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Propagule pressure and genetic diversity enhance colonization by a ruderal species: a multi-generation field experiment

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Abstract. Colonization is a critical filter, setting the stage for short-term and long-term population success. Increased propagule pressure (e.g., more founding individuals) usually enhances colonization; however, this pattern may be driven by purely numeric effects, population genetic diversity effects, or both. To determine the independent and interactive effects of propagule pressure and genetic diversity, we conducted a seed addition experiment in the field using the ruderal annual *Arabidopsis thaliana*. Propagule pressure treatments spanned five levels, from 32 to 960 seeds per 0.25-m^2 plot. Founder populations were composed of one, four, or eight genotypes and exposed to ambient or reduced levels of interspecific competition. Genotype monocultures were included to quantify additive vs. non-additive effects. Populations were followed for three generations, with abundance, population persistence and genotype retention (the proportion of introduced genotypes persisting over time) as the major response variables. Increased propagule pressure enhanced abundance immediately following introduction, particularly where nutrient availability was high and competition reduced. Greater propagule pressure also increased the likelihood of population persistence and genotype retention through three generations. However, most populations experienced rapid abundance declines over time, yielding no relationship between propagule pressure and third-generation abundance across persisting populations. Under reduced competition, increased genetic diversity led to a marginal increase in persistence through the third generation that was more pronounced, and statistically significant, in low nutrient conditions. Genetic diversity did not affect persistence through the first generation, thus indicating that genetic diversity effects strengthened over time. Nevertheless, genotypic mixture populations fell short of expectations based on performance in monocultures (negative non-additive effects). Increased genetic diversity was also associated with abundance declines, largely due to one particularly high-performing genotype in the lowest diversity treatments (i.e., genotypic identity effects). Overall, our results indicate that increases in both propagule pressure and genetic diversity can enhance colonization success but are highly context dependent. They also highlight novel ways in which both factors can impact the retention of introduced genetic diversity over time. Our findings pinpoint the determinants of a fundamental population process and have key implications for applications where enhanced or suppressed colonization is desired, including ecological restoration and invasive species management.

Key words: admixture; Arabidopsis thaliana; *complementarity; invasion biology; invasion genetics; negative density dependence; population bottleneck; population genetic diversity; propagule pressure; sampling effects; self-compatibility; weeds.*

Introduction

Colonization is a critical process that sets the stage for population growth, species persistence, and evolutionary change (Baker and Stebbins 1965). In most cases, colonizing populations are more likely to establish and spread when they are larger at founding: a greater number of founders buffer populations from demographic or environmental stochasticity and can reduce Allee effects (Sale 1982, Lockwood et al. 2005, 2009, Colautti et al. 2006, Poulsen et al. 2007, Courchamp et al. 2008, Simberloff 2009, Fauvergue et al. 2012, Blackburn et al. 2015). Yet, the statement that colonization is enhanced by increased propagule pressure (the number of founders per introduction event, more introduction events over time, or both) ignores substantial variability in the strength and even the likelihood of measurable propagule pressure effects among colonizing species and colonization scenarios. Multiple factors can

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influence the degree of colonization success resulting from a given degree of propagule pressure, including the strength of biotic and abiotic invasion resistance (D'Antonio et al. 2001, Thomsen et al. 2006, Duncan 2016), the quality of incoming propagules (Burgess and Marshall 2011), life history traits of the colonizer (Crawley 1986), and negative density dependence (Marshall and Keough 2003, Warren et al. 2012, Barney et al. 2016). Despite these well-documented complications, investigations into factors that may interact with propagule pressure are still relatively rare and underappreciated (Lockwood et al. 2005, Blackburn et al. 2015).

Beyond the potential direct effects noted above, increased propagule pressure may also enhance colonization indirectly, due to the fact that larger founder populations should tend to harbor more genetic and phenotypic diversity (Beirne 1975, Nei et al. 1975, Lande 1988, Lockwood et al. 2005, Dlugosch and Parker 2008, Simberloff 2009, Fauvergue et al. 2012, Rius and Darling 2014, Szűcs et al. 2014, Luque et al. 2016). The increased genetic diversity expected in larger founder populations may act via several different mechanisms to enhance colonization success. Increased diversity will often reduce the expression of genetic load in species that are prone to inbreeding depression (Firestone and Jasieniuk 2013, Hufbauer et al. 2013) and promote increased rates of adaptation post-introduction (Clegg and Allard 1972, Reznick and Ghalambor 2001, Novak and Mack 2005). These "evolutionary" mechanisms are closely related conceptually to the conservation genetics of small populations and, as such, have received a great deal of attention in the literature (Newman and Pilson 1997, Elam et al. 2007). Less commonly recognized are what we refer to as "ecological" effects of genetic diversity (Hughes et al. 2008), which accrue as a result of sampling and/or complementarity effects in large populations that harbor a phenotypically diverse suite of genotypes (Gamfeldt et al. 2005, Wennersten et al. 2012). These latter mechanisms might positively affect colonization success in high diversity populations even in the absence of evolutionary effects (i.e., those leading to changes in allele frequencies). In this paper, we look at the combined ecological and evolutionary effects of genetic diversity, focusing on the earliest generations post-introduction when we expect them to matter most for colonization success.

