Intraspecific Competitive Interactions Rapidly Evolve Via Spontaneous Mutations

Henning Nottebrock (✉ henning@nottebrock.net)

South Dakota State University <https://orcid.org/0000-0003-2238-2700>

Mao-Lun Weng

South Dakota State University

Matthew T. Rutter

College of Charleston, Charleston

Charles B. Fenster

South Dakota State University

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Abstract

Using a mechanistic eco-evolutionary trait-based neighborhood-model, we quantify the impact of mutations on intraspecific spatial interactions to better understand mechanisms underlying the maintenance of genetic variation and the potential effects of these evolved interactions on the population dynamics of *Arabidopsis thaliana*. We use 100 twenty-fifth generation mutation accumulation (MA) lines (genotypes) derived from one founder genotype to study mutational effects on neighbor responses in a field experiment. We created individual-based maps (15,000 individuals), including phenotypic variation, to quantify mutational effects within genotypes versus between genotypes on reproduction and survival. At small-scale (within 80 cm of the focal plant), survival is enhanced but seed-set is decreased when a genotype is surrounded by different genotypes. At large-scale (within 200 cm of the focal plant), seed set is facilitated by different genotypes while the same genotype has either no effect or negative effects. The direction of the interactions among MA lines suggests that at small scale these interactions may contribute to the maintenance of genetic variation and at large scale contribute to the survival of the population. This may suggest, that, mutations potentially have immediate effects on population and community dynamics by influencing the outcome of competitive and facilitatory interactions among conspecifics.

Introduction

Mutations are the ultimate source of genetic diversity; thus, their contribution to genetic variation is central to evolutionary process (reviewed in Halligan and Keightley 2009; Nei 2013). Although mutations must at some time contribute to adaptive evolution, their role in selection response relative to standing genetic variation has long been considered as secondary (Lynch and Keightley 2002). Given this perspective, it is not surprising that the contributions of mutations to eco-evolutionary processes is understudied. However, it is paradoxical to consider mutations as minor factors in adaptive response given that mutations and environmental context have played a prominent role in our understanding of evolutionary process since the earliest days of the neoDarwinian synthesis (Fisher 1930). From an ecological perspective, it is important to note that mutations are expressed in individuals having specific spatial locations and experiencing specific environmental conditions (Weng et al. 2021), including competition with conspecifics.

Our understanding of mutational contribution to an individual's fitness requires consideration of the local environment governing competitive relationships among genotypes. Only when the spatial relationship between traits and demographic parameters is explicitly described can robust hypotheses about the effects of individual variation on competitive outcomes be accurately formulated (Hart et al. 2016) and through extension, the effects of mutation on fitness. Furthermore, how mutations contribute to competitive interactions among conspecifics may increase or decrease genetic variation and influence levels of standing population genetic variation required for response to selection. Evolutionary processes, i.e., recurrent mutations and drift, gene flow, frequency and balancing selection, hybridization even epistasis (Fenster et al. 1997) are often considered sources of genetic variation (Barrett and Schluter,

2007). However, the link between genetic diversity and foundational ecological processes such as intraspecific competitive interactions are rarely considered even though Intraspecific competition is common (Nottebrock et al. 2017b) and, depending on its intensity relative to interspecific competition, can influence community dynamics (Nottebrock et al. 2017a). Intraspecific genetic variation contributing to individual trait variation and environmental adaptability may promote species coexistence by both increasing habitat heterogeneity and altering competitive hierarchies (Violle et al. 2012, Ehlers et al. 2016). However, intraspecific genetic variation may hinder species coexistence when intraspecific genetic variation is diminished by competition between individuals (Hart et al 2016). Thus, a complete understanding of evolutionary process requires linking intraspecific genetic diversity with spatial ecological interactions (Bolnick et al. 2011, Genung et al. 2011), especially by including mutational effects on competition in common garden experiments to be able to predict community dynamics (Violle et al. 2017)

We investigate the link between evolutionary genetics and spatial ecological interactions of mutation accumulation lines (MA lines) in the model plant organism *Arabidopsis thaliana* (Brassicaceae) to advance our understanding of the fitness effects of new mutations. Previous studies demonstrate the potential for *A. thaliana* genotypes to establish competitive hierarchies (Damgaard 2004, Cahill et al. 2005, Bossdorf et al. 2009, Baron et al. 2015) but they focus on interactions among genotypes from different populations. Here we take advantage of 25th generation *A. thaliana* mutation accumulation (MA) lines that were planted under field conditions in years 2004 and 2005 with spatial records of each individual each year (e.g., Rutter et al. 2010; 2012, Rutter et al. 2018) to quantify the potential contribution of de novo mutations to the generation of intraspecific competitive interactions (Fig. 1). We focus on the neighborhood effects of MA lines on focal plants from the same MA line (within genotypes) or different MA lines (between genotypes) to quantify the evolution of intraspecific genetic variation through the accumulation of spontaneous mutations. We implement trait-based neighborhood models (Nottebrock et al. 2017a, Nottebrock et al. 2017b, Lachmuth et al. 2017) to understand ecological mechanisms that may govern interactions within and between MA lines and which might influence the fitness effects of mutations.

Specifically, we ask: 1) Do spontaneous mutations rapidly (within 25 generations) introduce enough genetic variation among MA lines to influence intraspecific competition and facilitation of *A. thaliana*? 2) Do spontaneous mutations of MA lines contribute to competition, facilitation and selection promoting differential MA line survival and reproduction at different spatial scales? 3) How may competitive and facilitative effects potentially determine population and community dynamics? Answers to these questions also allow us to consider both the role of mutations to contributing to population genetic variation and to the genetic origins of population and community dynamics, contributing to a fuller understanding of the maintenance of biodiversity.

Methods

MA lines are generated from a single nearly homozygous individual founder and cultivated via limited effective population number. In the case of *A. thaliana*, this occurs through single seed descent, resulting in $N_e = 1$. Thus typical MA line cultivation results in an unbiased sample of mutation effects ranging from deleterious to advantageous, although lethal mutations are excluded (Lynch and Walsh 1998). Note that we do not expect lethal mutations to contribute to genetic variation associated with selection response and lethal mutations should only minimally contribute to community level dynamics. Each MA line accumulates independent spontaneous mutations. After the propagation of a set of MA lines through multiple generations, the genetic differences among the MA lines and between those lines and the founder reflect the input of mutation. Significant MA line effects for multiple traits, including performance and trait measures, were found under both field and greenhouse conditions (Rutter et al. 2010; Roles et al. 2016, Rutter et al. 2018). Each of the MA lines in our experiment is fixed for an average of 20 different sequence level mutations, single nucleotide mutations (SNMs) and indels combined (Ossowski et al. 2010, Rutter et al. 2012, Weng et al. 2019). To better understand interaction effects within and between MA lines and founders we are referring to intra-genetic and inter-genetic effects respectively throughout the manuscript.

