1    **Rapid evolution of spontaneous mutation increases genetic diversity facilitating plant**

2    **population survival**

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7

8    Abstract

9    Using a mechanistic eco-evolutionary trait-based neighborhood-model, we quantify the impact

10    of mutations on spatial interactions to better understand the potential effect of niche evolution

11    through mutations on the population dynamics of *Arabidopsis thaliana*. We use 100 twenty-

12    fifth generation mutation accumulation (MA) lines (genotypes) derived from one founder

13    genotype to study mutational effects on neighbor responses in a field experiment. We created

14    individual-based maps (15,000 individuals), including phenotypic variation, to quantify

15    mutational effects within genotypes versus between genotypes on reproduction and survival.

16    At small-scale, survival is enhanced but reproduction is decreased when a genotype is

17    surrounded by different genotypes. At large-scale, seed set is facilitated by different genotypes

18    while the same genotype has either no effect or negative effects. Mutations may provide a

19    mechanism for plants to quickly evolve niches and may drive competition, facilitation and

20    selection with profound consequences for future population and community dynamics.

21    Introduction

22    A complete understanding of population and community dynamics requires linking intraspecific

23    genetic diversity with spatial ecological interactions (Bolnick et al. 2011, Genung et al. 2011).

24    Evolutionary mechanisms -- mutation, drift, gene flow and selection -- are responsible for

25    intraspecific genetic variation contributing to both ecological structure and species diversity

26    (Hart et al. 2016). These community properties impact ecological mechanisms such as

27    competition and facilitation (Whitlock 2014). Competition and facilitation in turn affect

28    population and community dynamics that depend on variation in demographic rates (Chase et

29    al 2002, Solivers et al 2015). Demographic rates are influenced by spatial interactions of genetic

30    variation and this variation may contribute to species coexistence: genotypes can hinder or

31    favor the survival of each other by using similar or different resources with negative or positive

32    consequences for coexisting species (Hart et al. 2016, Hausch et al. 2018). Intraspecific genetic

33    variation contributing to individual trait variation and environmental adaptability may promote

34    species coexistence by both increasing habitat heterogeneity and altering competitive

35    hierarchies (Violle et al. 2012, Ehlers et al. 2016). However, intraspecific genetic variation may

36    hinder species coexistence when intraspecific genetic variation is diminished by competition

37    between individuals (Hart et al 2016). To fully understand the causes of coexistence

38    mechanisms, we need to integrate intraspecific evolutionary mechanisms with intraspecific

39    ecological mechanisms underlying spatial species interactions (Bolnick et al. 2011, Ehlers et al.

40    2016).

41

42   The number of studies exploring eco-evolutionary dynamics and their potential

43 feedbacks on population and community dynamics has dramatically increased over the last two

44 decades (Shefferson and Salguero-Gomez 2015). An important current issue in community and

45 ecosystem genetics research is determining the relevance of intraspecific genetic variation and

46 genetic differentiation (divergence) to ecological and evolutionary processes at the community

47 and ecosystem level (Genung et al. 2011, Pujol et al. 2018). Quantifying intraspecific trait

48 variation defining the fundamental niches of species is an important link between ecology and

49 evolution (Violle and Jiang 2009). Spatial structure is another important component of realistic

50 eco-evolutionary dynamics, such that in spatially structured populations, selection is

51 determined by the interplay between demographic and genetic structures (Lion et al. 2011).

52 Demographic structure describes the spatial distribution of individuals through birth, death and

53 migration resulting in spatial patterns, while genetic structure describes the spatial distribution

54 of genotypes. The amount and spatial pattern of genetic variation may constrain evolution of

55 traits influencing competitive ability of individuals (Wilson 2014). Moreover, competitive

56 abilities depend on species' niches. The strength of competition is determined by how much

57 individual niches overlap with each other (Hutchinson 1957, Holt 2009) and how long

58 coexistence has occurred (Connell 1980).

59

60   Species niche breadths are reflected by individual trait variability and intraspecific and

61 interspecific genetic and spatial interactions driven by environmental conditions. Thus,

62 intraspecific trait variability shaped by intraspecific genetic variation can influence ecological

63 mechanisms driving variation among individual persistence (Lankau 2009). Only when the

64  spatial relationship between traits and demographic parameters is explicitly described can

65  robust hypotheses about the effects of individual variation on competitive outcomes be

66  accurately formulated (Hart et al. 2016). Especially in controlled common garden environments,

67  genetic variation in one species can have predictable and heritable effects on associated

68  communities and ecosystems (Carr and Dudash 1995; Whitham et al. 2003, 2006; Johnson &

69  Stinchcombe 2007; Bailey et al. 2009; Johnson, Vellend & Stinchcombe 2009). Hence, coupling

70  evolutionary genetics with community ecology may advance our understanding of species

71  interactions and population and community dynamics (Baron et al. 2016), especially for

72  populations and communities that suffer environmental change (Bellard et al. 2012).

73

74      An important gap in our understanding of the link between evolutionary and ecological

75  processes is the nearly complete absence of data quantifying how rapidly genetic variation

76  governing within species competitive hierarchies evolves (Hausch et al. 2018). An important

77  source of novel population genetic variation is mutation. Therefore, we aim to investigate the

78  link between evolutionary genetics and spatial ecological interactions of mutation accumulation

79  lines (MA lines) in the model plant organism *Arabidopsis thaliana* (Brassicaceae) to advance our

80  understanding of the genetic origins of population and community dynamics, contributing to a

81  fuller understanding of the maintenance of biodiversity. We take advantage of 25th generation

82  *A. thaliana* mutation accumulation (MA) lines that were planted under field conditions in years

83  2004 and 2005 with spatial records of each individual each year (e.g., Rutter et al. 2010; 2012,

84  Rutter et al. 2018) (Fig. 1).

85

86           Here we focus on the neighborhood effects of MA lines on focal plants from the same

87       MA line (within genotypes) or different MA lines (between genotypes) to quantify the evolution

88       of intraspecific genetic variation through the accumulation of spontaneous mutations. We

89       implement trait-based neighborhood models (Nottebrock et al. 2017a, Nottebrock et al. 2017b,

90       Lachmuth et al. 2017) to understand ecological mechanisms of within and between MA lines

91       genetic variation to examine eco-evolutionary dynamics (Lion 2018). Specifically, we ask: 1) Do

92       spontaneous mutations rapidly introduce enough genetic variation among MA lines to influence

93       competition and facilitation of *A. thaliana*? 2) Do spontaneous mutations of MA lines

94       contribute to competition, facilitation and selection promoting differential MA line survival and

95       reproduction at different spatial scales? 3) How may competitive and facilitative effects

96       potentially determine population and community dynamics?