A rapidly growing body of evidence shows that increased genetic diversity can have meaningful ecological effects on populations, communities and ecosystems even within a single generation (Hughes and Stachowicz 2004, Schweitzer et al. 2005, Crutsinger 2006, Crawford and Rudgers 2013). Yet, ecological effects of genetic diversity on colonization are less well studied, with mixed evidence for enhanced colonization by more diverse founder populations (positive effects [Martins and Jain 1979, Ahlroth et al. 2003, Crawford and Whitney 2010]; no effects [Hovick et al. 2012, Erfmeier et al. 2013]). A recent meta-analysis (Forsman 2014) did find that higher genetic diversity increased colonization success on average; however, the analysis was not corrected for phylogenetic relationships among the study organisms (which ignores non-independence among species due to shared evolutionary histories; see Chamberlain et al. 2012), and many of the included studies used experimental designs that limit the degree to which inferences regarding genetic diversity effects can be made (e.g., pseudo-replicated designs that confound the effects of genetic diversity and genetic identity). Thus, we argue that the jury is still out on the general importance of genetic diversity for colonization success via primarily ecological mechanisms.

Given the lack of clarity regarding genetic diversity effects on colonization, it is not surprising that we know even less about the relative importance of, and potential interactions between, genetic diversity and propagule pressure on colonization success. These are critical knowledge gaps because larger founder populations will often more fully sample the available genetic and phenotypic diversity from a source region (Nei et al. 1975, Blackburn et al. 2015), thus confounding their effects in non-experimental systems. This problem is particularly germane within the context of biological invasions, where introductions from multiple native source populations can cause within-population diversity in the introduced range to exceed that in the native range (Kolbe et al. 2007, Dlugosch and Parker 2008). Additionally, although founder population sizes vary widely (Nuñez et al. 2011), we are unaware of clear theoretical expectations for how the magnitude of genetic diversity effects on colonization might vary with propagule pressure. However, the fact that most ecological effects of genetic diversity (not just on colonization) have been observed in species that naturally tend to occur at high relative abundances (e.g., seagrass [*Zostera marina*; Hughes and Stachowicz 2004], cottonwood [*Populus* sp.; Schweitzer et al. 2005], goldenrod [*Solidago altissima*; Crutsinger 2006], beachgrass [*Ammophila breviligulata*; Crawford and Rudgers 2013]) does lead to one potential expectation: that overall genetic diversity effects on colonization will be more pronounced when propagule pressure and thus intraspecific densities are the greatest. Such an effect could result from a combination of stronger intraspecific interactions within dense populations as well as greater representation of rare genotypes following colonization by a large number of individuals.

To our knowledge, six previous studies have jointly manipulated propagule pressure and genetic diversity to assess the interactive effects of both factors on colonization; most have been single-generation investigations under lab/greenhouse conditions (see Appendix S1: Table S1 for an overview). All of these studies (excepting Crawford and Whitney 2010) found that increased propagule pressure directly enhanced at least some metric of colonization success, but the effects of genetic diversity and interactions between genetic diversity and propagule

pressure were much less consistent. Increasing genetic diversity led to increased colonization regardless of founder population size in two studies: a field experiment with the water strider *Aquarias najas* (Ahlroth et al. 2003) and a greenhouse study with the plant *Arabidopsis thaliana* (Crawford and Whitney 2010). This contrasts with findings from a lab experiment on the oyster *Saccostrea glomerata* (Hedge et al. 2014) and a field experiment on the plant *Oenothera biennis* (Cook-Patton et al. 2017), in which genetic diversity effects were dependent on population size (a statistical interaction) but in opposing directions; genetic diversity enhanced colonization in large but not small populations in the former study and enhanced germination in small but not large populations in the latter. And lastly, increased genetic diversity had no effect on colonization in experiments with the plant *Senecio vernalis* (Erfmeier et al. 2013) and the beetle *Tribolium castaneum* (Vahsen et al. 2018), regardless of founder population size. Perhaps contributing to the inconsistency in perceived genetic diversity effects across systems and propagule pressure gradients, some of these experiments are pseudo-replicated (Appendix S1: Table S1), with all high diversity replicates consisting of exactly the same set of genotypes; such a design makes it impossible to distinguish the effects of genetic diversity from those of genotypic identity (see Huston and McBride 2002). Therefore, our expectation for greater genetic diversity effects on colonization in larger founding populations is only occasionally supported, and with important limitations.

Given these inconsistent findings, it is worth asking whether variation in biotic or abiotic conditions may influence the importance of genetic diversity for colonization, similar to their influence on the importance of propagule pressure. For both sampling and complementarity effects, resource availability and the degree of abiotic stress are likely candidates as potentially mediating factors (Mulder et al. 2001, Craven et al. 2016). Sampling effects represent the increased likelihood of one or more "good colonizer" genotypes being included in high diversity founder populations (Loreau and Hector 2001), and under increasingly stressful conditions the presence of rare stress-tolerant genotypes is likely to be increasingly important. Complementarity effects, in contrast, result from processes such as facilitation and resource partitioning that lead genotypes to perform differently in mixture than they do when growing alone (Loreau and Hector 2001). Because the importance of both facilitation and resource partitioning are likely be enhanced with increasing resource limitation (Craven et al. 2016, Siebenkäs et al. 2016) or stress (Bertness and Callaway 1994, Mulder et al. 2001, Reusch et al. 2005), complementarity effects should also strengthen under these conditions. Stronger genetic diversity effects following periods of stress have been documented in experiments with the seagrass *Zostera marina* (Hughes and Stachowicz 2004, 2009), yet to our knowledge, the consequences of variation in resource availability for genetic diversity effects have not yet been addressed.

A final contingency that is likely to be important in mediating the perceived effects of genetic diversity or propagule pressure is the length of time (in generations) following an introduction event. We are unaware of studies designed to assess how the magnitude of the numeric effects of propagule pressure may change over time, but presumably once introductions cease any enhancement to colonization success because of propagule inputs is likely to dissipate. In contrast, we expect genetic diversity effects to increase over time: even if genetic diversity effects are initially too subtle to be detected, they may still set the stage for measurable differences in persistence or population growth in later generations. Most studies that have measured temporal change in the effects of increased genetic diversity on other metrics of population success report those effects strengthening over time (Martins and Jain 1979, Reusch et al. 2005, Drummond and Vellend 2012, Wang et al. 2012, but see Hughes and Stachowicz 2009). It may be that such temporal patterns are the rule rather than the exception (as is the case for species diversity effects; see Cardinale et al. 2007) and that our current understanding is limited primarily by the lack of genetic-diversity–colonization experiments spanning multiple generations (Appendix S1: Table S1).