MA lines and field experiments

We used survival and seed set data of *A. thaliana* MA lines and the founder as assessed in field experiments in 2004 and 2005 from Rutter et al. (2010, 2012 and 2018) planted in a randomized design (Fig. 1). Rutter et al. (2010, 2012) planted seedlings of 100 MA lines and the founder at the four-leaf stage, approximately two weeks post germination, into a secondary successional field at Blandy Experimental Farm (BEF) in Virginia (39°N, 78°W). Each of the 100 MA lines was used to found up to five sublines to minimize biases due to maternal effects introduced by the specific location within the greenhouse. We founded six sublines from each of the six lines representing the premutation founder genotype. In 2003, subline plants were used to generate all seed utilized in all field experiments. In each planting, 7504 individuals were planted, 7000 individuals of 100 MA lines (70 replicates per MA line, 14 replicates per subline) and 504 individuals of the founder (14 replicates per subline). The planting environment corresponds to a spring ephemeral life-history, where plants germinate and complete the life-cycle in the spring. At the time of planting, vegetation was scant but present. By harvest, the *A. thaliana* individuals were dwarfed by naturally occurring vegetation, consisting of a mixture of mostly biennials and perennials typical of old field succession. We did not characterize the surrounding vegetation for our plots. Thus, we assess mutational contribution to intraspecific interactions against a background of a varying plant community.

The plot was arranged in 14 spatial blocks with each containing 12 sub-blocks (Fig. 1B) (total plot area approximately 35 x 25 m). Each block included one seedling from each subline and in total 7504 individuals. We used the spatial information of each individual within the described design and created a raster of all plant individuals with R packages (raster, maps, maptools). We used individual-based maps neighborhood matrices with exact spatial and trait information of each genotype. If all five sublines did not produce enough seedlings to distribute in all blocks, seedlings from other sublines of the same MA

line were overrepresented in blocks to maintain the same overall number of plants per MA line. Plants dying within the first 3 days of transplant (about 50 plants) were considered to have died from transplant shock and were replaced with another plant from the same MA line. Plants were censused weekly for survival. Plants were harvested by late May, by which time they had senesced. In 2004 a total of 5915 individuals including 394 founders survived. In 2005, a total of 4506 individuals survived including 302 founders. Plants were oven dried and biomass was measured. All fruits produced by each plant were counted and in combination with seed production used as the measurements of seed set. For our analysis, we used measurements of two response variables representing an important part of the life history of *A. thaliana* to calculate direct neighborhood effects on: a) the survival rate of plant individuals and b) individual seed set from plants that survived and produced fruits.

Statistical Analyses

We use eco-evolutionary trait-based neighborhood models that include intraspecific genetic variation and phenotypic variation expressed by plant trait biomass to analyze competition and facilitation between individuals of *A. thaliana*. We analyzed plant survival rate and focal seed set measurements from years 2004 and 2005 separately. For each year, we considered all individuals as focal plants in the analysis based on individual-based neighborhood matrices to analyze 1) rate of plant survival to reproduction and 2) seed set of those plants that survived to reproduction. We analyzed neighboring plants to focal plants in a radius of 80 cm (small-scale) or 200 cm (large-scale) of a given focal plant as two spatial scales in the neighborhood analyses (Fig. 1) to quantify selection, competition or facilitation between plants depending on their genotypic and phenotypic variation.

We used extensions of linear mixed models (package lme4, Bates et al. 2014) in R ver. 3.5.2 (www.r-project.org) to conduct neighborhood analyses of focal seed set and survival. We assumed binomial errors for the analyses of plant survival and Poisson errors for analyses of seed set. The mixed models described interactions among plants by including neighborhood indices as explanatory variables at two spatial scales in separate models. Neighborhood indices are spatial density effects of surrounding neighborhood plants that affect focal seed set and survival. For each plant, we used the Euclidian distance between the focal plant and the neighboring plants to compute response effects of within MA line or between MA line neighbors in a given radius around focal plants (Nottebrock et al. 2017b). Moreover, we used a neighborhood index that accounts for the decline of neighbor effects with distance from the focal plant (Uriarte et al. 2010) and summed the amount of biomass from all individuals in a radius of 80 cm or 200 cm respectively by a Gaussian interaction kernel (Lachmuth et al. 2018, Nottebrock et al. 2017, Damgaard 2004). We used random effects of block and subblock to correct for environmental variation between local heterogeneous conditions. Importantly, we correct for between MA line effects by including MA lines as a random effect. That is, we account for the fact that different MA lines may have different effects on a focal plant by treating these as random effects. In addition, including a random slope of biomass on each random intercept corrects for the intraspecific phenotypic variation depending on local conditions (sub-block and block differences) of plant focal individuals. Moreover, the weighted neighborhood density by plant biomass accounts for environmental variation

between neighboring plants. A detailed model description of survival and seed set models can be found in S1 supplementary text (Supplementary Material S1).

Neighborhood matrices of all individuals (individual-based maps) were used to analyze the effect of intra- and inter-genotypic neighbors on survival and focal seed set with spatial interaction kernels of neighborhood (plant biomass) density. By incorporating different genotypes and phenotypic variation, we can quantify how important genetic variation is for neighborhood models and if the phenotypic variation explains spatial interactions between individuals. We assume the consequences of genetic differences to be larger between MA lines than between any MA line with itself, or the founder with itself. This is a valid assumption since each MA line differs from the other by approximately $20 + 20 = 40$ mutations, while any two replicates within a MA line or the founder lines will differ by one generation, ≤ 2 mutations. On average founders should differ from the individual MA lines by roughly half the difference of the number of mutations differentiating MA lines. Thus, we simulated line effects from parameters derived from MA lines as random effects with the R package 'merTools' and the function 'plotREsim' in R 2018. Not surprisingly, because the founder performance was always the average of all MA lines, we found no difference between founder and MA line effects on a focal plant (see results). Consequently, in many of our analyses we refer to the founder line and MA lines as just lines.