97

98　Methods

99　MA lines are generated from a single nearly homozygous individual founder and cultivated via

100　limited effective population number. In the case of *A. thaliana*, this occurs through single seed

101　descent, resulting in Ne= 1. Thus typical MA line cultivation results in an unbiased sample of

102　mutation effects ranging from deleterious to advantageous, although lethal mutations are

103　excluded (Lynch and Walsh 1998). Each MA line accumulates independent spontaneous

104　mutations. After the propagation of a set of MA lines through multiple generations, the genetic

105　differences among the MA lines and between those lines and the founder reflect the input of

106　mutation. Significant MA line effects for multiple traits, including performance and trait

107　measures, were found under both field and greenhouse conditions (Rutter et al. 2010; Roles et

108　al. 2016, Rutter et al. 2018). Each of the MA lines in our experiment is fixed for an average of 20

109　different sequence level mutations, single nucleotide mutations (SNMs) and indels combined

110　(Ossowski et al 2010, Rutter et al. 2012, Weng et al. 2019).

111

112　*MA lines and field experiments*

113　We used survival and seed set data of *A. thaliana* MA lines and the founder as assessed in field

114　experiments in 2004 and 2005 from Rutter et al. (2010, 2012 and 2018) planted in a

115　randomized design (Fig. 1). Rutter et al. (2010, 2012) planted seedlings of 100 MA lines and the

116　founder at the four-leaf stage, approximately two weeks post germination, into a secondary

117　successional field at Blandy Experimental Farm (BEF) in Virginia (39°N, 78°W). Each of the 100

118　MA lines was used to found up to five sublines to minimize biases due to maternal effects

119    introduced by the specific location within the greenhouse. We founded six sublines from each

120    of the six lines representing the premutation founder genotype. In 2003, subline plants were

121    used to generate all seed utilized in all field experiments. In each planting, 7504 individuals

122    were planted, 7000 individuals of 100 MA lines (70 replicates per MA line, 14 replicates per

123    subline) and 504 individuals of the founder (14 replicates per subline).  The planting

124    environment corresponds to a spring ephemeral life-history, where plants germinate and

125    complete the life-cycle in the spring.  At the time of planting, vegetation was scant but present.

126    By harvest, the *A. thaliana* individuals were dwarfed by naturally occurring vegetation.

127

128        The plot was arranged in 14 spatial blocks with each containing 12 subblocks (Fig. 1B)

129    (total plot area approximately 35 x 25 m). Each block included one seedling from each subline

130    and in total 7504 individuals. We used the spatial information of each individual within the

131    described design and created a raster of all plant individuals with R packages (raster, maps,

132    maptools). We used individual-based maps neighborhood matrices with exact spatial and trait

133    information of each genotype. If all five sublines did not produce enough seedlings to distribute

134    in all blocks, seedlings from other sublines of the same MA line were overrepresented in blocks

135    to maintain the same overall number of plants per MA line. Plants dying within the first 3 days

136    of transplant (about 50 plants) were considered to have died from transplant shock and were

137    replaced with another plant from the same MA line. Plants were censused weekly for survival.

138    Plants were harvested by late May, by which time they had senesced. In 2004 a total of 5915

139    individuals including 394 founders survived. In 2005, a total of 4506 individuals survived

140    including 302 founders. Plants were oven dried and biomass was measured. All fruits produced

141    by each plant were counted and in combination with seed production used as the

142    measurements of seed set. For our analysis, we used measurements of two response variables

143    representing an important part of the life history of *A. thaliana* to calculate direct

144    neighborhood effects on: a) the survival rate of plant individuals and b) individual seed set from

145    plants that survived and produced fruits.


146

147    *Statistical Analyses*

148    We use eco-evolutionary trait-based neighborhood models that include intraspecific genetic

149    variation and phenotypic variation expressed by plant trait biomass to analyze competition and

150    facilitation between individuals of *A. thaliana*. We analyzed plant survival rate and focal seed

151    set measurements from years 2004 and 2005 separately. For each year, we considered all

152    individuals as focal plants in the analysis based on individual-based neighborhood matrices to

153    analyze 1) rate of plant survival to reproduction and 2) seed set of those plants that survived to

154    reproduction. We analyzed neighboring plants to focal plants in a radius of 80 cm (small-scale)

155    or 200 cm (large-scale) of a given focal plant as two spatial scales in the neighborhood analyses

156    (Fig. 1) to quantify selection, competition or facilitation between plants depending on their

157    genotypic and phenotypic variation.

158

159         We used extensions of linear mixed models (package lme4, Bates et al. 2014) in R ver.

160    3.3.3 (www.r-project.org) to conduct neighborhood analyses of focal seed set and survival. We

161    assumed binomial errors for the analyses of plant survival and Poisson errors for analyses of

162    seed set. The mixed models described interactions among plants by including neighborhood

163    indices as explanatory variables at two spatial scales in separate models. Neighborhood indices

164    are spatial density effects of surrounding neighborhood plants that affect focal seed set and

165    survival. For each plant, we used the Euclidian distance between the focal plant and the

166    neighboring plants to compute response effects of intra- (same genotype) or inter-genotypic

167    (different genotype) neighbors in a given radius around focal plants (Nottebrock et al. 2017).

