

# Population genetic diversity influences colonization success

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## Abstract

Much thought has been given to the individual-level traits that may make a species a successful colonizer. However, these traits have proven to be weak predictors of colonization success. Here, we test whether population-level characteristics, specifically genetic diversity and population density, can influence colonization ability on a short-term ecological timescale, independent of longer-term effects on adaptive potential. Within experimentally manipulated populations of the weedy herb *Arabidopsis thaliana*, we found that increased genetic diversity increased colonization success measured as population-level seedling emergence rates, biomass production, flowering duration, and reproduction. Additive and non-additive effects contributed to these responses, suggesting that both individual genotypes (sampling effect) and positive interactions among genotypes (complementarity) contributed to increased colonization success. In contrast, manipulation of plant density had no effect on colonization success. The heightened ability of relatively genetically rich populations to colonize novel habitats, if a general phenomenon, may have important implications for predicting and controlling biological invasions.

**Keywords:** *Arabidopsis thaliana*, colonization, complementarity, facilitation, genetic diversity, non-additive effects

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## Introduction

The colonization of novel habitats plays an important role in many ecological processes, from ecological succession to population dynamics and range expansion. Colonization requires species to both disperse to a novel environment and successfully survive and reproduce there. While much thought has been given to the individual-level traits that may make a species a successful disperser (Rees *et al.* 2001), far less attention has been paid to population-level characteristics (e.g. density, age structure, genetic variation) that may affect the probability of survival and expansion of the colonizing population. Traditionally, individual-level traits such as dispersal ability, generation time, and growth rate have received a great deal of consideration as predictors of colonization ability (for animals, see Sol 2007; for plants,

see Baker 1974; Mack *et al.* 2000; Kolar & Lodge 2001; Sakai *et al.* 2001; Rejmánek *et al.* 2005; Pyšek & Richardson 2007; Whitney & Gabler 2008). However, these traits are weak predictors (Perrins *et al.* 1992; Mack 1996), and characteristics arising at the population or species level (such as genetic diversity and population density) may offer greater explanatory power.

Variation in the genetic diversity of founder populations is extensive (reviewed in Novak & Mack 2005; Roman & Darling 2007; Dlugosch & Parker 2008) and has the potential to influence the success of colonization events. Many recent studies have found that populations of species colonizing novel habitats harbour genetic diversity as high as or higher than that found in populations in their native range (e.g. Kolbe *et al.* 2004; Genton *et al.* 2005). Sources of such high levels of diversity include admixture (defined here as the mixture of individuals from geographically and genetically distinct source populations) and gene flow among multiple independent introductions of the species. For example,

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multiple introductions of agriculturally important genotypes of reed canarygrass, *Phalaris arundinacea*, have led to higher within-population genetic diversity in parts of the grass's non-native range than in its native range (Lavergne & Molofsky 2007). Even in cases of small founder populations not subject to human-mediated dispersal, admixture can occur at high levels. During colonization of the small Galapagos island of Daphne Major by large ground finches *Geospiza magnirostris*, small immigrant populations ( $\leq 39$  genotyped individuals) were derived from as many as five genetically distinct source islands (Grant *et al.* 2001). Nevertheless, some colonization events may only involve a few individuals that represent a small fraction of the natural genotypic variation of the species, effectively creating a population bottleneck (e.g. Kliber & Eckert 2005; Puillandre *et al.* 2008).

Much work has focused on the long-term evolutionary consequences of bottlenecks and/or multiple introductions for the adaptive potential of founder populations; however, relatively little attention has been paid to the short-term effects of genetic diversity on colonization success. Colonizing species experience habitats that often differ in abiotic or biotic conditions relative to their native ranges, and genetic variation within these populations is expected to increase colonization success in novel conditions by allowing rapid adaptation (Sakai *et al.* 2001; Lee 2002; Holt *et al.* 2005). In contrast, short-term effects (traditionally termed 'ecological' effects, although clearly evolution can happen rapidly enough to conflate ecological and evolutionary time scales; see Antonovics 1976; Hairston *et al.* 2005) conceivably could play out within the first generation. For example, high levels of genetic diversity could help a population become established, either by increasing the odds that some individuals can withstand the novel conditions (lottery model or sampling effect), or by allowing more efficient or more complete use of resources (niche partitioning) (Huston 1997; Loreau & Hector 2001). Studies of species in their native habitats are consistent with this view (Hughes *et al.* 2008). For example, populations of *Clarkia pulchella* with relatively high levels of genetic diversity maintained larger population sizes over the course of four years than less genetically diverse populations (Newman & Pilon 1997). Within a single generation, increased genetic diversity increased population biomass in goldenrod (*Solidago*) (Crutsinger *et al.* 2006) and population resistance and resilience to disturbance in eelgrass (*Zostera*) (Hughes & Stachowicz 2004; Reusch *et al.* 2005). Additionally, higher levels of population-level genetic diversity in a barnacle species increased larval settling success (Gamfeldt *et al.* 2005), although post-settling performance (growth, reproduction) was not measured.