We used the trait values of neighbors to calculate trait-based neighborhood indices including plant biomass as a trait (Goldberg & Fleetwood, 1987; Goldberg & Landa, 1991; Cahill et al., 2005). We fitted eco-evolutionary trait-based neighborhood models at two different spatial scales for response variables (survival and seed set) for each of the two and both years. To address our objectives, we first analyzed models with differential effect in which within all MA lines and founder had a different effect on survival (A1, A2, Table 1) and seed set (B1, B2, Table1) than between MA line and founder neighbors at small-scale (s) and large-scale (l). In addition, we analyzed models with neutral effects on survival (A1, A2, Table 1) and seed set (B1, B2, Table 1) that included total neighbor density without the split between within and between MA line and founder neighbors at small-scale (s) and large-scale (l). To this end, all models were fitted with two separate neighborhood indices that were calculated from intra-and inter-genotypic neighbors. To justify the inclusion of individual plant biomass as trait-values for interacting plants in the model, we used AICc to compare the models with and without the trait-proxy (Burnham and Anderson 2002). We found that models perform generally better including biomass as a trait-proxy and calculated trait-based neighborhood indices for similar or different genotypes (MA lines) from biomass density ($\Delta AICc > 2$, Supplementary Material S2). All eco-evolutionary trait-based neighborhood models contained random effects of subblock nested in block at block scale and subblock scale on the intercept, MA line identity on the intercept and the focal trait-value (plant biomass) on the slope. Additionally, because direct environmental variables were not measured during the field experiments, we included in each model the individual's biomass to correct for environmental conditions for spatial autocorrelation. All variables are scaled and centered to assure comparability between predictor variables. Models of differential and neutral effects for 2004 and 2005 (Table 1, A1-A2, B1-B2) are fitted at small-scale (80cm scale) and at large-scale (200cm scale). Hereafter, the 80 cm scale models are referred to as "small-scale" models and the 200 cm scale models are referred to as "large-scale" models. Neighborhood indices, intra-

and intergenotypic variation and total variation of biomass density are included as inverse density variables ($1/1+\text{density}$). We compared models of differential and neutral effects through likelihood ratio tests (LRTs).

Results

At the scale of the sub-block (small scale), focal plants surrounded by plants of the same MA line or founder varied in biomass density between 0 kg to 0.039 kg and between 0.004 kg to 0.39 kg when surrounded by different plants from different MA lines or if the founder, surrounded by MA lines. At the scale of the block (large scale) in year 2004 focal plants surrounded by plants of the same MA line, or if founder, surrounded by other founders, varied in biomass from 0 kg to 0.04 kg, and if surrounded by plants from different MA lines, or if the founder, by MA lines, their biomass ranged between 0.04 kg to 0.59 kg (2005: small-scale similar genotypes 0 kg to 0.06 kg and different genotypes 0 kg to 0.51 kg; larger-scale similar genotypes 0 kg to 0.06 kg and different genotypes 0.06 kg to 0.78 kg). Small-scale and larger-scale effects on seed set and survival are described with distance parameter alpha (decline of neighbor effect with distance) (Supplementary Material S1). Seed set models show at small-scale for both years a mean effect distance of 27 cm and at larger-scale a mean distance effect of 79 cm (Supplementary Material S2). Below we show results of eco-evolutionary trait-based neighborhood models including plant biomass as a trait proxy (Supplementary Material S2).

Weighted neighbor effects of biomass density on MA lines and founders for plant survival

At the smaller-scale, survival rate is larger when a focal plant is surrounded by individuals from different lines (MA or founder) than when surrounded by plants of the same line for both years 2004 and 2005 (model A1 and A2; Table 2 and Fig. 2a). This finding is demonstrated by the superior performance of the differential model relative to the neutral model (year 2004: LRT: $\chi^2_{1\text{DF}} = 5.21$, $p < 0.05$; year 2005: LRT: $\chi^2_{1\text{DF}} = 14.73$, $p < 0.001$). The differential and neutral models of survival at large-scale have only non-significant effects (Table 2). In addition, comparing the AIC we found that models at large-scale perform worse than at small-scale for both 2004 and 2005 (Table 2). The distance kernel (alpha) at small-scale shows that neighboring plants that are from different lines (founder or MA lines), reduce plant survival by 50% at 53 cm in 2004 and 48 cm in 2005.

Weighted neighbor effects of biomass density on genotypes for seed set

At both small and large scales, the differential model performs better than the neutral model: at small scales (year 2004: LRT: $\chi^2_{1\text{DF}} = 52.48$, $p < 0.001$; year 2005: LRT: $\chi^2_{1\text{DF}} = 17.37$, $p < 0.001$; respectively) and at large scale (year 2004: LRT: $\chi^2_{1\text{DF}} = 679.44$, $p < 0.001$; year 2005: LRT: $\chi^2_{1\text{DF}} = 21.17$, $p < 0.001$; respectively). The small-scale model of seed set that included weighted biomass densities demonstrates the reduction of seed set for a focal plant is larger when surrounded by individuals from different lines relative to individuals from the same line (founder or MA line) for both years 2004 and 2005 (model B1 and B2; Table 2 and Fig. 2a). The difference between within and between line effects indicates that

neighbors that are from a different line have a stronger competitive effect on seed set than within line neighbors at small-scale. In contrast, at large-scale seed set increases when surrounded by individuals from different lines but decreases when surrounded by individuals within the same line for both years 2004 and 2005 (model B1 and B2; Table 2 and Fig. 2b). Comparing the AIC between small and large-scales, models at large-scale for 2004 and 2005 perform better (Table 2).

MA line and founder effects on plant survival and seed set

The distance kernel at small-scale in 2004 indicates a reduction of seed set (competition) whereas at large-scale are consistent with an increase of seed set (facilitation). Neighboring plants from all genotypes of *A. thaliana* at small-scale reduce 50% of focal seed set at 12 cm and at large-scale facilitate 50% of focal seed set at 75 cm (S2, for year 2005). The estimation of genotype effects (MA lines and founder) simulated as conditional means and expressed as odds ratios show hierarchical orders of MA line and founder competitive effects at small-scale (Fig. 3). We found no significance of simulated competitive effects of all MA lines and founder calculated from survival and seed set models at small-scale (ANOVA, $p > 0.1$, Fig. 4a). In addition, we found no significant correlation between competitive effects of MA lines and founder at large-scale. In addition, we did not find selective effects of MA lines and founder on the survival at small-scale (ANOVA, $p > 0.1$, Fig. 4b). However, we found strong correlation between competitive effects of MA lines and founder at small-scale and large-scale indicating a genetic trade-off (ANOVA, $F=460.07$, $P < 0.0001$, Fig. 4c).