168    Moreover, we used a neighborhood index that accounts for the decline of neighbor effects with

9

169     distance from the focal plant (Uriarte et al. 2010) and summed the amount of biomass from all

170     individuals in a radius of 80 cm or 200 cm respectively by a Gaussian interaction kernel

171     (Lachmuth et al. 2018, Nottebrock et al. 2017, Damgaard 2004). We used random effects of

172     block and subblock to correct for environmental variation between local heterogeneous

173     conditions. Importantly, we correct for between MA line effects by including MA lines as a

174     random effect. In addition, including a random slope of biomass on each random intercept

175     corrects for the intraspecifc phenotypic variation depending on local conditions of plant focal

176     individuals. Moreover, the weighted neighborhood density by plant biomass accounts for

177     environmental variation between neighboring plants. Our model parameters and a detailed

178     model description of subblock and block models can be found in S1 supplementary text

179     (Supplementary Material).

180

181          Neighborhood matrices of all individuals (individual-based maps) were used to analyze

182     the effect of intra- and inter-genotypic neighbors on survival and focal seed set with spatial

183     interaction kernels of neighborhood (plant biomass) density. By incorporating different

184     genotypes and phenotypic variation, we can quantify how important genetic variation is for

185     neighborhood models and if the phenotypic variation explains spatial interactions between

186     individuals. We assume the consequences of genetic differences to be larger between MA lines

187     than between any MA line with the founder. This is a valid assumption since each MA line

188     differs from the other by approximately 20 + 20 = 40 mutations, while any two replicates within

189     a MA line will differ by one generation, $\leq$ 2 mutations. Thus, we simulated line effects from

190     parameters derived from MA lines as random effects with the R package 'merTools' and the

191     function 'plotREsim' in R 2018.

192

193         We used the trait values of neighbors to calculate trait-based neighborhood indices

194     including plant biomass as a trait (Goldberg & Fleetwood, 1987; Goldberg & Landa, 1991; Cahill

195     et al., 2005). We fitted eco-evolutionary trait-based neighborhood models at two different

196     spatial scales for response variables (survival and seed set) for each of the two and both years.

197     To address our objectives, we first analyzed models with differential effect in which intra-

198     genotypic neighbors (within all MA lines and founder) had a different effect on survival (A1, A2,

199     Table 1) and seed set (B1, B2, Table1) than inter-genotypic neighbors at small-scale (s) and

200     large-scale (l). In addition, we analyzed models with neutral effects on survival (A1, A2, Table 1)

201     and seed set (B1, B2, Table 1) that included total neighbor density without the split between

202     intra-genotypic and inter-genotypic neighbors at small-scale (s) and large-scale (l). To this end,

203     all models were fitted with two separate neighborhood indices that were calculated from intra-

204     and inter-genotypic neighbors. To justify the inclusion of individual plant biomass as trait-values

205     for interacting plants in the model, we used AICc to compare the models with and without the

206     trait-proxy (Burnham and Anderson 2002). We found that all models perform better including

207     biomass as a trait-proxy ($\Delta$AICc > 2). All eco-evolutionary trait-based neighborhood models

208     contained random effects of subblock nested in block at block scale and subblock scale on the

209     intercept, MA line identity on the intercept and the focal trait-value (plant biomass) on the

210     slope. Additionally, because direct environmental variables were not measured during the field

211     experiments, we included in each model the individual's biomass to correct for environmental

212     conditions for spatial autocorrelation. All variables are scaled and centered to assure

213     comparability between predictor variables. Models of differential and neutral effects for 2004

214     and 2005 (Table 1, A1-A2, B1-B2) are fitted at small-scale (80cm scale) and at large-scale

215     (200cm scale). Hereafter, the 80 cm scale models are referred to as "small-scale" models and

216     the 200 cm scale models are referred to as "large scale" models. Neighborhood indices, intra-

217     and intergenotypic variation and total variation of biomass density are included as inverse

218     density variables (1/1+density). We compared models of differential and neutral effects

219     through likelihood ratio tests (LRTs).

220

221    Results

222    Focal plants surrounded by plants of the same genotypes varied from 0 to 6 individuals at small-

223    scale (sub-block) and 5 to 6 individuals at large-scale (block). After determining that eco-

224    evolutionary trait-based models perform better when including plant biomass as a trait proxy to

225    calculate trait-based neighborhood indices we found that all models including plant biomass

226    perform better than models including only neighborhood density ($\Delta$AIC > 2, Supplementary

227    Material S2).

228

229    *Weighted neighbor effects of biomass density on genotypes for plant survival*

230    At small-scale, survival rate is larger when surrounded by inter-genotypic than intra-genotypic

231    neighbors for both years 2004 and 2005 (model A1 and A2; Table 2 and Fig. 2a). This difference

232    of survival rate between intra- and inter-genotypic plants indicates that inter-genotypic

233    neighbors select for genotypic diversity and show stronger competitive effects on the survival

234    of intra-genotypic neighbors at small-scale. This finding is demonstrated by the superior

235    performance of the differential model relative to the neutral model (year 2004: LRT: $\chi^2_{1DF}$ =

236    5.21, p < 0.05; year 2005: LRT: $\chi^2_{1DF}$ = 14.73, p < 0.001). The differential and neutral models of

237    survival at large-scale have only non-significant effects (Table 2). In addition, comparing the AIC

238    we found that models at large-scale perform worse than at small-scale for both 2004 and 2005

239    (Table 2). We therefore will only discuss small-scale effects on survival. The distance kernel

240    (alpha) at small-scale shows that neighboring plants of different genotypes reduce plant

241    survival by 50% at 53 cm in 2004 and 48 cm in 2005.