Thus, the available data indicate that increased genetic diversity could translate into higher population growth rates and higher initial dispersal to habitats for colonizing species.

However, if our goal is to examine how increased genetic variation in a founding population influences colonization success, the aforementioned experiments are not ideal, as they utilized genotypes that evolved in a common environment in their native ranges and were designed to address different questions. A more direct test of the hypothesis would examine population performance in an introduced or novel environment and create diversity treatments from divergent genotypes from multiple source locales, mimicking the admixture process.

To examine how genetic diversity may affect a species' ability to colonize a novel environment, we chose to use the model organism *Arabidopsis thaliana* (Brassicaceae). *Arabidopsis thaliana* has been widely used in molecular biology studies, resulting in the accessibility of numerous ecotypes with well-characterized genetic and phenotypic variation (Mitchell-Olds 2001; Pigliucci 2002). It also is a widespread weed that has colonized numerous habitats on four continents (Clarke 1993) and thus provides an excellent model system for examining questions at the interface of genetics, ecology, and invasion biology (Weltzin *et al.* 2003). By manipulating genetic diversity within populations of *A. thaliana* and measuring colonization success, we focus attention on whether high genetic diversity can promote invasion success on a short-term, 'ecological' timescale. We used soil-filled trays in a greenhouse as the novel environment to be colonized. While this approach clearly lacks the realism of the field, it does increase the conservatism of the test for effects of genetic diversity (e.g. the more uniform soil and climatic conditions should decrease opportunities for complementarity in resource use, relative to the field). We also manipulated plant density. We included density as a factor because it should influence the degree of interaction between individual plants, and we hypothesized that such interactions among genotypes may be an important mechanism influencing colonization success. Specifically, we address the question: Does greater population-level genetic diversity and/or density increase the ability of a species to initially colonize a novel environment via enhanced survivorship, growth, and/or reproduction?

## Methods

### *Plant material*

*Arabidopsis thaliana* is a predominantly selfing, weedy herb with a hypothesized origin in Eurasia (Mitchell-Olds

**Table 1** *Arabidopsis* accessions included in the experiment

Number	ABRC stock number	Name	Country
1	CS6643	Burren	Ireland
2	CS6660	Canary Islands	Spain
3	CS1084	Coimbra	Portugal
4	CS6673	Columbia	USA
5	CS6674	Catania	Italy
6	CS22614	Cape Verdi Islands	Cape Verdi
7	CS6688	Edinburgh	United Kingdom
8	CS1144	Espoo	Finland
9	CS6736	Hilversum	Netherlands
10	CS20	Landsberg erecta	Germany
11	CS6792	Mühlen	Poland
12	CS1380	Martuba	Libya
13	CS6805	Nossen	Germany
14	CS22661	New Zealand	New Zealand
15	CS6824	Oystese	Norway
16	CS6839	Poppelsdorf	Germany
17	CS6850	Rschew	Russia
18	CS6857	San Feliu	Spain
19	CS6874	Tsu	Japan
20	CS6889	Wilna	Russia
21	CS6891	Wassilewskija	Russia
22	CS6897	Wü	Germany
23	CS690	Zurich	Switzerland

2001; Pigliucci 2002). Twenty-three ecotypes were obtained from the *Arabidopsis* Biological Resource Center housed at Ohio State University. Stocks of each of these ecotypes have generally been bred from a single seed and maintained as an inbred line (*Arabidopsis* Biological Resource Center, Columbus, OH, USA), so we consider each ecotype to represent a single genotype. We chose accessions (Table 1) that maximized microsatellite marker diversity (King *et al.* 1993; Innan *et al.* 1997; Kover & Schaal 2002) and also represented a broad swath of the species range. During the summer of 2006, *Arabidopsis* plants were reared from seed in a common growth chamber for bulk seed production and to reduce potential maternal environmental effects. Seeds were collected from 4 to 8 maternal plants of each genotype for use in the experiment.

### Experimental design

We examined the effects of genetic diversity and density on colonization success by factorially manipulating population genetic richness (1, 2, 4 or 8 genotypes) and plant density (low density vs. high density) in a common greenhouse environment. Low density populations consisted of eight individuals (0.05 indivs/cm<sup>2</sup>), and high density populations had 16 individuals (0.10 indivs/cm<sup>2</sup>). These densities are somewhat higher than

those reported for adult populations of *A. thaliana* established in agricultural fields (0.001–0.02 indivs/cm<sup>2</sup>; Goss 2005) but are lower than those observed in some invasive populations in North America (J. Stinchcombe, University of Toronto, personal communication). Each population was planted in a 12.5 × 12.5 × 6 cm (L × W × H) pot filled with Metromix 200 soil (Sun Gro Horticulture, Canada, Ltd). Seeds were planted in a grid to ensure equal growing space. Each pot was placed within a larger soil-filled tray (30 × 30 × 6 cm) to simulate a founding population located in a disturbed, open habitat with no competitors. Plants could (and did) root through holes in the central pot to access soil in the larger tray.