Discussion

We are able to quantify individual spatial interactions between and within genotypes (MA lines and founder) using a mechanistic eco-evolutionary trait-based neighborhood model. We demonstrate intraspecific genetic variation due to spontaneous mutations can shape competitive abilities of genetically different individuals of *A. thaliana*. Notably, these differences arose in just 25 generations of mutation and in the absence of natural selection. Furthermore, these differences are so strong that we are able to quantify variation in competitive effects within our analytical framework despite treating the composition of the surrounding vegetation as a component of our random plot differences. Many of the mutations differentiating the MA lines also appear in nature, contributing to *A. thaliana* genetic polymorphism (Weng et al. 2019; Monroe et al. 2022). Thus, it may not be surprising that these very same mutations appear to contribute to dynamics having ecological implications. Below we discuss how these scale effects provide insight on the evolutionary processes depending on standing genetic variation and potential ecological processes underlying community assembly and coexistence.

Maintenance of genetic variation and fitness effects

Seed-dispersal is limited in space because the *A. thaliana* fruit do not dehiscently explode as they do in related species (Hofhuis and Hay 2017), although a seed bank ensures some dispersal through time (Falahati-Anbaren et al. 2014). Limited seed dispersal suggests that *A. thaliana* plants will typically interact with related individuals. Consequently, a relevant question is how mutations may contribute to

these potential interactions. At small-scale, competitive effects of different lines have opposed impacts on survival and seed set. Plant survival is higher when surrounded by neighbors from different lines (MA and founder) suggesting that genetic diversity introduced by de novo mutation should be promoted by a frequency dependent process (Delph and Kelly 2013). However, effects on focal seed sets were reversed between small and large scales: intra-genotypic neighbors have a stronger effect on survival at small scale, but inter-genotypic neighbors have stronger competitive effects on focal seed sets at small-scale, whereas at large-scale seed set is facilitated by inter-genetic neighbors. At large-scale, the intra-line effect on survival turns into less competitive effects on seed set. In contrast, different genotypes show stronger facilitative effects within the population at large-scale, maybe because local populations of genetically variable plants are more competitive against other species, which will need to be verified with future experiments that monitor the surrounding plant community. Overall, these results demonstrate the complexity of quantifying the fitness effects of mutations when tested in nature. Likely depending on density and other specific environmental conditions, mutations may contribute to increased survival of the rare genotype and may contribute to the persistence of local populations competing with other species.

Potential community implications for mutation competitive and facultative effects.

We quantified stronger statistical signals of effect sizes between lines than within lines. This result suggests that niche variation among individuals due to mutations may result in niche expansion or reduction (Ehlers et al. 2016). However, these competitive effects only occur between plants that survive to reproduction and affect seed-set. The neighbor effect increasing genetic diversity of *A. thaliana* populations may also have a positive effect on the coexistence of competing species (Vellend 2006). If we assume that the increase of genetic diversity due to spontaneous mutations of *A. thaliana* affects the extent of individual plant niches, at large-scale the inclusion of other plant species should result in stronger competitive effects of *A. thaliana* with other plant species (Hausch et al. 2018). We demonstrate that seed-set of focal *A. thaliana* individuals is facilitated by increasing variation of surrounding lines suggesting that a more diverse population of *A. thaliana* may be better competitors with the surrounding vegetation. However, *A. thaliana* of different genotypes show higher competition than within genotypes, when the survival of inter-genotypic neighbors is higher, which is perhaps due to the expansion of their individual niches due to more variation in plant traits.

Antagonistic interactions between genotypes on different spatial scales may result in genetic trade-offs when mutations are advantageous or deleterious, which over many generations could provide a strong stabilizing force maintaining both species and genetic diversity in this system and may promote coexistence (Lankau 2008). Thus, spontaneous mutation could also provide an additional evolutionarily stabilizing effect on community dynamics. Our study demonstrates the potential for a fundamental evolutionary process, mutation, to have profound consequences for community structure. When *A. thaliana* is rare, selection would favor genotypes that compete well and enhance the population's survival relative to that of its interspecific competitor (Lankau 2009). In contrast, when *A. thaliana* is common and the interspecific competitor is rare, selection may favor *A. thaliana* genotypes that are good intraspecific

competitors. This trade-off may result in a decrease in the interspecific competitive ability of *A. thaliana*, effectively increasing the competitor's fitness relative to that of *A. thaliana* (Lankau 2009, Lankau and Strauss 2007). However, the genetic trade-off between intra-and interspecific competitive abilities due to mutation remains unknown because our dataset only includes performance of *A. thaliana* individuals without quantifying the surrounding intraspecific environment (Chesson 2000, Adler et al. 2007).

Competitive Hierarchies of MA lines and Founder lines

Our result demonstrates scale dependent competition and facilitation (Nottebrock et al. 2017b) providing further evidence that in a relative short evolutionary time scale spontaneous mutations may change the competitive hierarchies between founders and specific MA lines due to advantageous or deleterious mutations (Rutter et al. 2010). In contrast to Masclaux et al. 2010, we found differential responses to similar genotypes vs different genotypes in *A. thaliana* depending on the neighbor effect on the plant survival or seed set. However, the interaction between similar genotypes and different genotypes seems to depend on the strength of the competitive abilities of the accession, while we have one accession and heredity is low by *A. thaliana*. Comparisons between MA lines and founder demonstrate that competitive hierarchies follow different orders and competitive effects occur at different life-history stages at different spatial scales. Eco-evolutionary processes might reflect spatial selection for diversified genotypes because of niche evolution and individuals of different genotypes that survived to reproduction have stronger competitive abilities (Ehlers et al. 2016). Moreover, the hierarchical order of competitive effects between MA lines and founders shows strong variation. Because our design reflected MA lines for only the Columbia founder, we must, however, be cautious in making general attributions of mutation effects on population dynamics.

Eco-evolutionary dynamics

Populations can adapt evolutionarily to their environment on a time scale equivalent to that of ecological processes and affect present day species interactions, i.e., coexistence (Fussmann et al. 2007). Yet, sustained and rapid climate change could deplete genetic variance faster than it can be replenished by mutation (Fournier-Level et al. 2016). In our study, we show that only 25 generations are enough to influence present day plant interactions of *A. thaliana* in the presence of other plant species. Possible effects of mutations on trait mechanisms might reflect the increased seed set of *A. thaliana* at large-scale, because of the presence of another plant species allowing the establishment and growth of *A. thaliana* (Ehlers et al. 2016). Many traits can influence competition and facilitation between individuals of different genotypes (e.g. Chapin et al. 1993; Caradus and Woodfield 1998; Hausmann et al. 2005). Intraspecific competition between *A. thaliana* individuals tends to be higher than between interspecific competitors (Lankau and Strauss 2007, Van Dam and Baldwin 1998; Tiffin 2002, Strauss and Irwin 2004). Such spatial mechanisms might be described by the scale difference of competition at small-scale and facilitation at large-scale between different *A. thaliana* genotypes. Competition and facilitation are therefore dependent on the extension or reduction of individual niches, which is based on trait changes due to spontaneous mutations. However, we are not able to directly link our results to benefactor

or antagonistic plants, because we focused our experiment on *A. thaliana* densities and fitness components. Nevertheless, genotypic-specific interactions are well studied. A number of studies of *A. thaliana* MA lines demonstrate mutation effects on plant traits such as leaf weight, flowering time, trichome density, number of leaves at bolting, duration of vegetative and flowering period (Camara and Pigliucci 1999, Rutter et al. 2010, Stearns and Fenster 2016). It is conceivable that the increase in variance of these traits through spontaneous mutations could contribute to the evolution of competitive hierarchies, which can happen over a short evolutionary time scale.