In the current study, we report on a three-generation experiment assessing the independent and interactive effects of propagule pressure and population genetic diversity on colonization success in the field. We created 534 experimental founder populations of *Arabidopsis thaliana*, a ruderal mustard for which positive effects of genetic diversity on colonization success have previously been demonstrated in the greenhouse (Crawford and Whitney 2010). The current study builds on those findings by assessing colonization (population and genotype persistence and abundance) over multiple generations in the field (Texas, USA) and by assessing the importance of genetic diversity factorially across a wide propagule pressure gradient. Specifically, we ask how the importance of propagule pressure and genetic diversity change over time and in response to both natural variation in resource availability and manipulated variation in the strength of interspecific competition.

Materials and Methods

Study system

Arabidopsis thaliana (hereafter *Arabidopsis*) is an annual, ruderal species with a global distribution, occurring as a weed in many regions beyond its native Eurasian range (Clarke 1993, Mitchell-Olds 2001, Platt et al. 2010, Alonso-Blanco et al. 2016), including Texas, where our study was conducted (Nesom 2009). *Arabidopsis* has been used previously in field and greenhouse studies to investigate ecological questions regarding colonization and invasion (Weltzin et al. 2003, Crawford and Whitney 2010), naturally occurring levels of variation in

phenology (Donohue et al. 2005*a*, *b*), population dynamics (Montesinos et al. 2009) and herbivore responses to plant genetic diversity (Kotowska et al. 2010).

We randomly selected 25 natural accessions of *Arabidopsis* (see Appendix S1: Table S2) that were both available through the Arabidopsis Biological Resource Center as single-seed descent lines and that were genotyped by Platt et al. (2010), to ensure ready availability of distinct genetic markers that would permit genotype assignment of field-collected material. The accessions were sourced from natural populations that we expected would vary in meaningful traits, although we did not select genotypes on the basis of traits. To reduce maternal environmental effects, we bulk-produced seeds from our entire pool of genotypes in a growth chamber set to 16 h of daylight; thus, all seeds in our experiment were produced under the same conditions.

Planting design

The experiment took place in an early successional field in southeastern Texas, USA (29°55′32″ N, 95°55′20″ W) dominated by short grasses and forbs. Prior to sowing *Arabidopsis*, all plots were disked and later sprayed with a 2% solution of glyphosate to create a disturbed, low-competition habitat. All plots were separated by at least 5 m to minimize dispersal among plots. This distance was assumed to be sufficient based on wind tunnel trials with 30–40 cm tall *Arabidopsis* plants in which 85% of seeds moved <2 m (Wender et al. 2005) and based on an expectation that our field-grown plants would be substantially shorter (indeed, >99.5% of 1,235 plants measured in year three were <20 cm tall) and thus less prone to long-distance dispersal. These assumptions were supported by the fact that, over three years, we found only a single *A. thaliana* plant in the interstitial zone between plots (defined as >1 m beyond a plot perimeter); genetic assignments indicated that it had established ~3 m from its source population and thus did not arise from a preexisting local seed bank. No *Arabidopsis* populations occur at or near the study site (S. M. Hovick *personal observation*), with the nearest documented population at least 250 km away (Turner et al. 2003).

Founder populations were created by adding seeds to 0.25-m^2 plots on 16–17 November 2012 so they could overwinter naturally in the field before germination. Seeds for each plot were counted manually in the lab and mixed with a small amount of sand in 2.5-mL microtubes to facilitate their even distribution when sprinkled across the plot area. Our main experiment used a randomized complete block design with three treatments: seed number (SeedNum; 32, 96, 160, 320, or 960 seeds per plot), genetic diversity (GenDiv; seeds from one, four, or eight genotypes) and interspecific competition (Comp; additional herbicide to reduce vegetation density vs. no additional herbicide). All treatments were replicated once in each of nine experimental blocks to account for potential heterogeneity across our study site, for a total of 270 seed addition plots in the main experiment.

Average recruitment from seed to reproductive individuals was ~5% in preliminary field studies; thus, we designed our range of SeedNum treatments to be sufficient for capturing nearly the full range of scenarios from extreme seed limitation to seed saturation. We did not include plots without *Arabidopsis* added to assess background emergence from the seed bank because it did not occur in the region, although such plots would have provided extra confidence that *Arabidopsis* was absent from the site. Additional herbicide applications for the Comp treatment were implemented in early autumn 2013 and 2014 (i.e., prior to the second and third growing seasons), when *Arabidopsis* was present only in the seed bank and could only be affected by the herbicide indirectly, via changes to the density of neighboring vegetation.

In genetic diversity experiments, small pool sizes (where "pool size" refers to the number of genotypes from which replicates are drawn) create the twin problems of nonindependence of replicates within a treatment and increasing similarity among treatment levels as diversity increases (Huston and McBride 2002). To minimize these issues, our genetic diversity treatments were implemented as random draws of one, four, or eight different accessions selected without replacement from a pool of 25 accessions. We set the additional constraints that all replicate one-genotype selections were unique, replicate four-genotype mixtures could have no more than two accessions in common, and replicate eight-genotype mixtures could have no more than three accessions in common; selections violating these constraints were discarded and replaced with a new selection. This design led to low genotypic similarity values across replicates and treatment levels well within norms currently in the literature (~0.25 or less; Weltzin et al. 2003, Crawford and Whitney 2010). Each random draw of one, four, or eight accessions was repeated across all plots occurring in a single block, yielding nine independent sets of accessions for each level of our genetic diversity treatment.