A major component of plant colonization success is initial survival, or germination followed by seedling emergence. To accurately measure emergence, we carefully planted one *Arabidopsis* seed in each grid position by painting the seed onto the soil with a toothpick. In order to examine how genetic diversity affected population growth and reproduction independently of seedling emergence success, we also included a separate 'overseeding' treatment in which, rather than planting a single seed, we sowed three to 10 or more seeds in each grid position using a pipettor and seeds suspended in water. After emergence, the extra plants in this 'overseeding' treatment were weeded, leaving one plant per position and mimicking 100% seedling emergence.

We added additional replicates to allow partitioning of additive versus non-additive responses. Additive responses occur when there are no interactions among genotypes; in this case, population responses would be entirely predicted by summing the responses of their component genotypes in monoculture. Non-additive responses occur when there are interactions (e.g. facilitation, niche partitioning, competition) among genotypes that cause the population response to be significantly higher or lower than the sum of the responses of the component genotypes (Hughes *et al.* 2008). To allow partitioning of additive and non-additive effects of genetic diversity, all genotypes not randomly selected for the 1-genotype experimental treatment were grown in high and low density monocultures. The high density monocultures included both overseeding and no overseeding treatments. Therefore, monoculture populations of each genotype were replicated either three or four times. This resulted in 199 populations (four genetic diversity levels × 2 density levels × 2 overseeding levels × 10 replicates, plus 13 monocultures × 2 density levels + an overseeding treatment for the 13 high density populations).

To minimize problems associated with nonindependence of replicates within a treatment, and increasing similarity among treatment levels as diversity increases

(Huston & McBride 2002), genotypes were randomly chosen from a relatively large pool of 23 genotypes. Genotype combinations were then discarded (and new genotype combinations generated randomly) to meet the following criteria: replicates of the 1- and 2-genotype treatments were allowed no genotypes in common, replicates of the 4-genotype treatment were allowed only one genotype in common, and replicates of the 8-genotype treatment could share no more than three genotypes. EstimateS software (Colwell 2005) was used to calculate similarity indices. Similarity estimates were low, and compared favorably to those in other recent diversity experiments (Weltzin *et al.* 2003 and references therein): The average Jaccard coefficient of similarity within 4- and 8-genotype treatments was 0.06 and 0.178, respectively. Between treatments, the average Jaccard similarity coefficient was 0.075 for 2- and 4-genotype treatments, 0.084 for 2- and 8-genotype treatments, and 0.141 for 4- and 8-genotype treatments.

After planting, the populations were cold stratified at 4 °C for 8 days. Populations were then placed in the Rice University greenhouse on 28 November 2006. Temperatures in the greenhouse were allowed to vary with ambient temperatures (but were not allowed to fall below 10 °C or exceed 29 °C) to simulate a novel outdoor environment. Populations were watered as needed and no supplemental lighting or fertilization was implemented. The experiment was terminated when the majority (>80%) of the plants had senesced, on 4 April 2007.

#### Response variables

We assessed several estimates of population performance, including seedling emergence, biomass, flowering duration, and reproduction. Population-level estimates of biomass and reproduction were calculated by summing values for the individual plants that comprised them. We scored seedling emergence percentage for each population in the no-overseeding treatment approximately four weeks following the end of the stratification period, after it appeared that most plants had germinated. Once the first plant bolted (21 December 2006), we recorded reproductive status (bolting, flowering, or producing fruits) of each plant in each population every two to three days until 25 January 2007. Then, we switched to recording reproductive status of all plants every 7 days until early April. Flowering duration was calculated as the number of days between the initiation of flowering by the earliest flowering plant in a population and the initiation of flowering by the latest flowering plant in that population. In mid-April, all above-ground biomass (including rosettes, flowering stalks, seed pods, and any senesced

leaves) was harvested, dried to constant weight, and weighed.

To estimate reproduction, allometric equations relating biomass to fruit production were developed for all 23 genotypes individually. At least seven plants from each genotype chosen randomly across treatments were assessed for fruit number and dry biomass; additional plants were then sampled until an  $r^2 \geq 0.8$  was reached for each genotype (except genotype 8, for which  $r^2 = 0.31$ ,  $n = 44$  plants sampled). For statistical analyses involving genotype 8, actual fruit values for 44 plants were used, while allometric equations were employed for the 37 remaining individuals of that genotype.