Conclusion

Rapid evolution of *A. thaliana* intraspecific competitive interactions due to spontaneous mutation alone appears to be of the size and direction necessary to promote the maintenance of genetic variation. Furthermore, mutation based evolution of intraspecific competitive interactions may have consequences for population and community dynamics. In particular, our findings about the influence of mutations on competitive hierarchies among phenotypes in a given environment (Levine and HilleRisLambers 2009) may demonstrate that the discovery of the underlying eco-evolutionary nature of competition in *A. thaliana* supports abiotic or biotic ecological processes to form plant niches (Hutchinson 1957, Bruno et al. 2003, Colwell and Rangel 2009). Moreover, selection and trait evolution favor population survival of *A. thaliana* in the wild, which stresses the importance of combining spatial ecological and evolutionary mechanisms for our understanding of population and community dynamics to support the maintenance of biodiversity (Violle et al. 2017). Finally, non-neutral intraspecific processes may determine species coexistence, because genetic diversity is promoted by having stronger competitive abilities at small-scale and stabilizing population survival at large-scale (Clark et al. 2010). Depending on the time of environmental changes, species may adapt to environmental change by shifting their fundamental niches (Clark 2010). The combination of intraspecific genotypic variation and spatial interactions might advance our understanding of community dynamics, especially of rapid evolution (Koch et al. 2014, Turcotte and Levine 2016).

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To be added

Conflicts of interest/Competing interests (include appropriate disclosures)

The authors claim no conflict of interests

Ethics approval (include appropriate approvals or waivers)

Not applicable

Consent to participate (include appropriate statements)

Not applicable

Consent for publication (include appropriate statements)

Not applicable

Availability of data and material (data transparency)

The spatial data will be uploaded upon acceptance to the dryad database. Genetic data can be found at NCBI Short Read Archive (SRA) with the accession number of SRP133100 and <https://doi.org/10.25386/genetics.6456065>.

Code availability (software application or custom code)

Not applicable

Authors' contributions:

HN, CBF and MTR conceived the idea; CBF and MTR designed the experiment and collected the data. HN developed the study idea and model design, analyzed the data and interpreted the results. HN led the writing and drafted a first version of the article. All critically contributed to the drafts and results interpretation and gave final approval for publication.

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References

1. Adler P, B., HilleRisLambers Janneke & Levine J. M. (2007). A niche for neutrality. *Ecology Letters*, 10, 95–104.
2. Agrawal, A.A., Hastings, A.P., Johnson, M.T.J., Maron, J.L. & Salminen, J.-P. (2012). Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science*, 338, 113–116.
3. Antonovics, J. (1976). The Nature of Limits to Natural Selection. *Annals of the Missouri Botanical Garden*, 63, 224–247.
4. Bailey JK et al. 2009 From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. **Phil. Trans. R. Soc. B** 364, 1607–1616. (doi:10.1098/rstb.2008.0336)

5. Baron E., Richirt J., Villoutreix R., Amsellem L., Roux F. & Bennett A. (2015). The genetics of intra- and interspecific competitive response and effect in a local population of an annual plant species. *Functional Ecology*, 29, 1361–1370.
6. Bataillon, T. (2003). Shaking the 'deleterious mutations' dogma? *Trends in Ecology & Evolution*, 18, 315–317.
7. Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *arXiv:1406.5823 [stat]*.
8. Bellard C., Bertelsmeier C., Leadley P., Thuiller W. & Courchamp F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.
9. Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.
10. Bossdorf Ol., Prati D., Auge H. & Schmid B. (2004). Reduced competitive ability in an invasive plant. *Ecology Letters*, 7, 346–353.
11. Burnham and Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach. 2d ed. New York: Springer-Verlag
12. Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory, 7.
13. Cahill, F. J., Kembel, S. W. and Gustafson, D. J. (2005), Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*. *Journal of Ecology*, 93: 958-967. doi:10.1111/j.1365-2745.2005.01013.x
14. Cahill, J.F., Elle, E., Smith, G.R. & Shore, B.H. (2008). Disruption of a belowground mutualism alters interactions between plants and their floral visitors. *Ecology*, 89, 1791–1801.
15. Camara, M. d. and M. Pigliucci. (1999). Mutational contributions to genetic variance-covariance matrices: An experimental approach using induced mutations in *Arabidopsis thaliana*. *Evolution* 53 (6), 1692-1703
16. Caradus, J. & Woodfield, D. *Plant and Soil* (1998) 200: 63.
<https://doi.org/10.1023/A:1004296707631>
17. Carr, D. E. and Dudash, M. R. (1996), Inbreeding depression in two species of *Mimulus* (Scrophulariaceae) with contrasting mating systems. *American Journal of Botany*, 83: 586-593. doi:10.1002/j.1537-2197.1996.tb12743.x
18. Castellanos Maria Clara, Donat-Caerols Santiago, González-Martínez Santiago C., Verdú Miguel & Gómez-Aparicio Lorena. (2014). Can facilitation influence the spatial genetics of the beneficiary plant population? *Journal of Ecology*, 102, 1214–1221.
19. Chapin, F. S. III, Autumn, K., & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *American Naturalist*, 142, S78–S92.
20. Chase, J. M. et al. 2002. The interaction between predation and competition: a review and synthesis. – *Ecol. Lett.* 5: 302–315.