To determine whether any effects of genetic diversity were due to additive vs. non-additive effects, all 25 genotypes were sown in replicated monocultures (n = 3 replicates). Replicating all treatment combinations was not feasible; thus, monocultures were sown at two levels of seed addition (96 or 960 seeds per plot) and two levels of interspecific competition (implemented as in the main experiment) in each of three blocks. Nine genotypes were grown in monocultures as part of the main experiment, which we used for one of the three replicates for those genotypes. The additional two replicates for these nine genotypes plus three replicates for the remaining 16 genotypes required sowing an additional 264 plots. Thus, the entire experiment consisted of 224,064 seeds sown into 534 plots (270 plots in the main experiment plus 264 additional monoculture plots).

Data collection

We censused each plot four times during the 2012–2013 growing season (7–17 February, 4–5 March, 18–20 March, and 16 April–2 May) by marking every individual with a toothpick, which allowed us to track population dynamics over time and clearly note individuals that germinated but died prior to flowering. Plots were similarly censused for the total number of flowering individuals present during the second and third generations post-introduction to assess changes in abundance over time. We conducted three censuses each in the 2013–2014 growing season (10–13 December, 19–22 February, and 15–19 April) and the 2014–2015 growing season (21–23 February, 16–18 March, and 13-17 April).

Leaf tissue was collected from flowering plants in the four- and eight-genotype mixture plots so that genotypic identities of successful colonizers could be determined. In each population in each generation, we collected tissue from either all plants or from up to 20 plants per census, whichever number was lower. Leaves were kept on ice in the field and then stored at −80°C until DNA extraction with Qiagen DNeasy Plant Kits (Qiagen, Venlo, The Netherlands). A subset of single nucleotide polymorphisms (SNPs) developed by Platt et al. (2010) for distinguishing *Arabidopsis* accessions (38 out of 149 markers; their multiplex plate 1) were identified by Agena Bioscience (San Diego, California, USA), using their iPLEX Assay and MassARRAY system. Two SNPs were dropped due to poor resolution. We used the R package allelematch to assign a genotypic identity to unknown samples, omitting from analysis any sample with data for <50% of the 36 SNPs and those that could not be assigned unambiguously to an accession that had been initially introduced to a given population (Galpern et al. 2012; https://cran.rproject.org/package=allelematch). The analyses we present here are based on genotype identifications for 61% of all flowering plants from genotypic mixture plots in year one and 34% in year three (see Appendix S1: Fig. S1 for a flowchart detailing sample sizes throughout sample collection and processing). For each of the four- and eight-genotype mixture plots, we then multiplied observed abundance from field-based censuses (which were blind to genotype) by the proportional abundances of individual genotypes from tissue collections to estimate the number of individuals per genotype. As a methodological check, we followed the same genotype assignment protocol described above for a random subset of third-generation plants from one-genotype plots (74 plants from 24 different plots); our genotype assignment methods matched 100% of the field-collected samples to the expected genotype added as seed to each plot, further indicating no between-plot movement of *Arabidopsis* seeds.

To estimate effectiveness of our Comp treatment, we quantified variation in the abundance of co-occurring vegetation among plots by visually estimating the percent of each plot lacking vegetation (i.e., bare ground) using a modified Daubenmire scale (Daubenmire 1959). Bare ground estimates were repeated annually in early February just prior to peak *Arabidopsis* activity, both before (year 1) and after (years 2 and 3) the Comp treatments had been initiated.

In addition to arranging treatments by block to account for environmental variability, we also collected soil nutrient availability data at every plot in the first growing season using ion resin capsules (Unibest, Kennewick, Washington, USA). We collected two soil cores (2×5 cm deep) just outside the plot boundaries, combined them into a single sample and refrigerated them until being incubated in the lab. We submerged the capsules in a slurry of 50 g soil and 200 mL deionized water and left them to incubate for five days. Because of the long incubation period, our measures can be interpreted as an upper threshold to plant-available nutrients (K. J. Borgman, *personal communication*). After incubation, capsules were rinsed and sent to Unibest for their full nutrient analysis, which reports concentrations of total N (NO_3-N plus NH_4-N), P, K, Al, B, Ca, Cu, Fe, Mg, Mn, Na, S, and Zn.

Soil nutrient data were incorporated into analyses by first reducing the dimensionality of the full data set using principal components analysis (PCA). Nutrient data were transformed as necessary so distributions were approximately normal and PCA was conducted using the covariance matrix with the vegan package in R (Oksanen et al. 2018; https://cran.r-project.org/package=vegan). Variation in nutrient availability among plots was best described using the first two PC axes (Appendix S1: Fig. S2), the first of which correlated positively with Fe and Mg (with Fe and Mg concentrations explaining 84.2% of variation in PC1 scores based on multiple regression), and the second of which correlated positively with N, P, and K (with soil N, P, and K explaining 85.3% of variation in PC2 scores). Because PC2 is most closely related to macronutrients that directly influence plant performance (vs. PC1, which may indicate variation in pH and thus *indirect* effects on nutrient availability), in all subsequent analyses we use PC2 alone as a general index of nutrient availability (denoted as Nutrients).

Statistical analyses

All analyses were done using R version 3.5.1 (R Development Core Team 2016).

Effectiveness of competition treatments.—To assess whether vegetation was similar across plots before the Comp treatment had been implemented, and to document divergence thereafter, we compared the percent bare ground in response to Comp using separate *t* tests for data from each year of the experiment.