#### Statistical analyses

We tested for treatment effects on colonization success of the *Arabidopsis* populations using  $M/ANCOVA$  models that included the treatments genetic diversity (a continuous variable), density, overseeding, and all possible interactions (Proc GLM, SAS Institute 2003). Results treating genetic diversity as a fixed categorical factor using  $M/ANOVA$  models did not differ from those obtained with genetic diversity as a continuous variable using  $M/ANCOVA$  models. The latter is standard practice for analyses of diversity (Tilman *et al.* 1996; Hughes & Stachowicz 2004; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Crawford *et al.* 2007) and we have opted to retain this approach. In all models, the overseeding treatment never significantly affected the response variables (because seedling emergence was high and because plants with fewer neighbors were able to grow larger). Therefore, for clarity, this treatment was removed from the models and the final data analysis was limited to the effects of genetic diversity, density, and the diversity  $\times$  density interaction.

The following response variables were examined: percentage seedling emergence (only for the populations with no overseeding), above-ground biomass, flowering duration, and fruit number. Following a  $MANCOVA$  finding significant treatment effects on all response variables considered together, we performed protected  $ANCOVA$  (Scheiner 2001) on each response. All data met assumptions of normality of residuals and homogeneity of variances, except for the analysis of fruit number, where two outliers were excluded to improve normality. To test if population performance for the four traits was positively correlated, the six pairwise correlations were examined for all populations in all treatments (except for percentage seedling emergence, where the overseeding treatment populations were excluded).

We then tested whether responses to genetic diversity were additive or non-additive in nature by conducting Monte Carlo simulations. Artificial populations matching

the genotypic composition of each of the experimental polycultures were constructed by randomly sampling trait values (with replacement) from individual plants growing in monoculture, following the general logic of Johnson *et al.* (2006) and Crawford *et al.* (2007). Sampling only occurred within a density level (e.g. a given artificial low-density population was constructed only from individuals in low-density monocultures). We then examined the distribution of trait values for 9999 sets of artificial populations and calculated 95% confidence intervals. When actual means fell outside these intervals we inferred non-additive effects of genetic diversity. Monte Carlo simulations were programmed using SAS macro language (SAS Institute 2003); the code is available on request from the authors.

**Results**

Increased genetic diversity within founding populations of *Arabidopsis* significantly increased population-level seedling emergence, biomass, flowering duration, and reproduction (Tables 2 and 3). In monoculture, 66% of the planted seeds emerged, compared to 82% of the seeds in the highest diversity treatment ( $F_{1,75} = 12.24$ ,  $P = 0.0008$ ) (Fig. 1a). This pattern arose because most genotypes showed increased per-capita germination rates in higher-diversity environments: 18 of the 23 genotypes (78%) responded positively to increased genetic diversity (i.e. showed significantly positive correlations between genetic diversity level and germina-

tion percentage). Populations with the highest genetic diversity also produced 69% more biomass than monocultures ( $F_{1,155} = 23.53$ ,  $P < 0.0001$ ) (Fig. 1b). On average, the 8-genotype treatment flowered for 25 days longer than the 1-genotype treatment ( $F_{1,155} = 43.46$ ,  $P < 0.0001$ ) (Fig. 1c), and produced ≈1400 (20%) more fruits ( $F_{1,153} = 5.80$ ,  $P = 0.0274$ ) (Fig. 1d).

Populations with high performance for one response variable did not necessarily perform well across all response variables. Three of the five relationships between response variables were significantly positively correlated. Percentage seedling emergence was significantly correlated with both biomass (Pearson's  $r = 0.23$ ,  $P = 0.003$ ) and flowering duration ( $r = 0.27$ ,  $P = 0.0005$ ), and flowering duration was significantly correlated with biomass ( $r = 0.25$ ,  $P = 0.0014$ ). However, these correlations were generally weak. The correlation between biomass and fruit production is not presented, since fruit number was calculated from allometric equations using biomass as the predictor variable.

In contrast to the substantial effects of genetic diversity, plant density did not significantly affect percentage seedling emergence, biomass, or fruit production. This potentially counterintuitive result was the result of larger per-capita values for biomass and fruit production in low-density populations that compensated for lower absolute numbers of plants (data not shown). There was a marginally significant trend for longer flowering periods in high-density populations relative to low-density populations ( $F_{1,155} = 3.45$ ,  $P = 0.065$ ). There were no significant density by genetic diversity interactions (Tables 2, 3), suggesting that the effects of genetic diversity did not depend on the initial population size or level of intraspecific competition tested in this experiment.

Significant non-additive effects of genetic diversity were detected for all four response variables. Diversity treatments containing either 4 or 8 genotypes of *Arabidopsis* emerged more often than expected under additivity (Fig. 2). However, when populations contained only two genotypes, they germinated less often than expected under the additive model.