242 *Weighted neighbor effects of biomass density on genotypes for seed set*

243 At both small and large scales, the differential model performs better than the neutral model:

244 at small scales (year 2004: LRT: $\chi^2_{1DF}$ = 52.48, p < 0.001; year 2005: LRT: $\chi^2_{1DF}$ = 17.37, p < 0.001;

245 respectively) and at large scale (year 2004; LRT: $\chi^2_{1DF}$ = 679.44, p < 0.001; year 2005: LRT: $\chi^2_{1DF}$ =

246 21.17, p < 0.001; respectively). The small-scale model of seed set that included weighted

247 biomass densities demonstrates the reduction of seed set is larger when surrounded by inter-

248 genotypic than intra-genotypic neighbors for both years 2004 and 2005 (model B1 and B2;

249 Table 2 and Fig. 2a). The difference between intra- and inter-genotypic plants indicates that

250 inter-genotypic neighbors have a stronger competitive effect on seed set than intra-genotypic

251 neighbors at small-scale. In contrast, at large-scale seed set increases when surrounded by

252 inter-genotypic neighbors but decreases when surrounded by intra-genotypic neighbors for

253 both years 2004 and 2005 (model B1 and B2; Table 2 and Fig. 2b). Comparing the AIC between

254 small and large-scales, models at large-scale for 2004 and 2005 perform better (Table 2).

255

256 *Genotype effects on plant survival and seed set*

257 The distance kernel at small-scale in 2004 indicates a reduction of seed set (competition)

258 whereas at large-scale are consistent with an increase of seed set (facilitation). Neighboring

259 plants from all genotypes of *A. thaliana* at small-scale reduce 50% of focal seed set at 23 cm

260 and at large-scale facilitate 50% of focal seed set at 86 cm. The estimation of genotype effects

261 (MA lines and founder) simulated as conditional means and expressed as odds ratios show

262 hierarchical orders of MA line and founder competitive effects at small-scale (Fig. 3). We found

263    no significance of simulated competitive effects of all MA lines and founder calculated from

264    survival and seed set models at small-scale (ANOVA, $p > 0.1$, Fig. 4a). In addition, we found no

265    significant correlation between competitive effects of MA lines and founder at large-scale. In

266    addition, we did not find selective effects of MA lines and founder on the survival at small-scale

267    (ANOVA, $p > 0.1$, Fig. 4b). However, we found strong correlation between competitive effects

268    of MA lines and founder at small-scale and large-scale indicating a genetic trade-off (ANOVA,

269    $F=460.07$, $P< 0.0001$, Fig. 4c).

270

271    Discussion

272    We are able to quantify individual spatial interactions between and within genotypes (MA lines

273    and founder) using a mechanistic eco-evolutionary trait-based neighborhood model. We

274    demonstrate intraspecific genetic variation due to spontaneous mutations can shape

275    competitive abilities of genetically different individuals *of A. thaliana*. Notably, these

276    differences arose in just 25 generations of mutation and in the absence of natural selection.

277    Many of the mutations differentiating the MA lines also appear in nature, contributing to *A.*

278    *thaliana* genetic polymorphism (Weng et al., 2019). Plant survival is higher when surrounded by

279    inter-genotypic neighbors supporting genetic diversity. Effects on focal seed sets were reversed

280    between small and large scales; inter-genotypic neighbors have stronger negative (competitive)

281    or positive (facilitative) effects than intra-genotypic neighbors on focal seed sets at small-scale

282    or large-scale, respectively. Moreover, at small-scale, competitive effects of different MA lines

283    have similar impacts on survival and seed set. At large-scale, the intra-genotypic effect on

284    survival turns into less competitive effects on seed set. In contrast, different genotypes show

285    stronger facilitative effects within the population at large-scale, maybe because plants are more

286    competitive against other species. Below we discuss how these scale effects provide insight on

287    community assembly and potential coexistence.

288

289    *Selection, Competition and Facilitation*

290    Because of stronger statistical signals of effect sizes between genotypes than within genotypes,

291    niche variation may result in niche expansion or reduction (Ehlers et al. 2016). However, these

292    competitive effects only occur between plants that survive to reproduction and affect seed-set.

293    The neighbor effect on plant survival suggests kin recognition despite our randomized field

294    experiment that likely reduced the spatial autocorrelation of genotypes (Hamilton 1964,

295    Kubisch et al. 2013). Seed-dispersal is limited in space because the *A. thaliana* fruit do not

296    dehiscently explode as they do in related species (Hofhuis and Hay 2017), although a seed bank

297    ensures some dispersal through time (Falahati-Anbaren et al. 2014). The neighbor effect

298    increasing genetic diversity of *A. thaliana* populations can have a positive effect on the

299    coexistence of competing species (Vellend 2006). If we assume that the increase of genetic

300    diversity due to spontaneous mutations of *A. thaliana* affects the extent of individual plant

301    niches, at large-scale the inclusion of other plant species should result in stronger competitive

302    effects of *A. thaliana* with other plant species (Hausch et al. 2018). We demonstrate that *A.*

303    *thaliana* individuals increase their competitive abilities with an increase of genetic diversity,

304    perhaps due to the expansion of their individual niches due to more variation in plant traits.

305

306        Antagonistic interactions between genotypes on different spatial scales may result in

307    genetic trade-offs when mutations are advantageous or deleterious, which over many

308    generations could provide a strong stabilizing force maintaining both species and genetic

309    diversity in this system and promote coexistence (Lankau 2008). Thus, spontaneous mutation

310    could also provide an additional evolutionarily stabilizing effect on community dynamics. Our

311    study demonstrates the potential for a fundamental evolutionary process, mutation, to have

312    profound consequences for community structure. When *A. thaliana* is rare, selection would

313    favor genotypes that compete well and enhance the population's survival relative to that of its

314     interspecific competitor (Lankau 2009). In contrast, when *A. thaliana* is common and the

315     interspecific competitor is rare, selection would favor *A. thaliana* genotypes that are good

316     intraspecific competitors. This trade-off may result in a decrease in the interspecific competitive

317     ability of *A. thaliana*, effectively increasing the competitor's fitness relative to that of *A.*

318     *thaliana* (Lankau 2009, Lankau and Strauss 2007). However, the genetic trade-off between

319     intra-and interspecific competitive abilities due to mutation remains unknown because our

320     dataset only includes performance of *A. thaliana* individuals without quantifying the

321     surrounding intraspecific environment (Chesson 2000, Adler et al. 2007).