Realized genotypic richness and its retention over time.—We used genetic assignment data to document whether our GenDiv treatments varied in the number of *Arabidopsis* genotypes present across populations (realized genotypic richness), expecting that some genotypes

would fail to establish or go locally extinct over time. We estimated genotypic richness in all non-monoculture plots in both the first and third generations, assessing treatment effects using a linear model with a Poisson distribution (identity link). Because GenDiv treatments differ in the number of originally introduced genotypes, we also calculated genotype retention as the proportion of introduced genotypes persisting to a given point in time. Genotype retention was analyzed using a linear model with a Gaussian distribution (identity link).

For genotypic richness and genotype retention, as well as our primary metrics of colonization success (see *Colonization success*), we used the following analytical procedures for model selection and statistical inference. Our predictors of interest were the main effects of the SeedNum, GenDiv, and Comp treatments, the effect of natural variability in soil nutrients (Nutrients), and all interactions. Other than Comp, we treated all predictors as continuous variables. We used a step-down approach to simplify initial models, using likelihood-ratio (LR) tests to justify dropping non-significant interactions (Bolker et al. 2009) until reaching a best-fit model or until only the main effects remained; model selection based on AIC gave identical results. Preliminary analyses revealed complex interactions with the Comp treatment term; thus, low- and high-competition treatments were analyzed separately. We excluded Block from our final analyses because LR tests did not support its inclusion in addition to Nutrients, which represents relevant environmental variation at a much finer spatial scale. Last, we assessed whether any SeedNum effects were better characterized as nonlinear by using LR tests to compare our final models with those in which SeedNum^2 was added as an additional predictor. All inferences regarding significance of parameter estimates are based on Wald tests and Type III sums of squares, from the car package (Fox and Weisberg 2011; https://cran.r-project.org/package=car). Unless otherwise indicated, we report error using the standard error of the mean.

For genotype retention only, quadratic relationships (from adding SeedNum^2 to models) appeared to fit our data poorly, so we compared quadratic models with nonlinear models parameterized to fit a saturating function (the Michaelis-Menton equation) using the nls command in base R. Nonlinear models were specified as $Y \sim \text{MaxRet}(\text{SeedNum-Xshift})/(\text{KRet} + \text{SeedNum-Xshift}) + (\beta_{\text{Nut}} \times \text{Nutrients}) + (\beta_{\text{GD}} \times \text{GenDiv})$, where MaxRet is maximum genotype retention (the asymptote), KRet is the value of SeedNum where the curve reaches its half-maximum, Xshift is a parameter that allows the curve to shift left or right to permit a non-zero intercept, and β_{Nut} and β_{GD} are the estimated effects of Nutrients and GenDiv, respectively (both of which can shift the overall curve up or down). Model comparisons were based on AIC. Inferences regarding parameters from nonlinear models are based on *t* statistics.

Colonization success.—Our fundamental metric of colonization success is the abundance of flowering individuals, as these have the potential to contribute to future population growth. We present two separate analyses of these data: (1) changes in abundance over time and (2) persistence through, and abundance in, the third generation.

1. Changes in abundance over time.—In our first analysis, we used a repeated measures framework to investigate changes in abundance over time. We specified a first-order autoregressive correlational structure across three years of abundance data using the R package nlme (Pinheiro et al. 2017; https://cran.r-project.org/package=nlme). Abundances were square-root transformed and zero values retained.

2. Persistence and abundance in year three.—Second, we conducted a focused assessment of persistence through, and abundance in, year three, the final year of our surveys. Many *Arabidopsis* populations went extinct after the first and second growing seasons; thus, we used hurdle models to describe variation in year three population presence/absence separately from abundance, which was analyzed only for those populations with at least one individual present. We modeled persistence using a binomial generalized linear model (GLM) with the logit link function and abundance using a truncated negative binomial GLM (Zuur et al. 2009) with the log link function; for the latter analysis we used the R package VGAM (Yee 2010; https://cran.r-project.org/package=VGAM). In all cases, tests for overdispersion in our final models (using the overdisp_fun function; *available online*)[4] were non-significant (all $P > 0.25$).

Additive vs. non-additive effects.—To determine whether performance in genotypic mixtures (i.e., four- and eight-genotype populations) resulted just from sampling effects or additionally from non-additive effects such as complementarity or interference among different genotypes, we used a standard approach, comparing observed performance in mixtures with expectations based on performance in monoculture plots (Loreau and Hector 2001). Sampling and complementarity effects are determined by assessing the colonization ability of all component genotypes in monoculture and then calculating an additive expectation for colonization in high diversity plots based on the relative abundance of each genotype in the founder population; deviations in observed performance from this additive expectation indicates some degree of non-additive effects (Loreau and Hector 2001). Because monocultures were sown in only a subset of all five *SeedNum* treatment levels (96 or 960 seeds), and because we knew that performance was influenced by plot-level nutrient availability, we used an approach modified from Mulder et al. (2001) to calculate expected performance. For these analyses, we focused on two performance metrics from the main experiment: persistence through and abundance

[4] https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#-model-diagnostics

in the third year post-introduction (omitting locally extinct populations from the latter analysis). Analyses were conducted separately on high and low competition plots, and because few populations persisted under high competition conditions the abundance analysis was only possible with low competition plots. Expectations were calculated in three steps. First, using data from all monoculture plots (n = 300), we calculated genotype-specific parameter estimates for the likelihood of persistence (using binomial GLM and a logit link function) and abundance (using zero-truncated Poisson GLM and a log link) with the following model: $Y \sim$ Nutrients + SeedNum + Genotype. Second, for each performance metric (Y), we used these parameter estimates to predict the performance of all component genotypes from plots in the main experiment (including one-genotype treatments). Last, we aggregated per-genotype predicted values within plots to calculate expectations at the population level. Per-genotype abundances were predicted using a value of SeedNum equal to that of the entire population and then aggregated simply by averaging across all genotypes in the plot; this helped account for observed density dependency in abundance (see *Changes in abundance over time*). In contrast, individual genotype persistence probabilities were predicted using a value of SeedNum equal to SeedNum/GenDiv (i.e., per-genotype seed input), reflecting the assumptions that persistence was density-independent at the population level and independent across genotypes. The resulting persistence probabilities were aggregated by calculating the union of all per-genotype probabilities within a population, using the inclusion-exclusion principle (Shiryaev 2016). This method is appropriate when calculating the probability that at least one introduced genotype persists, which is sufficient for persistence at the population level.