**Table 2** MANCOVA results for the effects of genetic diversity and density on *Arabidopsis* population-level seedling emergence, biomass, and reproduction

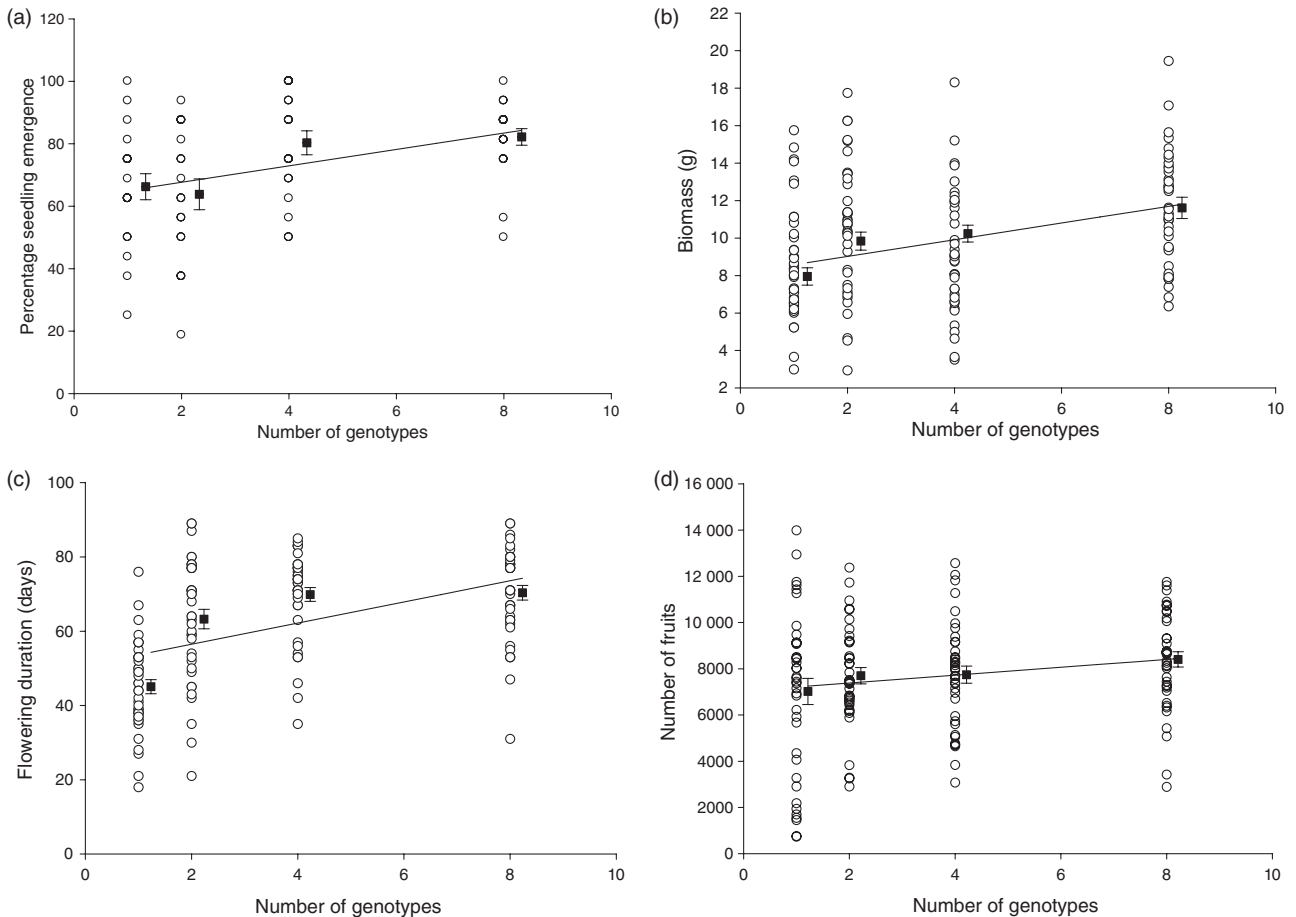
	d.f.	Pillai's Trace	F	P
Genetic diversity	1,150	0.2890	15.24	<b>&lt;0.0001</b>
Density	1,150	0.0274	1.06	0.3783
GD × density	1,150	0.0222	0.85	0.4945

Bold *P*-values are significant at  $P < 0.05$ .

**Table 3** ANCOVA results for the effects of genetic diversity and density on *Arabidopsis* population-level seedling emergence, biomass, and reproduction

	% Seedling emergence				Aboveground biomass				Flowering duration				Number of fruits			
	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>	d.f.	F	P	R <sup>2</sup>
Model	3,75	4.77	<b>0.0042</b>	0.16	3,155	9.11	<b>&lt;0.0001</b>	0.15	3,155	17.05	<b>&lt;0.0001</b>	0.25	3,153	3.05	<b>0.0303</b>	0.06
Genetic diversity	1	12.24	<b>0.0008</b>		1	23.53	<b>&lt;0.0001</b>		1	43.46	<b>&lt;0.0001</b>		1	4.96	<b>0.0274</b>	
Density	1	0.52	0.4724		1	0.34	0.5585		1	3.45	0.065		1	0.00	0.9460	
GD × density	1	1.71	0.1944		1	0.36	0.5521		1	0.11	0.7354		1	1.28	0.2606	

Bold *P*-values are significant at  $P < 0.05$ .