21. Chave, J., Muller-Landau, H.C. & Levin, S.A. (2002). Comparing Classical Community Models: Theoretical Consequences for Patterns of Diversity. *The American Naturalist*, 159, 1–23.
22. Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
23. Clark, J.S. (2010). Individuals and the Variation Needed for High Species Diversity in Forest Trees. *Science*, 327, 1129–1132.
24. Colwell, R.K. & Rangel, T.F. (2009). Hutchinson's duality: The once and future niche. *PNAS*, 106, 19651–19658.
25. Connell, J. (1980). Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. *Oikos*, 35(2), 131-138. doi:10.2307/3544421
26. Damgaard, C. (2004). Inference from plant competition experiments: the effect of spatial covariance. *Oikos*, 107, 225–230.
27. Delph, Lynda F and Kelly, John K (2014). On the importance of balancing selection in plants
28. Publication date 2014/1, New Phytologist, Volume 201 Pages 45-56
29. Dudley, S. A., Murphy, G. P., File, A. L. and Robinson, D. (2013), Kin recognition and competition in plants. *Funct Ecol*, 27: 898-906. doi:10.1111/1365-2435.12121
30. Ehlers, B.K., Damgaard, C.F. & Laroche, F. (2016). Intraspecific genetic variation and species coexistence in plant communities. *Biology Letters*, 12, 20150853.
31. Exposito-Alonso M, Becker C, Schuenemann VJ, Reiter E, Setzer C, Slovak R, et al. (2018) The rate and potential relevance of new mutations in a colonizing plant lineage. *PLoS Genet* 14(2): e1007155. <https://doi.org/10.1371/journal.pgen.1007155>
32. Falahati-Anbaran, M., Lundemo, S. and Stenøien, H. K. (2014), Seed dispersal in time can counteract the effect of gene flow between natural populations of *Arabidopsis thaliana*. *New Phytol*, 202: 1043-1054. doi:10.1111/nph.12702
33. Fisher C.K. and Mehta P.(2014). The transition between the niche and neutral regimes in ecology. *Proc Natl Acad Sci USA* 111:13111–13116
34. Fournier-Level A, et al.(2016) Predicting the evolutionary dynamics of seasonal adaptation to novel climates in *Arabidopsis thaliana*. *Proc Natl Acad Sci USA* 113(20):E2812–E2821.
35. Fridley, J.D. & Grime, J.P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, 91, 2272–2283.
36. Fussmann G. F., Loreau M. & Abrams P. A. (2007). Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, 21, 465–477.
37. Genung, M. A., Schweitzer, J. A., Úbeda, F. , Fitzpatrick, B. M., Pregitzer, C. C., Felker-Quinn, E. and Bailey, J. K. (2011), Genetic variation and community change – selection, evolution, and feedbacks. *Functional Ecology*, 25: 408-419. doi:10.1111/j.1365-2435.2010.01797.x
38. Hamilton, W. D. 1964. The genetical evolution of social behaviour. *I & II. J. Theor. Biol.* 7:1–52.

39. Hart, S. P., Schreiber, S. J., Levine, J. M. and Coulson, T. (2016), How variation between individuals affects species coexistence. *Ecol Lett*, 19: 825-838. doi:[10.1111/ele.12618](https://doi.org/10.1111/ele.12618)
40. Hart, S. P., Freckleton, R. P., Levine, J.M. & Kroon, H. (2018). How to quantify competitive ability. *Journal of Ecology*, 0.
41. Hausmann N. J., Juenger T. E., Sen S., Stowe K. A., Dawson T. E., et al., 2005. Quantitative trait loci affecting δC^{13} and response to differential water availability in *Arabidopsis thaliana*. *Evolution* 59: 81–96
42. Hofhuis, H. and Hay, A. (2017), Explosive seed dispersal. *New Phytol*, 216: 339-342. doi:[10.1111/nph.14541](https://doi.org/10.1111/nph.14541)
43. Holt, R.D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *PNAS*, 106, 19659–19665.
44. Hubbell S.P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19, 166–172.
45. Hutchinson G.E. (1957). *Concluding remarks. Cold Spring Harbor Symp Quant Biol* 22:415–427.
46. Johnson, M.T.J. Stinchcombe, J.R. An emerging synthesis between community ecology and evolutionary biology *Trends Ecol. Evol.*, 22 (2007), pp. 250-257
47. Johnson, M.T.J., Vellend, M. & Stinchcombe, J.R. (2009). Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philosophical Transactions of the Royal Society of London B* 364:1593-1605.
48. Kerwin et al. (2015) Natural genetic variation in *Arabidopsis thaliana* defense metabolism genes modulates field fitness | eLife Lens. <https://lens.elifesciences.org/05604/>. Last accessed 4 May 2018.
49. Koch, H., Frickel, J., Valiadi, M. & Becks, L. (2014). Why rapid, adaptive evolution matters for community dynamics. *Front. Ecol. Evol.*, 2.
50. Kubisch A. *et al.* (2013). Kin competition as a major driving force for invasions. *Am. Nat.* 181: 700–706
51. Lachmuth S., Henrichmann C., Horn J., Pagel J., Schurr F.M. & Rafferty N. (2018). Neighbourhood effects on plant reproduction: An experimental–analytical framework and its application to the invasive *Senecio inaequidens*. *Journal of Ecology*, 106, 761–773.
52. Lankau, R.A. (2011). Rapid Evolutionary Change and the Coexistence of Species. *Annual Review of Ecology, Evolution, and Systematics*, 42, 335–354.
53. Lankau, R.A. & Strauss, S.Y. (2007). Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science*, 317, 1561–1563.
54. Lankau R. A., Wheeler E., Bennett A. E. & Strauss S. Y. (2010). Plant–soil feedbacks contribute to an intransitive competitive network that promotes both genetic and species diversity. *Journal of Ecology*, 99, 176–185.