We used paired t tests to compare observed vs. expected (monoculture-based) performance at the plot level, inferring non-additivity when these deviated. Bonferroni corrections were used to control the family-wise error rate within each set of comparisons. Single-genotype populations from the main experiment were included in all analyses as a check against our methods since for these plots, observations should not differ from expectations.

Genotype-specific variation in colonization.—By randomly assigning *Arabidopsis* genotypes to GenDiv treatments, we expected that some populations would by chance include particularly good or poor colonizer genotypes. To assess the nature of these compositional influences on perceived GenDiv effects, we categorized genotypes in the tails of the performance distribution as good or poor colonizers, based on realized abundances in year three monoculture plots. To categorize genotypes, we used a data set with one observation per genotype-plot combination, fitting the following model in R with glmer: Abundance ~ Genotype + Nutrients + (1|SeedNum) + (1|Comp); thus, we considered our treatments as random effects and Nutrients as a fixed effect covariate. We specified a Gamma GLM with log link, adding 0.005 to all values so zeros could be included and then used Tukey-adjusted pairwise comparisons to group genotypes with similar colonization ability. Based on these groupings, we categorized most genotypes as intermediate in their colonization ability, and categorized as good (n = 2) or poor (n = 4) those genotypes that differed in predicted abundance from a core central group (those ranked above or below the c and d groupings in Fig. 6).

Results

Effectiveness of competition treatments

Our competition treatment produced significant differences in vegetation cover once it was implemented after the first growing season. Prior to initiating the herbicide applications, plots assigned to both groups were sparsely vegetated to a similar extent (t_{268} = 0.93, P = 0.354), with percentage bare ground during the first growing season estimated at 50.0% ± 1.7% and 52.3% ± 1.8% (mean ± 1 SEM) in what would become the high and low competition plots, respectively. The plots diverged thereafter, with 10.7% ± 1.1% vs. 52.4% ± 1.5% bare ground in high vs. low competition plots in the second growing season (t_{268} = 23.20, $P < 0.001$) and 9.1% ± 0.6% vs. 19.1% ± 1.1% in the third (t_{268} = 8.00, $P < 0.001$).

Realized genetic diversity and its retention over time

Our GenDiv treatments were successful in establishing founder populations that varied in realized genotypic richness (mean richness in year one: 0.98 ± 0.02 in one-genotype, 3.39 ± 0.91 in four-genotype, and 6.04 ± 0.19 in eight-genotype populations). However, genotype *retention* declined as genetic diversity increased in both years one and three (negative values of β_{GenDiv} in Table 1), indicating that higher diversity introductions lost proportionally more genotypes compared to lower diversity introductions (Fig. 1). This pattern is consistent with expectations, as fewer seeds per genotype were added in higher vs. lower GenDiv treatments to maintain a given level of SeedNum.

Genotype retention in year 1 was similar in what would become high vs. low competition plots (Fig. 1a vs. b; P = 0.730 for the Comp effect in a model with all plots from the main experiment), but in year three genotype retention and thus realized genotypic richness was reduced in high-competition plots (Fig. 1c vs. d; $P < 0.001$). As a result, realized genotypic richness in year three varied with our GenDiv treatments only in low competition conditions (β_{GenDiv} = 0.104, $P < 0.001$; mean richness 0.56 ± 0.07 in one-genotype, 1.49 ± 0.18 in four-genotype, and 1.49 ± 0.20 in eight-genotype populations) and not in high competition (βGenDiv=0.0004, P = 0.994; mean richness 0.27 ± 0.07 in one-genotype, 0.27 ± 0.09 in four-genotype, and 0.29 ± 0.09 in eight-genotype populations).

TABLE 1. Analyses on the retention of *Arabidopsis* genotypic richness in the first and third years post-introduction.

	Year 1 genotype retention				Year 3 genotype retention			
Source	Parameter estimate	SE	t	P	Parameter estimate	SE	χ^2	P
Low competition								
Intercept	—	—	—	—	**0.360**	**0.075**	**23.18**	**<0.001**
Nutrients PC	0.030	0.042	0.71	0.480	**0.188**	**0.075**	**6.25**	**0.012**
Seed number	—	—	—	—	**0.002**	**0.0004**	**14.45**	**<0.001**
Genetic diversity	**−0.030**	**0.006**	**−5.47**	**< 0.001**	**−0.053**	**0.010**	**29.24**	**<0.001**
Seed number^2	—	—	—	—	**−0.000001**	**0.0000004**	**10.94**	**<0.001**
MaxRet	**1.07**	**0.04**	**26.36**	**<0.001**	—	—	—	—
KRet	5.08	5.34	0.95	0.343	—	—	—	—
Xshift	15.88	15.69	1.01	0.313	—	—	—	—
High competition								
Intercept	—	—	—	—	**0.211**	**0.048**	**19.30**	**<0.001**
Nutrients PC	0.011	0.046	0.25	0.806	0.083	0.064	1.66	0.197
Seed number	—	—	—	—	**0.0002**	**0.0001**	**4.74**	**0.030**
Genetic diversity	**−0.033**	**0.006**	**−5.46**	**< 0.001**	**−0.033**	**0.008**	**15.59**	**<0.001**
MaxRet	**1.07**	**0.049**	**21.68**	**< 0.001**	—	—	—	—
KRet	8.92	10.85	0.82	0.412	—	—	—	—
Xshift	−13.00	49.27	−0.26	0.79	—	—	—	—

Notes: Retention is a proportion, calculated as realized genotypic richness relative to the number of genotypes introduced via our initial genetic diversity (GenDiv) treatments. Separate models were run for low and high competition plots and for genotype retention in years 1 and 3 (n = 135 for each analysis). Parameters from nonlinear models are presented for year 1 data and from general linear models for year 3 data. Note that, for nonlinear models, MaxRet is asymptotic maximum genotype retention, an indicator of number of seeds (SeedNum) effects.