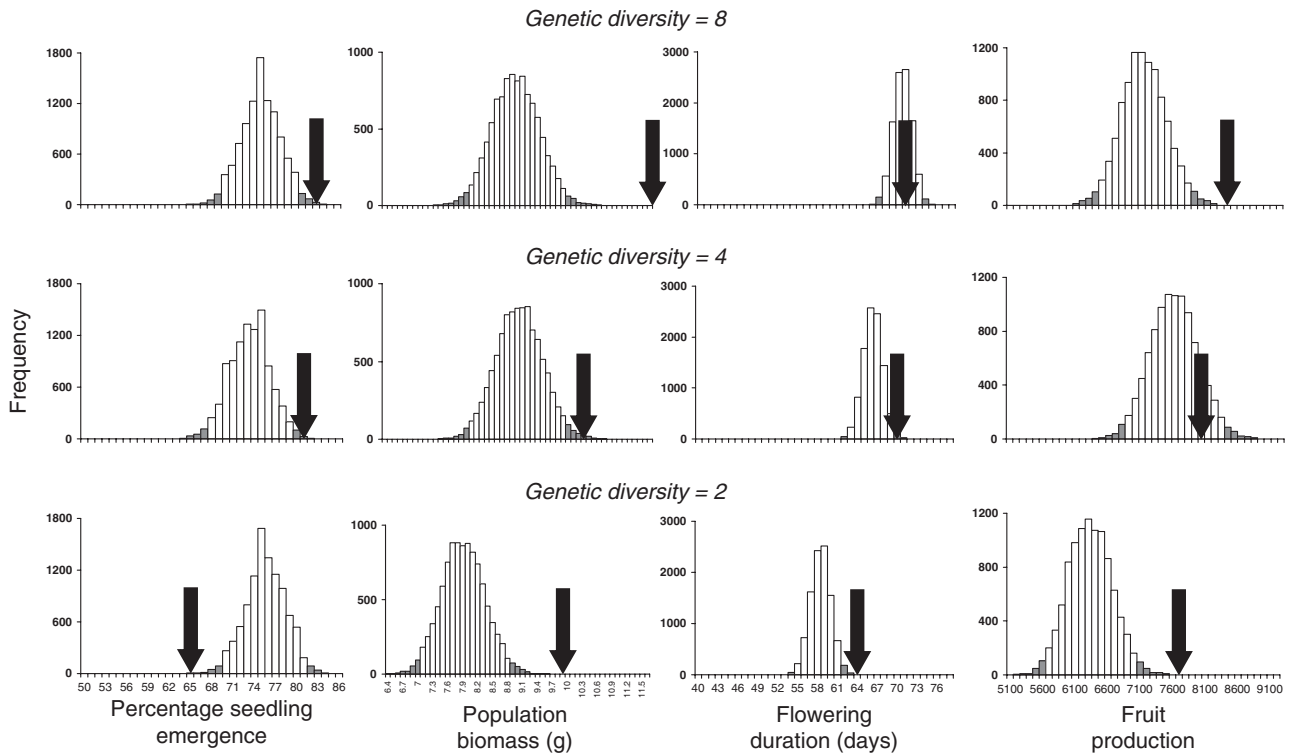
**Fig. 1** Response of population-level seedling emergence, biomass, and reproduction to genetic diversity. Open circles are population-level values. In panel a, an individual circle represents on average 2.2 populations (range 1–8); circles overlap completely because seedling emergence was necessarily scored in discrete intervals. Black squares are treatment means ( $\pm$ SE) and are offset for clarity. [Correction added after online publication 18 February 2010: panel (a) was replaced.]

All diversity levels produced significantly more biomass than predicted from the additive model, with the most diverse (8-genotype) treatment massing 30% more than expected under nonadditivity (Fig. 2). Populations showed significant positive non-additive responses for flowering duration in the 2- and 4-genotype (but not 8-genotype) treatments (Fig. 2). Diversity treatments containing either 2 or 8 genotypes produced more fruits than expected, and the highest diversity treatment produced nearly 1300 more fruits than expected under additivity (Fig. 2).