55. Latzel, V., Allan, E., Bortolini Silveira, A., Colot, V., Fischer, M. & Bossdorf, O. (2013). Epigenetic diversity increases the productivity and stability of plant populations. *Nat Commun*, 4, 2875.
56. Laure, G. Zimmermann N. E., Levine J. M., Adler P. B. & Wootton T (2017). The effects of intransitive competition on coexistence. *Ecology Letters*, 20, 791–800.
57. Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.
58. Lion, S. (2018) Theoretical approaches in evolutionary ecology: Environmental feedback as a unifying perspective. *Am. Nat.* 191, 21–44.
59. Lynch, M., and B. Walsh. (1998). Genetics and analysis of quantitative traits. Sinauer Associates, Inc., Sunderland, MA.
60. Masclaux, F., Hammond, R. L., Meunier, J. , Gouhier-Darimont, C. , Keller, L. and Reymond, P. (2010), Competitive ability not kinship affects growth of *Arabidopsis thaliana* accessions. *New Phytologist*, 185: 322-331. doi:10.1111/j.1469-8137.2009.03057.x
61. Monroe, J. G., Srikant, T., Carbonell-Bejerano, P., Becker, C., Lensink, M., Exposito-Alonso, M., Klein, M., Hildebrandt, J., Neuman, M., Kliebenstein, D., Weng, M-L., Imbert, E., Agren, Å, J.,
62. Rutter, M.T., Fenster, C.B., Weigel, D.. Mutation bias reflects natural selection in *Arabidopsis thaliana*. bioRxiv 2020.06.17.156752; doi: <https://doi.org/10.1101/2020.06.17.156752>, *Nature in press*.
63. Mukai, T. (1964). The Genetic Structure of Natural Populations of *Drosophila Melanogaster*. I. Spontaneous Mutation Rate of Polygenes Controlling Viability. *Genetics*, 50, 1–19.
64. Nei, M. (2013). Mutation-driven evolution. Oxford University Press
65. Nottebrock H., Schmid B., Mayer K., Devaux C., Esler K. J., Böhning-Gaese K., *et al.* (2017a). Sugar landscapes and pollinator-mediated interactions in plant communities. *Ecography*, 40, 1129–1138.
66. Nottebrock H., Schmid B., Treurnicht M., Pagel J., Esler K. J., Böhning-Gaese K., *et al.* (2017b). Coexistence of plant species in a biodiversity hotspot is stabilized by competition but not by seed predation. *Oikos*, 126.
67. Ossowski, S., K. Schneeberger, J. I. Lucas-Lledó, N. Warthmann, R. M. Clark, R. G. Shaw, D. Weigel, and M. Lynch. (2010). The rate and molecular spectrum of spontaneous mutations in *Arabidopsis thaliana*. *Science* 327:92–94.
68. Roles, A. J., and J. K. Conner. (2008). Fitness effects of mutation accumulation in a natural outbred population of wild radish (*Raphanus raphanistrum*): comparison of field and greenhouse environments.. *Evolution*, 62: 1066-1075. doi:10.1111/j.1558-5646.2008.00354.x
69. Roles, A. J., M. T. Rutter, C. B. Fenster and J. K. Conner. (2016). Field measurement of genotype by environment interaction for fitness caused by spontaneous mutations in *Arabidopsis thaliana*. *Evolution*, 70: 1039-1050.
70. R Development Core Team (2011). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

71. Rutter, M. T., F. H. Shaw and C. B. Fenster. (2010). Spontaneous mutation parameters for *Arabidopsis thaliana* measured in the wild. *Evolution*, 64: 1825-1835.
72. Rutter, M., A. Roles, J. Conner, R. Shaw, F. Shaw, K. Schneeberger, S. Ossowski, D. Weigel and C. B. Fenster. (2012). Brief Communication: Fitness of *Arabidopsis thaliana* mutation accumulation lines whose spontaneous mutations are known. *Evolution*, 66: 2335-2339.
73. Rutter, M. T., A. J. Roles, and C. B. Fenster. (2018). Quantifying natural seasonal variation in mutation parameters with mutation accumulation lines. *Ecology and Evolution*, <https://doi.org/10.1002/ece3.4085>
74. Schaack, S., Allen, D.E., Latta, L.C., Morgan, K.K. & Lynch, M. (2013). The effect of spontaneous mutations on competitive ability. *Journal of Evolutionary Biology*, 26, 451–456.
75. Shaw, R.G., Byers, D.L. & Darms, E. (2000). Spontaneous Mutational Effects on Reproductive Traits of *Arabidopsis thaliana*. *Genetics* 155:369–378.
76. Shaw, F. H., C. J. Geyer, and R. G. Shaw. (2002). A comprehensive model of mutations affecting fitness and inferences for *Arabidopsis thaliana*. *Evolution* 56:453–463.
77. Shefferson Richard P, Salguero-Gómez Roberto & Rees Mark. (2015). Eco-evolutionary dynamics in plants: interactive processes at overlapping time-scale and their implications. *Journal of Ecology*, 103, 789–797.
78. Soliveres, S., Smit, C. & Maestre, F.T. (2015). Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biol Rev Camb Philos Soc*, 90, 297–313.
79. Soliveres Set al. (2015). Intransitive competition is widespread in plant communities and maintains their species richness. **Ecol. Lett.** 18, 790–798. doi:10.1111/ele.12456
80. Stearns, F. W. and C. B. Fenster. (2016). The effect of induced mutations on quantitative traits in *Arabidopsis thaliana*: Natural versus artificial conditions. *Ecology and Evolution*, doi: 10.1002/ece3.2558
81. Strauss, S.Y. & Irwin, R.E. (2004). Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annu. Rev. Ecol. Evol. Syst.*, 35, 435–466.
82. Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990). On the Relationship between r/K Selection and Environmental Carrying Capacity: A New Habitat Templet for Plant Life History Strategies. *Oikos*, 58, 239–250.
83. Tiffin, P. (2002). Competition and time of damage affect the pattern of selection acting on plant defense against herbivores. *Ecology*, 83: 1981-1990. doi:10.1890/0012-9658(2002)083[1981:CATODA]2.0.CO;2
84. Tilman D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. **Proc. Natl Acad. Sci. USA** 101, 10 854–10 861. doi:10.1073/Pnas.0403458101
85. Turcotte, M.M. & Levine, J.M. (2016). Phenotypic Plasticity and Species Coexistence. *Trends Ecol. Evol. (Amst.)*, 31, 803–813.

86. Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., John Kress, W., Erickson, D., *et al.* (2010). Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecol. Lett.*, 13, 1503–1514.
87. Van Dam, N. M. and Baldwin, I. T. (1998), Costs of jasmonate-induced responses in plants competing for limited resources. *Ecology Letters*, 1: 30-33. doi:10.1046/j.1461-0248.1998.00010.x
88. Vellend Mark & Geber Monica A. (2005). Connections between species diversity and genetic diversity. *Ecology Letters*, 8, 767–781.
89. Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., *et al.* (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27, 244–252.
90. Violle, C. & Jiang, L. (2009). Towards a trait-based quantification of species niche. *J Plant Ecol*, 2, 87–93.
91. Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J.B., Cadotte, M.W., *et al.* (2017). Functional Rarity: The Ecology of Outliers. *Trends in Ecology & Evolution*, 32, 356–367.
92. Weng, M.-L., Becker, C., Hildebrandt, J., Rutter, M.T., Shaw, R.G., Weigel, D. and Fenster, C.B. 2019. Fine-Grained Analysis of Spontaneous Mutation Spectrum and Frequency in *Arabidopsis thaliana* Genetics, 211, 703-714. doi.org/10.1534/genetics.118.301721
93. Weng, M.-L., Ågren, J., Imbert, E., Nottebrock, H., Rutter, M.T., and Fenster, C.B. 2021. Fitness effects of mutation in natural populations of *Arabidopsis thaliana* reveal a complex influence of local adaptation. *Evolution*, 75: 330-348. doi.org/10.1111/evo.14152
94. Whitham, T. G., Young, W. P., Martinsen, G. D., Gehring, C. A., Schweitzer, J. A., Shuster, S. M., Wimp, G. M., Fischer, D. G., Bailey, J. K., Lindroth, R. L., Woolbright, S. and Kuske, C. R. (2003), Community and ecosystem genetics: A consequence of extended phenotype. *Ecology*, 84: 559-573. doi:10.1890/0012-9658(2003)084[0559:CAEGAC]2.0.CO;2
95. Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J. *et al.* (2006). A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.*, 7, 510–523.
96. Whitlock R. & Lortie C. (2014). Relationships between adaptive and neutral genetic diversity and ecological structure and functioning: a meta-analysis. *Journal of Ecology*, 102, 857–872.

