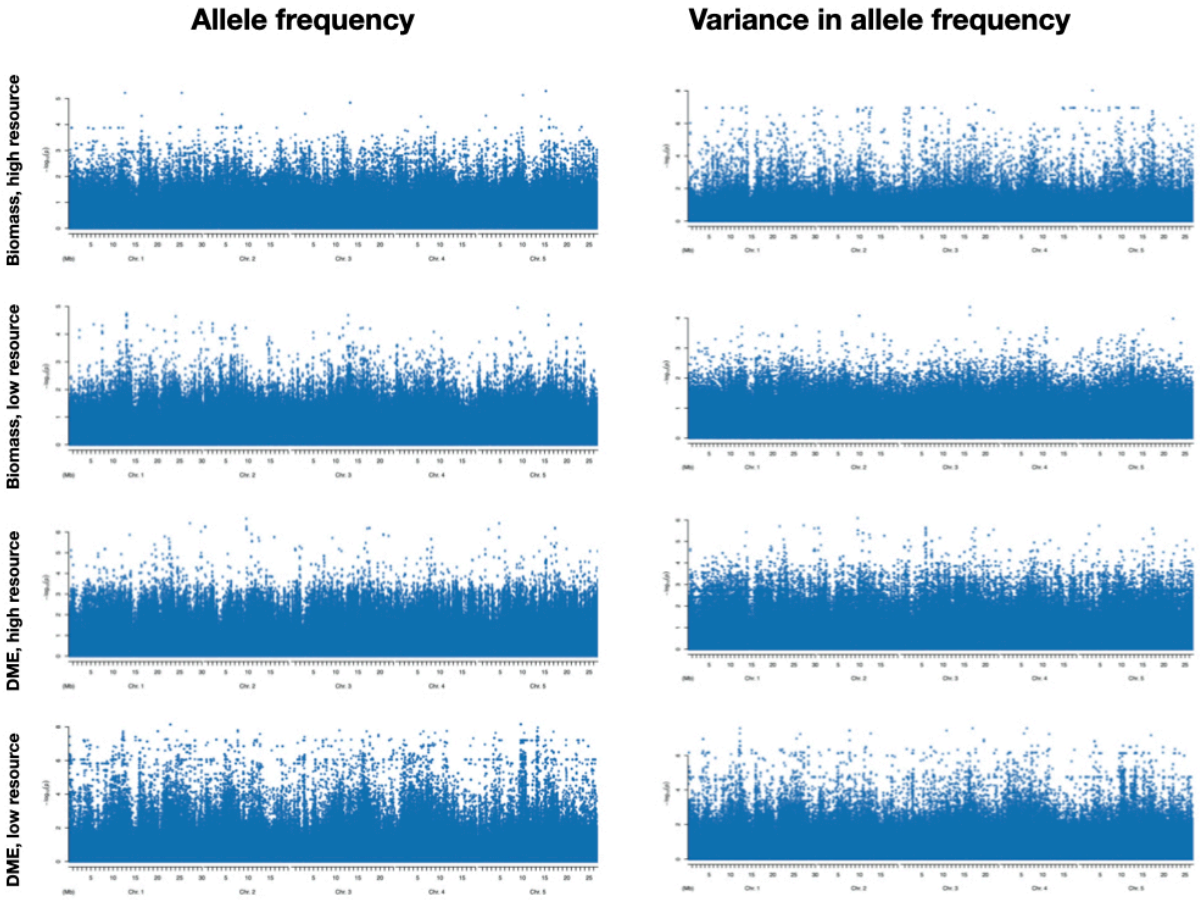
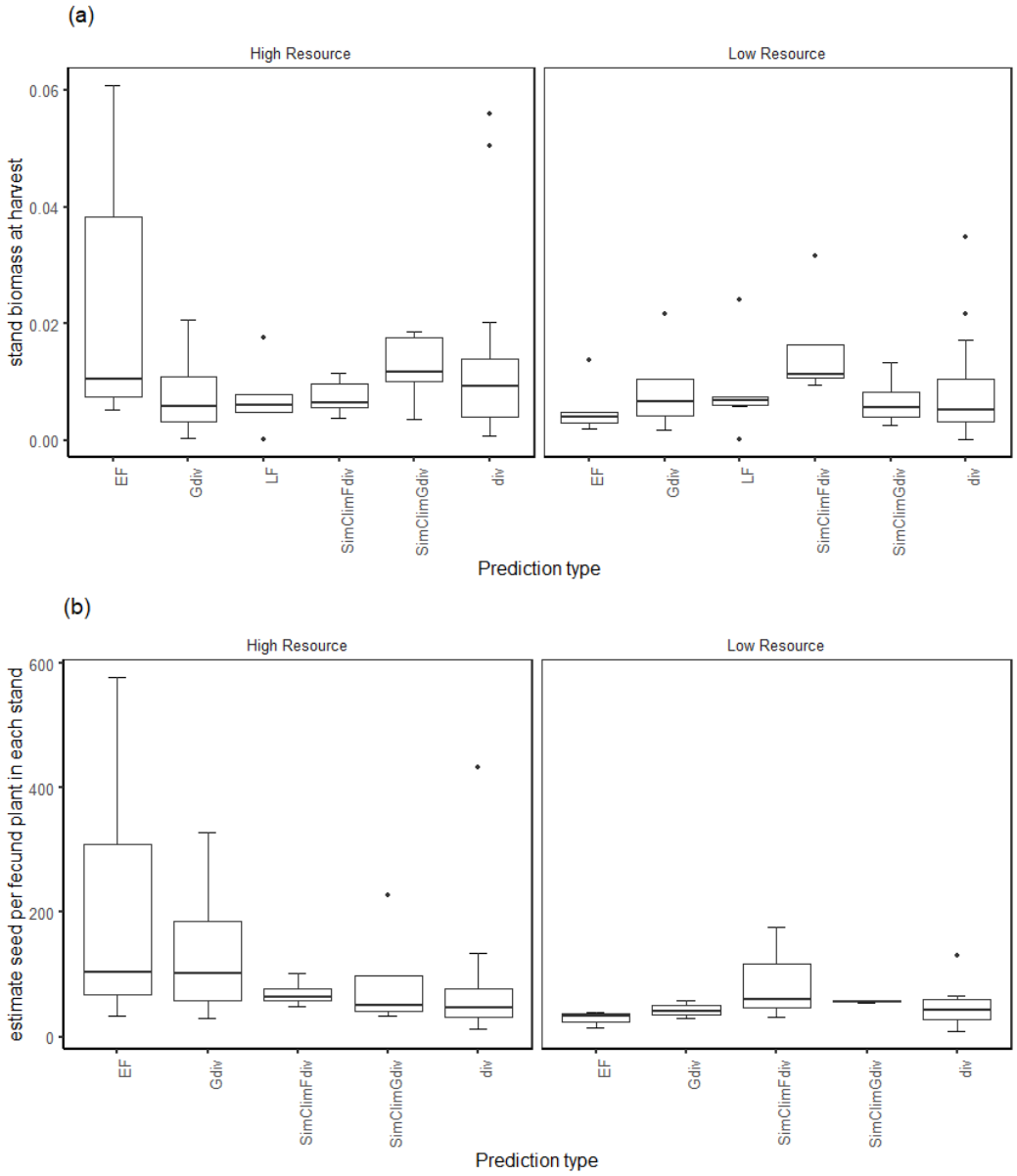
Figure S5. Biomass and fecundity performance of prediction stands in high and low resource environments. Performance of prediction plots and random polyculture plots in high and low resource environments. Criteria for prediction plots described in text. ‘EF’ = ‘early flowering’, 12 stands. ‘Gdiv’ = genetic diversity criterion, 11 stands. ‘LF’ = ‘late flowering’, 11 stands. ‘SimClimFdiv’ = similar climate, flowering time diversity criterion, 10 stands. ‘SimClimGdiv’ = similar climate, genetic diversity criterion, 11 stands. ‘div’ = all remaining randomly assembled polyculture stands, 55 stands. (a) Per plant biomass at harvest. (b) Plot level Estimated seed number. Because only two stands from the LF criteria produced fruit, it was not included in analyses of fecundity.