## Discussion

Our results show that higher levels of genetic diversity within experimental founder populations of *Arabidopsis thaliana* are associated with increased initial seedling emergence, flowering duration, biomass, and reproduction. The lack of strong correlations between the response

variables indicates that positive effects of genetic diversity on population performance accrued during multiple stages of the plants' life cycle. The patterns are influenced by an interaction among the genotypes in a population, as evidenced by the non-additive effects of diversity on all responses. In contrast, density had no significant effect on any of the measured responses, nor did it modify the effect of genetic diversity on these responses. This suggests that the interactions occurring among genotypes that produced non-additive responses were present at both density levels. Our results suggest that, on a short-term, 'ecological' timescale, high levels of genetic diversity could aid a population colonizing a new habitat by increasing the probability the population will survive, grow, and reproduce under novel conditions. Thus, the ecological consequences of genetic diversity and admixture in founder populations may be profound and determine whether the longer-term effects of genetic diversity on adaptation ever come into play.



**Fig. 2** Non-additive effects of genetic diversity for four population-level response variables: percentage seedling emergence, flowering duration, biomass, and number of fruits. Shown are the distributions of trait values for 9999 sets of artificial populations, constructed in Monte Carlo simulations by randomly sampling response variable values from individual plants growing in monoculture. Shaded bars highlight the area outside of the 95% confidence intervals. Arrows indicate the location of the actual (observed) means.

### Consequences of genetic diversity

While several recent ecological studies have examined the relationship between genetic diversity and population processes (Newman & Pilson 1997; Hughes & Stachowicz 2004; Gamfeldt *et al.* 2005; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006), these studies have not specifically addressed how genetic diversity within populations influences colonization success. They have employed genotypes of the focal species that evolved in a common environment within the species' native range and do not always measure the population variables relevant to colonization success. Populations of colonizing species may frequently be composed of distantly related genotypes from multiple locations in the range of the species, and furthermore are likely to face novel biotic and abiotic conditions. Under these conditions, we found that genetic diversity is capable of influencing colonization success.

While a positive effect of increased genetic diversity on population biomass production has previously been documented (e.g. Crutsinger *et al.* 2006), to our knowledge, no study has found that genetically diverse populations display significantly higher reproduction. Johnson *et al.* (2006) found that some genotypes of

*Oenothera biennis* had a greater fitness when grown in diverse populations relative to monocultures. We found that this response scaled up to the population-level, with more diverse populations producing more fruits than less diverse populations.

We also found that higher levels of genetic diversity promoted flowering duration, a novel result. This characteristic is likely to be an important determinant of colonization success for many plant species; a longer flowering period increases the chances that a population will overlap with pollinators that may vary in seasonal abundance (Rathcke & Lacey 1985). This could be critically important in novel environments, as co-evolved pollinators are unlikely to be present; however, pollinator attraction is clearly less important for highly self-compatible species such as *Arabidopsis thaliana* (Abbott & Gomes 1989).

Our finding that genetic diversity influenced seedling emergence success is another novel and perhaps counterintuitive result. We hypothesize that seed-seed or seedling-seed interactions are responsible. There is a substantial literature documenting seed-seed and seedling-seed interactions (e.g. Inouye 1980; Bergelson & Perry 1989; Murray 1998; Dyer *et al.* 2000; Lortie & Turkington 2002; Turkington *et al.* 2005). In these

experiments, the emergence behavior of seedbank seeds (either percentage or timing) is altered by their density or seedling density. For example, Murray (1998) manipulated seed density in *Eragrostis curvula* and found that seeds planted at higher densities emerged at higher per-capita rates. Further experiments using leachates are consistent with soilborne chemical cues; for example, Bergelson & Perry (1989) found that leachate from germinating seeds accelerated emergence timing of *Senecio vulgaris* and *Capsella bursa-pastoris* seeds, relative to plain water. In our system, we hypothesize that high-diversity treatments are more likely to contain one or more early-germinating genotypes, and that these early germinants modify the chemical environment of the remaining seedbank and cause an increase in emergence percentage. Currently we are conducting further experiments to test this hypothesis, to isolate the mechanism, and to examine whether such behaviour may be adaptive.

Despite the growing body of experimental evidence that genetic diversity has important ecological consequences, few studies have examined the importance of genetic diversity relative to other population-level factors (Hughes *et al.* 2008). This is a critical next step in judging the importance of genetic diversity for ecological processes. In our experiment, we manipulated the density of individual plants as well as genetic diversity. We hypothesized that these factors are important because they could alter the strength of interaction among individuals. We found no significant effect of density on any of the response variables, except for a trend for high density populations to flower longer than low density populations (Table 3). Therefore, we conclude that genetic diversity was a more important driver of colonization success than density for *A. thaliana* under our experimental conditions.