Significant effects ($P < 0.05$) are shown in boldface type; —, not tested.

In both the first and third years post-introduction, realized genotypic richness increased in response to higher levels of the SeedNum treatments, indicating that increased propagule pressure contributed to initial levels of genetic diversity as well as its retention over time (Table 1, Fig. 1). The relationship between propagule pressure and proportional genotype retention was nonlinear in most cases, with the exception of year three retention in populations exposed to high competition (Fig. 1d). A saturating function fit the first year genotype retention data better than did models with a SeedNum^2 term (ΔAIC = 5.7 and 0.8 for low and high competition plots, respectively; see Figs. 1a, b). In contrast, the quadratic model was a better fit to year three data from low competition plots compared to a saturating function (ΔAIC = −2.8; see Fig. 1c), reflecting diminished genotype retention in the highest density founder populations relative to populations with intermediate founder densities (mean genotype retention across GenDiv treatments: 0.21 ± 0.06 in 32-seed; 0.27 ± 0.07 in 96-seed; 0.38 ± 0.07 in 160-seed; 0.52 ± 0.10 in 320-seed; and 0.47 ± 0.09 in 960-seed founder populations).

Changes in abundance over time

Population sizes in the first generation reflected our wide range of SeedNum treatments (Fig. 2). Increasing propagule pressure led to greater abundances, but the relationship was nonlinear and apparently saturating ($P < 0.001$ for SeedNum^2 in both competition treatments; Table 2), indicating that our largest founder populations were establishment limited rather than seed limited. Abundances declined over time in most populations, and these declines were particularly apparent where initial propagule pressure was the greatest (SeedNum × Time interactions; Table 2, Fig. 2).

Soil nutrient availability affected variation in abundances over time, but the nature of these effects was not consistent across SeedNum and GenDiv treatments. In both competitive environments, the positive effects of increased nutrients accrued primarily to populations with the greatest propagule pressure (SeedNum × Nutrient interactions; Table 2; Appendix S1: Fig. S3); these effects were dampened in high competition relative to low competition conditions (Appendix S1: Fig. S3). In low competition, the relationship between nutrient availability and abundance also depended on population genetic diversity, with these patterns shifting over time (a GenDiv × Nutrient × Time interaction; see Fig. 3). High genetic diversity populations (4 or 8 genotypes) had a consistently positive nutrient–abundance relationship in all three generations. In contrast, low genetic diversity populations were initially insensitive to nutrients, but by generation three showed a strong positive nutrient–abundance relationship.

Persistence through the third generation

Empirical patterns.—Initial population establishment was uniformly high, with 98.9% of our main experiment