322

323     *Competitive Hierarchies of MA lines and Founder lines*

324     Our result show scale dependent competition and facilitation (Nottebrock et al. 2017b)

325     providing further evidence that in a relative short evolutionary time scale spontaneous

326     mutations may change the competitive hierarchies between founders and specific MA lines due

327     to advantageous or deleterious mutations (Rutter et al. 2010). In contrast to Masclaux et al.

328     2010, we found differential responses to similar genotypes vs different genotypes in *A. thaliana*

329     depending on the neighbor effect on the plant survival or seed set. However, the interaction

330     between similar genotypes and different genotypes seems to depend on the strength of the

331     competitive abilities of the accessions (this study). Comparisons between MA lines and founder

332     demonstrate that competitive hierarchies follow different orders and competitive effects occur

333     at different life-history stages at different spatial scales. Eco-evolutionary processes might

334     reflect spatial selection for diversified genotypes because of niche evolution and individuals of

335     different genotypes that survived to reproduction have stronger competitive abilities (Ehlers et

18

336    al. 2016). Moreover, the hierarchical order of competitive effects between MA lines and

337    founders shows strong variation.

338

339    *Eco-evolutionary dynamics*

340    Populations can adapt evolutionarily to their environment on a time scale equivalent to that of

341    ecological processes and affect present day species interactions, i.e., coexistence (Fussmann et

342    al. 2007). Yet, sustained and rapid climate change could deplete genetic variance faster than it

343    can be replenished by mutation (Fournier-Level et al. 2016). In our study, we show that only 25

344    generations are enough to influence present day plant interactions of *A. thaliana* in the

345    presence of other plant species. Possible effects of mutations on trait mechanisms might reflect

346    the increased seed set of *A. thaliana* at large-scale, because of the presence of another plant

347    species allowing the establishment and growth of *A. thaliana* (Ehlers et al. 2016). Many traits

348    can influence competition and facilitation between individuals of different genotypes (e.g.

349    Chapin et al. 1993; Caradus and Woodfield 1998; Hausmann et al. 2005). Intraspecific

350    competition between *A. thaliana* individuals tends to be higher than between interspecific

351    competitors (Lankau and Strauss 2007, Van Dam and Baldwin 1998; Tiffin 2002, Strauss and

352    Irwin 2004). Such spatial mechanisms might be described by the scale difference of competition

353    at small-scale and facilitation at large-scale between different *A. thaliana* genotypes.

354    Competition and facilitation are therefore dependent on the extension or reduction of

355    individual niches, which is based on the ability to advance or distract traits due to spontaneous

356    mutations. However, we are not able to directly link our results to benefactor or antagonistic

357    plants, because we focused in our experiment on *A. thaliana* densities and fitness components.

19

358    Nevertheless, genotypic-specific interactions are well studied. A number of studies of *A.*

359    *thaliana* MA lines demonstrate mutation effects on plant traits such as leaf weight, flowering

360    time, trichome density, number of leaves at bolting, duration of vegetative and flowering

361    period (Camara and Pigliucci 1999, Rutter et al. 2010, Stearns and Fenster 2016). It is

362    conceivable that the increase in variance of these traits through spontaneous mutations could

363    contribute to the evolution of competitive hierarchies.

364

365    *Consequences for population and community dynamics*

366    Competition between genetically different individuals of *A. thaliana* at small-scale and

367    facilitation at large-scale has important implications for population structure (Cahill et al. 2005).

368    Plants may cooperate by competing less, or act selfishly by competing more (Dudley et al.

369    2013). However, kin recognition might be the result of kin selection when occurring in a

370    heterogeneous environment with various genotypes (Hamilton 1964). Especially, at large-scale,

371    we show that different genotypes facilitate seed set that stabilize the population dynamics by

372    increasing the performance of neighboring plant individuals (Latzel et al. 2013, Castellanos et al.

373    2014). Thus, selection for diversified genotypes might reveal a coexistence mechanism, because

374    mutations at a short time scale (25 generations) are able to alter the competitive hierarchies of

375    *A. thaliana* individuals of different genotypes. These genotypes might expand or reduce their

376    niches and can therefore act more competitive against strangers (Ehlers et al 2016). Moreover,

377    variation in competitive ability among genotypes due to mutation can lead to intransitive

378    competitive hierarchies at a small-scale, and allow coexistence of competitors at large-scale

379    when there is no single dominant competitor (Vellend and Geber 2005, Taylor and Aarssen

380    1990, Laure et al. 2017). This might also reflect the genetic trade-off between competitive

381    abilities of MA lines of small-scale competition and of large-scale facilitation (Timan 2004). Low

382    competition between *A. thaliana* individuals at small-scale transmits into low facilitation

383    between different species at larger scale. In turn, strong competition within *A. thaliana* at

384    small-scale results in weaker competition between different species at large-scale. Thus, the

385    constant input of mutation to genetic variation of competitive hierarchies suggests that genetic

386    variation is likely never a limiting factor in the evolution of those traits that influence plant

387    community dynamics.

388

389    *Implementation of eco-evolutionary trait-based model for population and community ecology*

390    In ecology, two primary contrasting models are crucial to population and community dynamics

391    for understanding the maintenance of biodiversity: the niche and neutral theories of ecology

392    (Fisher and Mehta 2015). The niche theory claims that niches are determined by the difference

393    of abiotic or biotic ecological processes e.g. competition or facilitation (Hutchinson 1957, Bruno

394    et al. 2003, Colwell and Rangel 2009) whereas the neutral theory predicts that ecological

395    processes are neutral and are solely modified by stochasticity (Hubbel 2005). Although it is still

396    under debate which model predicts the dynamic properties of communities and determines the

397    maintenance of biodiversity (Violle et al. 2017), both models miss the importance of

398    evolutionary mechanisms and individual variation influencing population and community

399    dynamics (Violle et al. 2012). The difference of competition and facilitation between or within

400    genotypes demonstrates that evolutionary mechanisms that shape individual variation could

401    change hierarchies of intra-specific interactions in natural plant populations over a short

402    evolutionary time scale. Our results are concordant with the niche theory stressing the

403    changing of competitive hierarchies among phenotypes in a given environment (Levine and

404    HilleRisLambers 2009, Nottebrock et al. 2017). Moreover, selection and trait evolution favor

405    population survival of *A. thaliana* in the wild, which stresses the importance of combining

406    spatial ecological and evolutionary mechanisms for our understanding of population and

407    community dynamics.