#### *Additive and non-additive effects of genetic diversity*

We found that non-additive effects generally led to increased population performance in the founder populations. Non-additive effects were found in 10 of the 12 comparisons, with the exceptions being the 8-genotype treatment for flowering duration and the 4-genotype treatment for fruit production. Only with the 2-genotype treatment for seedling emergence percentage was a significant negative, non-additive effect detected. This pattern could have been caused by competition between early-germinating and late-germinating genotypes. Other work has found significant non-additive positive effects of genetic diversity for population biomass (Crutsinger *et al.* 2006), but we also document non-additive effects for population seedling emergence percentage, flowering duration, and fruit production. This

suggests that positive interactions among genotypes may be critically important for population survival and growth in novel conditions. Positive interactions that may be occurring in this system include resource partitioning and facilitation. Resource partitioning can occur when genotypes utilize resources at different rates, leading to more efficient utilization of the available suite of resources. Since resource partitioning assumes that competition for resources among individuals within a genotype is stronger than competition between genotypes, individuals in more diverse populations would suffer less from competition, allowing them to maximize growth and fitness. Facilitation may occur when the presence of one genotype modifies the environment in a way that benefits other genotypes. The presence of a beneficial genotype in a more diverse population could lead to greater individual growth and fitness. Further experimentation on this system could elucidate which of these factors contribute to the positive, non-additive responses we found.

Additive effects of diversity can also be inferred from the randomizations. For biomass, flowering duration, and fruit production, as the number of genotypes present in the populations increases, so does the expected mean of the response. For example, the mean of flowering duration makes an obvious shift from approximately 59 days when two genotypes are present to almost 71 days when eight genotypes are present (Fig. 2). Additive effects of diversity could be attributed to the sampling effect, where individuals with a relatively large effect on the response are more likely to be included in more diverse populations. For example, populations with higher diversity have a greater likelihood of containing genotypes that flower very early and very late, effectively increasing the duration of the flowering period.

#### *Caveats*

Since our experiment was conducted in a very controlled environment, an interesting question is how the effects of genetic diversity will change in magnitude and direction under more complex ecological scenarios, such as in field situations. For example, mixtures of distinct plant genotypes are known to alter disease dynamics in crop plants (Mundt 2002). Similarly, when grown in polyculture, herbivore-susceptible genotypes of a plant may benefit from associational resistance when growing next to less susceptible genotypes (*sensu* Tahvanainen & Root 1972). Alternatively, particularly attractive genotypes may negatively affect more resistant plants via associational susceptibility, as has been found for attack of a galling midge (*Rhopalomyia solidaginis*) on genotypes of *Solidago altissima* (Crawford *et al.*



2007). Thus, genetic diversity will likely have complex effects on colonization success in populations subject to disease, pest attack, and other abiotic and biotic factors.

A second caveat arises from the choice of genotypes used in the experiment. Given that genotypes were drawn from a wide geographic range and have known phenotypic differences (e.g. in size and flowering time; ABRC, Columbus, OH, USA), effects of genetic diversity found in this study could be larger than that associated with typical founder populations. However, one can also imagine founder populations in which very high levels of phenotypic diversity would be present, for example, introductions of ornamental plants in which morphological diversity is explicitly sought (see below). For *A. thaliana* in particular, a recent analysis of the genetic structure of Eurasian populations suggests that they are isolated by distance (Beck *et al.* 2008). Therefore, if multiple introductions from several source populations occurred, relatively high levels of genetic diversity could result.

#### Conservation implications

Our finding that increased genetic diversity leads to increased colonization success in our experimental system suggests that admixed founder populations of exotic species may have improved ability to become established. Several studies of successful invasive species have found that populations are characterized by a relatively large amount of genetic diversity (e.g. Kolbe *et al.* 2004; Genton *et al.* 2005). High levels of genetic diversity are likely found in species that have been introduced multiple times to an area. Such admixture may be exceedingly common during particular types of dispersal events; for example, Roman & Darling's (2007) review found that 66% of reports on invasions mediated by ballast water showed levels of within-population genetic diversity at least as high in the introduced range as the native range. Similarly, agriculturally or horticulturally important species may become invasive after introductions of distinct genotypes with different desirable qualities. For example, many genotypes of reed canary grass (*Phalaris arundinacea*) were introduced to Eurasia and North America for forage and soil stabilization (Lavergne & Molofsky 2004).

In general, our results suggest that population-level characteristics should be considered in addition to the individual-level traits (e.g., growth rate, dispersal ability, and generation time; see Whitney & Gabler 2008 for a review) that are the typical focus of invasive species risk assessment schemes. Furthermore, exclusion, quarantine and control procedures for invasive species would likely benefit from practices that limit admixture or focus on species prone to admixture.

#### Conclusion

While much theory suggests that genetic diversity should allow populations of colonizing species to adapt to their new environments (Sakai *et al.* 2001; Lee 2002; Holt *et al.* 2005; Novak & Mack 2005; Dlugosch & Parker 2008), little thought has been given to the short-term ('ecological') consequences of genetic diversity that precede any evolutionary changes. Both additive and non-additive effects were important determinants of increased colonization success in our system, suggesting that both genetic identity of the colonists and interactions among genotypes may have profound influences on the relative success or failure of a colonization event. The genetic diversity present in colonizing populations may be a useful metric for predicting colonization success.

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