Tables

Table 1

Table of all different eco-evolutionary trait-based neighborhood models including intraspecific variation to test our three objectives of density effects on survival and seed set of *A. thaliana*. Differential models split the neighbor responses into within genotypes and between genotypes. Neutral models describe the overall neighbor response without differentiating between genotypes. All models include random effects of plant biomass on the slope, subblock or block and MA-line on the intercept (see Fig. 1 for design), and respectively depending on small (s) or large-scale (l) (for more details see method section).

	Year 2004	Year 2005	Model
Individual survival	A1 (s,l)	A2 (s,l)	Differential
	A1 (s,l)	A2 (s,l)	Neutral
Seed set	B1 (s,l)	B2 (s,l)	Differential
	B1 (s,l)	B2 (s,l)	Neutral

Table 2

The coefficient and AIC from eco-evolutionary trait-based neighborhood models of the *Arabidopsis thaliana* field experiment in the years 2004 and 2005. Models include intraspecific genetic variation defined as intra-genotypic (within genotypes) and inter-genotypic (between genotypes) variation. Models are shown at two different spatial scales: weighted subblock density (80cm radius) and weighted block density (200cm radius). All scales include variables of neutral effects (absence of intra- and inter-genotypic variation (total sum of all neighboring genotypes)) and differential effects (presence of intra- and inter-genotypic variation (split of neighboring genotypes in intra- and inter-genotypic genotypes)). Thus, neighbor identity is split into intra- and inter-genotypes as differential effects or are combined as neutral effects, which includes all neighbors. P-value levels <0.05*, <0.005**, <0.001*** and >0.05^{ns}.

Survival model							
(A1) 2004		(s) Small scale (80cm)		AIC	(l) Larger scale (200cm)		AIC
		<i>Intra</i>	<i>Inter</i>		<i>Intra</i>	<i>Inter</i>	
<i>Weighted density</i>							
MA Lines	neutral	-0.02 ^{ns}		7551.7	0.004 ^{ns}		7644.5
	differential	-0.02 ^{ns}	-0.37**	7548.6	0.15 ^{ns}	-0.30 ^{ns}	7644.2
(A2) 2005		(s) Small scale (80cm)		AIC	(l) Larger scale (200cm)		AIC
		<i>Intra</i>	<i>Inter</i>		<i>Intra</i>	<i>Inter</i>	
<i>Weighted density</i>							
MA lines	neutral	0.03 ^{ns}		9637.3	0.03 ^{ns}		9872.9
	differential	-0.02 ^{ns}	-0.28***	9626.1	0.05 ^{ns}	-0.10 ^{ns}	9873.3
Seed set model							
(B1) 2004		(s) Small scale (80cm)		AIC	(l) Larger scale (200cm)		AIC
		<i>Intra</i>	<i>Inter</i>		<i>Intra</i>	<i>Inter</i>	
<i>Weighted density</i>							
MA lines	neutral	-0.02***		52982	0.03		52944
	differential	-0.02*	-0.07***	52841	0.03***	0.15***	52939
(B2) 2005		(s) Small scale (80cm)		AIC	(l) Larger scale (200cm)		AIC
		<i>Intra</i>	<i>Inter</i>		<i>Intra</i>	<i>Inter</i>	
<i>Weighted density</i>							
MA lines	neutral	-0.008*		49103	-0.008*		49049
	differential	-0.009**	-0.09***	49095	-0.01*	0.16***	49026

Figures

Figure 1

(A) 100 Mutation accumulation lines (here example of four MA-lines) of *Arabidopsis thaliana* derived from a single founder (Columbia) after 25 generations with a mutation rate of ~ 0.7 per generation (Weng et al. 2019). Each MA line has a unique genotype that differs from the founder. Fundamental niche of individual genotypes (different dashed and dotted lines) and founder genotype (black line) are distributed within the hypothetical fundamental niche of a population of *A. thaliana* (bold black line). Axes represent niche axis (resource-use, environmental factors, etc.). (B) Planting design of *A. thaliana* in a natural field experiment showing spatial biomass variation of individual survivors in 2004.

Figure 2

The barplots show standardized coefficient effect sizes and associated standard errors of eco-evolutionary trait-based neighborhood models at small-scale (a, c) and large-scale (b, d) for all MA-lines for the survival model (a, b) and the seed set model (c, d). Intra-genotypic effects (yellow) and inter-genotypic effects (grey) are presented for 2004 and 2005. Coefficient effect sizes indicate reduction or an increase of seed set depending on biomass density of intra-or inter-genotypic neighbors. In addition, coefficient effect sizes indicate a reduction of survival of intra or inter-genotypic neighbors.

Figure 3

The effect range on seed set (a), (b) and survival (c) computed from eco-evolutionary trait-based neighborhood models shown as odds ratios for year 2004 (for 2005 see Supplementary Material). (a) Shows the hierarchical competitive order of MA lines and founder for the seed set model including range effects of each MA line and founder as random intercepts and the trait proxy biomass as random slopes at small-scale and (b) at large-scale. (c) Shows the hierarchical selective order of MA lines and founder for the survival model including range effects of each MA line and founder as random intercepts at small-scale.

Figure 4

Correlation of the simulated conditional mean represented as odds ratio of same genotypes (MA lines) reducing or increasing the effect sizes of the seed set model and of the survival model at small-scale or large-scale for 2004, respectively. For year 2005 see supplementary material. Each point represents different genotypes of *A. thaliana*. Negative values means lower effect sizes on the survival or seed set and positive values means increasing the effect sizes on the survival or seed set. a) Relationship between survival and seed set model. b) Relationship between survival and seed set model. c) Relationship between small-scale survival and large-scale seed set model. Since we are plotting effect sizes, the positive correlation in panel c reflects a trade-off between competition and facilitation (see results).

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