408

409    Conclusion

410    Rapid evolution of *A. thaliana* due to spontaneous mutation alone has profound consequences

411    for population and community dynamics. Competition of *A. thaliana* individuals is genotype-

412    dependent and *A. thaliana* is not a single weak competitor among co-occurring plant species

413    (Ehlers et al. 2016, Soliveres et al 2017). Moreover, the discovery of the underlying eco-

414    evolutionary nature of competition in *A. thaliana* supports a shift from species-based to

415    individual-based community ecology. This would lead to a more predictive ecological theory

416    (Violle et al 2017). We show that including the intraspecific genetic variation and phenotypic

417    variation as separate aspects to a trait-based neighborhood model increases the predictive

418    power to understand population and community dynamics. In particular, non-neutral

419    intraspecific processes may determine species coexistence, because genetic diversity is

420    promoted by having stronger competitive abilities at small-scale and stabilizing population

421    survival at large-scale (Clark et al. 2010). Additionally, our study demonstrates higher genetic

422    diversity increases population survival due to rapid evolution with implications to forecast the

423    fate of species and functional diversity in response to environmental changes (Violle et al 2012).

424    Depending on the time of environmental changes, species may adapt to environmental change

425    by shifting their fundamental niches (Clark 2010). The combination of intraspecific genotypic

426    variation and spatial interactions might advance our understanding of community dynamics,

427    especially of rapid evolution (Koch et al. 2014, Turcotte and Levine 2016). Incorporating genetic

428    variation and the eco-evolutionary process for determining standing levels of genetic variation

429    will provide a better understanding of species interactions underlying the maintenance of

430    biodiversity.

431

432    Keywords (10 for indexing purpose): trait-based community ecology, spontaneous mutations,

433    competition, facilitation, niche evolution, intraspecific genetic variation, intraspecific

434    phenotypic variation, *Arabidopsis thaliana*, mutation accumulation lines, eco-evolutionary

435    dynamics.

436

437    Figures and Tables
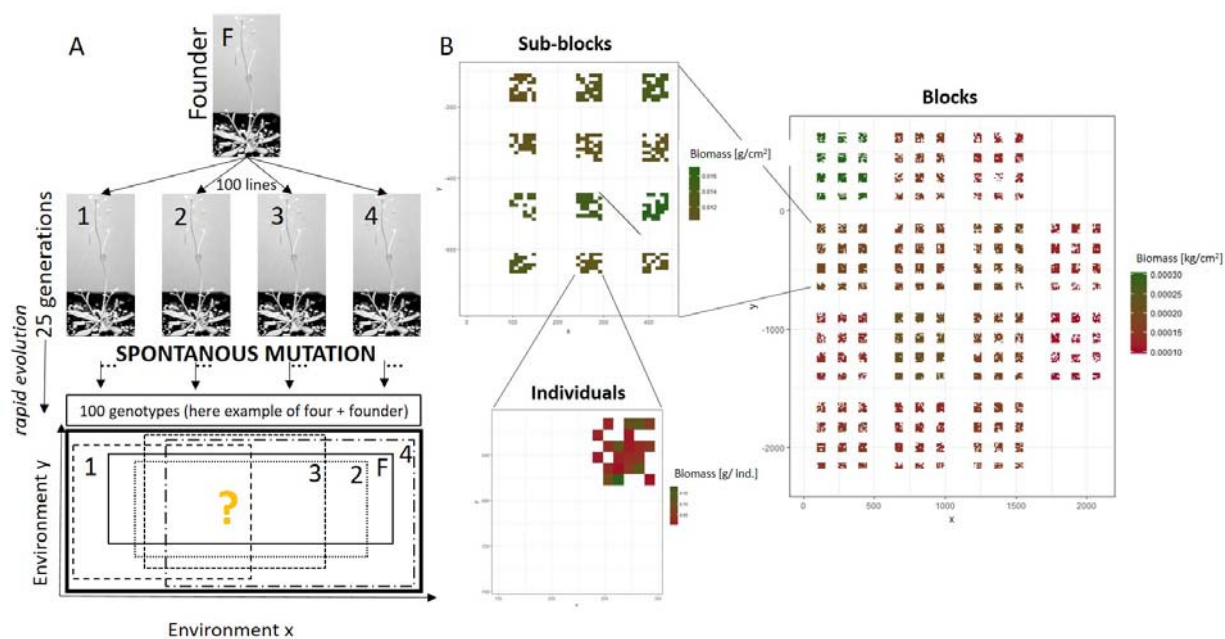


438

439    Figure 1. (A) 100 Mutation accumulation lines (here example of four MA-lines) of *Arabidopsis*

440    *thaliana* derived from a single founder (Columbia) after 25 generations with a mutation rate of

441    ~0.7 per generation (Weng et al. 2019). Each MA line has a unique genotype that differs from

442    the founder. Fundamental niche of individual genotypes (different dashed and dotted lines) and

443    founder genotype (black line) are distributed within the hypothetical fundamental niche of a

444    population of *A. thaliana* (bold black line). Axes represent niche axis (resource-use,

445    environmental factors, etc.). (B) Planting design of *A. thaliana* in a natural field experiment

446    showing spatial biomass variation of individual survivors in 2004.

447

| | 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 |

448

449 Table 1. Table of all different eco-evolutionary trait-based neighborhood models including

450 intraspecific variation to test our three objectives of density effects on survival and seed set of

451 *A. thaliana*. Differential models split the neighbor responses into within genotypes and

452 between genotypes. Neutral models describe the overall neighbor response without

453 differentiating between genotypes. All models include random effects of plant biomass on the

454 slope, subblock or block and MA-line on the intercept (see Fig. 1 for design), and respectively

455 depending on small (s) or large-scale (l) (for more details see method section).

**Survival model**

| (A1) 2004 | | (s) Small scale (80cm) | | AIC | (l) Larger scale (200cm) | | AIC |
|---|---|---|---|---|---|---|---|
| | | *Intra* | *Inter* | | *Intra* | *Inter* | |
| *Weighted density* | | | | | | | |
| 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 |
|---|---|---|---|---|---|---|---|
| | | *Intra* | *Inter* | | *Intra* | *Inter* | |
| *Weighted density* | | | | | | | |
| 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 |
|---|---|---|---|---|---|---|---|
| | | *Intra* | *Inter* | | *Intra* | *Inter* | |
| *Weighted density* | | | | | | | |
| MA lines | neutral | -0.02*** | | 52982 | 0.03 | | 52944 |
| | differential | -0.02** | -0.07*** | 52948 | *0.03**** | *0.15**** | 52939 |

| (B2) 2005 | | (s) Small scale (80cm) | | AIC | (l) Larger scale (200cm) | | AIC |
|---|---|---|---|---|---|---|---|
| | | *Intra* | *Inter* | | *Intra* | *Inter* | |
| **Weighted density** | | | | | | | |
| **MA** | neutral | -0.008* | | 49103 | -0.008* | | 49049 |
| **lines** | differential | -0.009** | -0.09*** | 49095 | -0.01* | 0.16*** | 49026 |

456

457  Table 2. The coefficient and AIC from eco-evolutionary trait-based neighborhood models of the

458  *Arabidopsis thaliana* field experiment in the years 2004 and 2005. Models include intraspecific

459  genetic variation defined as intra-genotyptic (within genotypes) and inter-genotypic (between

460  genotypes) variation. Models are shown at two different spatial scales: weighted subblock

461  density (80cm radius) and weighted block density (200cm radius). All scales include variables of

462  neutral effects (absence of intra- and inter-genotypic variation (total sum of all neighboring

463  genotypes)) and differential effects (presence of intra- and inter-genotypic variation (split of

464  neighboring genotypes in intra- and inter-genotypic genotypes). Thus, neighbor identity is split

465  into intra- and inter-genotypes as differential effects or are combined as neutral effects, which

466  includes all neighbors. P-value levels <0.05*, <0.005**, <0.001*** and >0.05[ns].

467
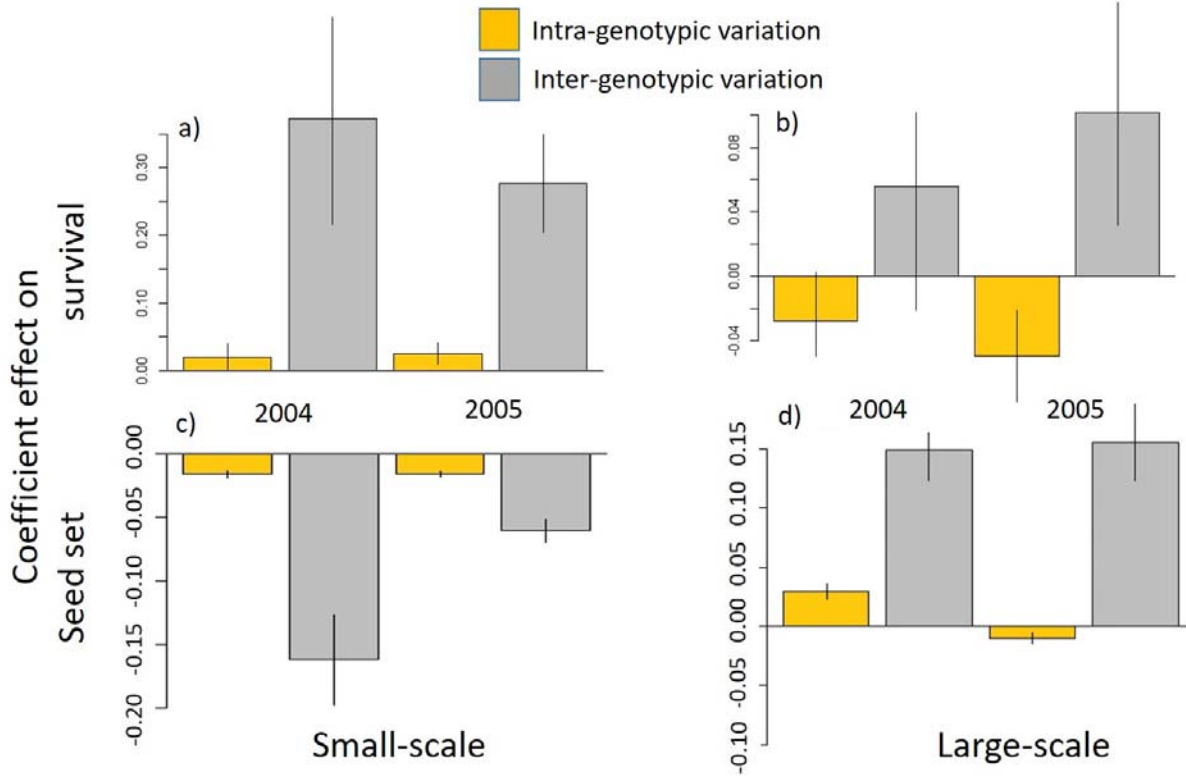
Figure 2. The barplots show standardized coefficient effect sizes and associated standard errors

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

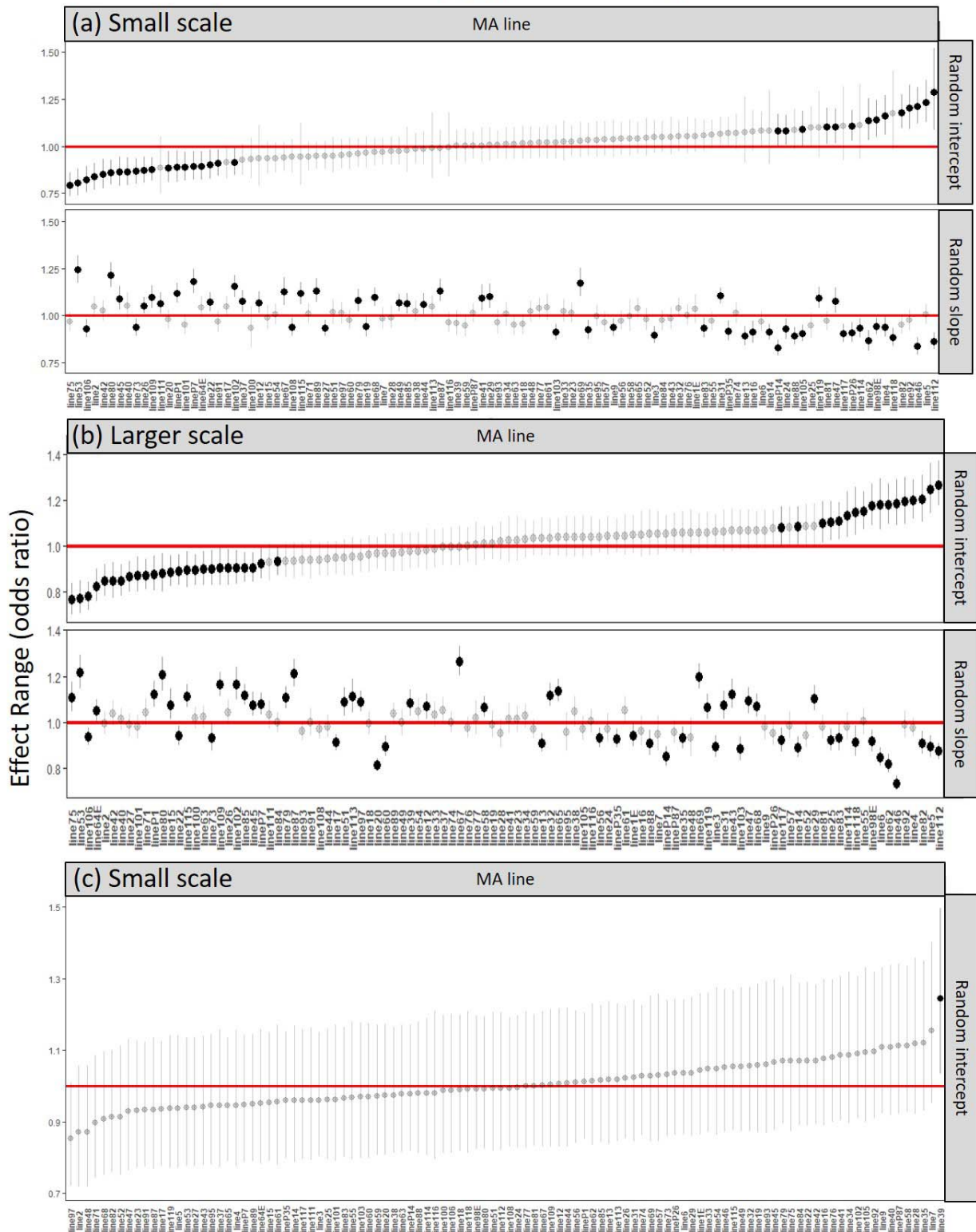effects (yellow) and inter-genotypic effects (grey) are presented for 2004 and 2005. Coefficient

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.

475

476

477    Figure 3. The effect range on seed set (a), (b) and survival (c) computed from eco-evolutionary

478    trait-based neighborhood models shown as odds ratios for year 2004 (for 2005 see

479    Supplementary Material). (a) Shows the hierarchical competitive order of MA lines and founder

480    for the seed set model including range effects of each MA line and founder as random

481    intercepts and the trait proxy biomass as random slopes at small-scale and (b) at large-scale. (c)

482    Shows the hierarchical selective order of MA lines and founder for the survival model including

483    range effects of each MA line and founder as random intercepts at small-scale.

484
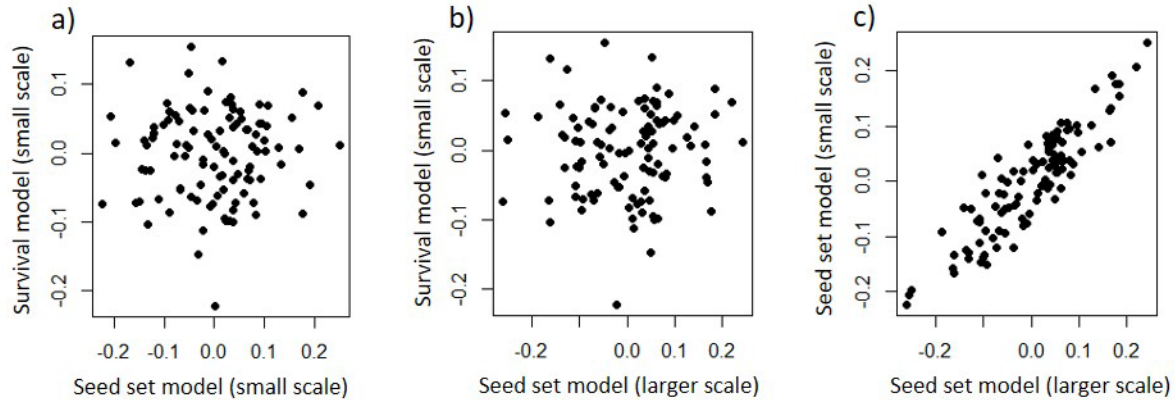
Figure 4. Correlation of the simulated conditional mean represented as odds ratio of same genotypes (MA lines) reducing or increasing the effect sizes of the seed set model and of the survival model at small-scale or large-scale for 2004, respectively. For year 2005 see supplementary material. Each point 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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