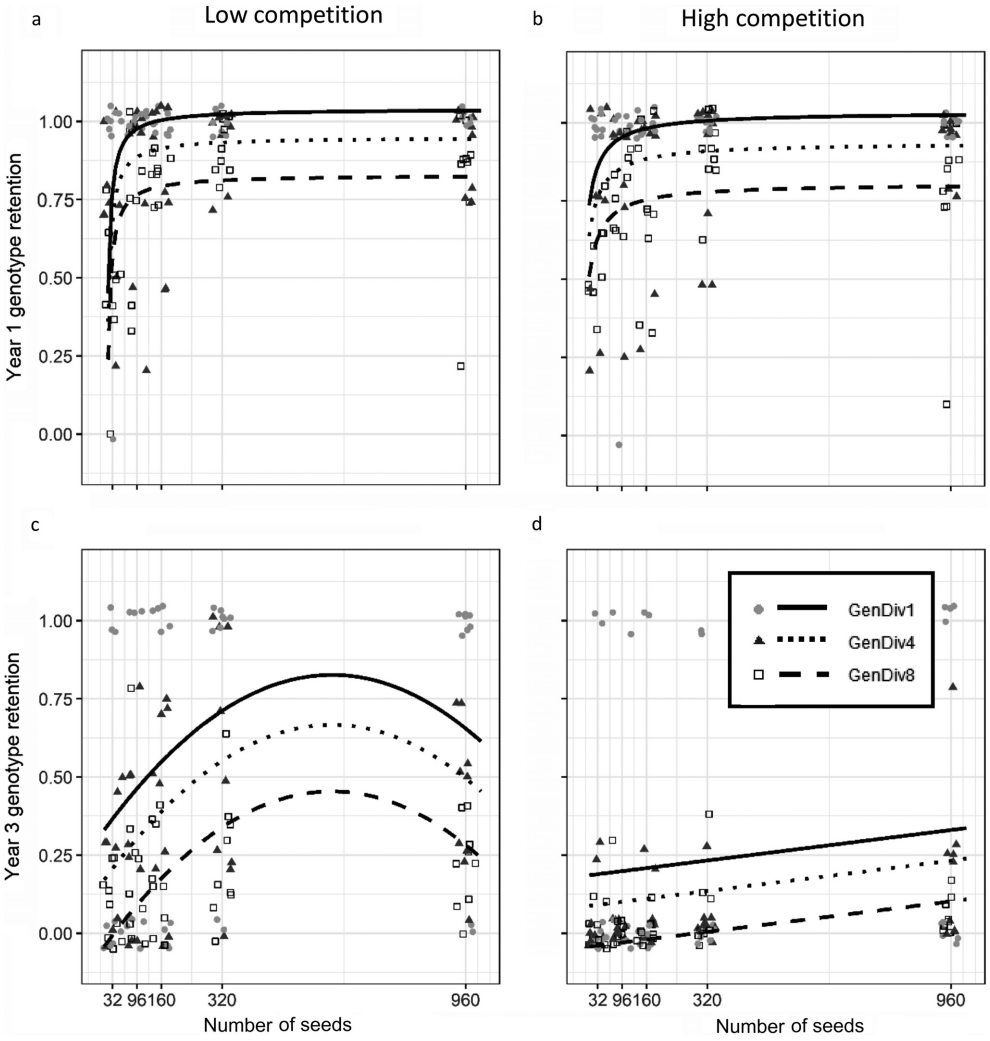

FIG. 1. *Arabidopsis* genotype retention in the (a, b) first and (c, d) third years post-introduction. GenDiv1, GenDiv4 and GenDiv8 refer to populations that were originally founded by 1, 4, or 8 genotypes, respectively. Data and best-fit lines from model parameter estimates are presented separately for (a, c) low competition and (b, d) high competition plots. Note that all values have been jittered slightly in both directions to facilitate interpretation.

founder populations (267 of 270) yielding at least one reproductive individual in the first year. We detected no significant effects of SeedNum nor of GenDiv treatments ($P = 0.172$ and 0.563, respectively) on year one establishment; thus, variation in persistence through year three reflects variation in the likelihood of local extinction during years two and three.

In the low competition treatment, 68.1% of populations (92 of 135) persisted through the third generation. Under these conditions, population persistence was more likely with increased propagule pressure, but significant nonlinearity (a SeedNum^2 effect; see Table 3) indicated an apparently saturating effect of increased propagule pressure, with no difference in persistence between our two highest SeedNum treatments (Fig. 4a). Persistence through the third generation was also enhanced by increasing genetic diversity in the founder population, though the effect was marginally significant ($\beta_{\text{GenDiv}} = 0.130$, $P = 0.074$; Fig. 4b solid line, Table 3); out of 45 populations per GenDiv treatment, single-genotype populations persisted in only 25 (55.6%), compared to 34 and 33 (~75%) for four- and eight-genotype populations, respectively. Close inspection of the data, as well as significant GenDiv × Nutrient interactions from the time series analysis, led us to suspect that GenDiv treatment differences in persistence may have been more pronounced in low nutrient plots. We therefore reran the persistence analysis excluding plots from the highest 25th percentile of soil nutrient availability. As expected, this post-hoc analysis yielded results that were qualitatively identical to those with the full data set, but with a significant increase in persistence as genetic diversity increased ($\beta_{\text{GenDiv}} = 0.238$, $P = 0.015$, $n = 101$; Fig. 4b dashed line).

In the high competition treatment, only 23.7% of *Arabidopsis* populations (32 of 135) persisted through the third generation. Persistence under these conditions was most likely in populations initiated with the very largest founder populations (Table 3; Fig. 4c), with 44.4% of the 960-seed populations surviving compared to 11–22% in all other SeedNum treatments. Third-generation persistence was marginally greater with increasing soil nutrients (Table 3) and unaffected by genetic diversity (Fig. 4d).

Tests for non-additive effects on persistence.—We found strong evidence of negative non-additive effects for persistence through year three in both competition treatments. In low competition, although increased diversity lead to enhanced persistence these observations fell far short of additive expectations (Fig. 4b, open circles) in both eight-genotype ($t_{44} = 4.0$, $P < 0.001$) and four-genotype populations ($t_{44} = 3.0$, $P = 0.004$; inferences based on Bonferroni adjusted $\alpha_{crit} = 0.017$). Persistence of single-genotype populations did not differ from expectations ($P = 0.812$). Propagule pressure appeared to influence these discrepancies, with more significant observed vs. expected differences occurring in the smallest founding populations of genotypic mixtures (see Fig. 4a, Table 4). The fact that expected persistence probabilities approached one with increasing genetic diversity reflected increases in the maximum per-genotype expectation for persistence in populations with more genotypes (maximum per-genotype expectations ranged from 0.10 to 0.90 in one-genotype plots, from 0.29 to 1.0 in four-genotype plots, and from 0.85 to 1.0 in eight-genotype plots).

Negative non-additivity was stronger in high than low competition conditions, although patterns were qualitatively the same (Figs. 4c, d). Both increased diversity and reduced seed inputs led to a greater discrepancy between observed and expected persistence, based on paired *t* tests (eight-genotype $t_{44} = 7.60$, $P < 0.001$; four-genotype $t_{44} = 4.36$, $P < 0.001$; one-genotype $P = 0.202$; see Table 4 for differences within SeedNum levels).

Third-generation abundance

Empirical patterns.—In the 92 populations that persisted under reduced competition conditions (i.e., excluding zeros), third-generation abundance increased in response to increasing soil nutrients (Table 3) and declined with increasing genetic diversity (Table 3, Fig. 5). The negative effect of genetic diversity was influenced by two outlier populations in the single-genotype treatment with abundances of 405 and 226 plants, both of which were monocultures of the same high-performing genotype (Se-0; see Appendix S1: Table S2). Excluding both outliers rendered the *GenDiv* effect non-significant (Fig. 5 inset). Propagule pressure had no effect on abundances of populations that persisted through the third-generation ($P = 0.711$).

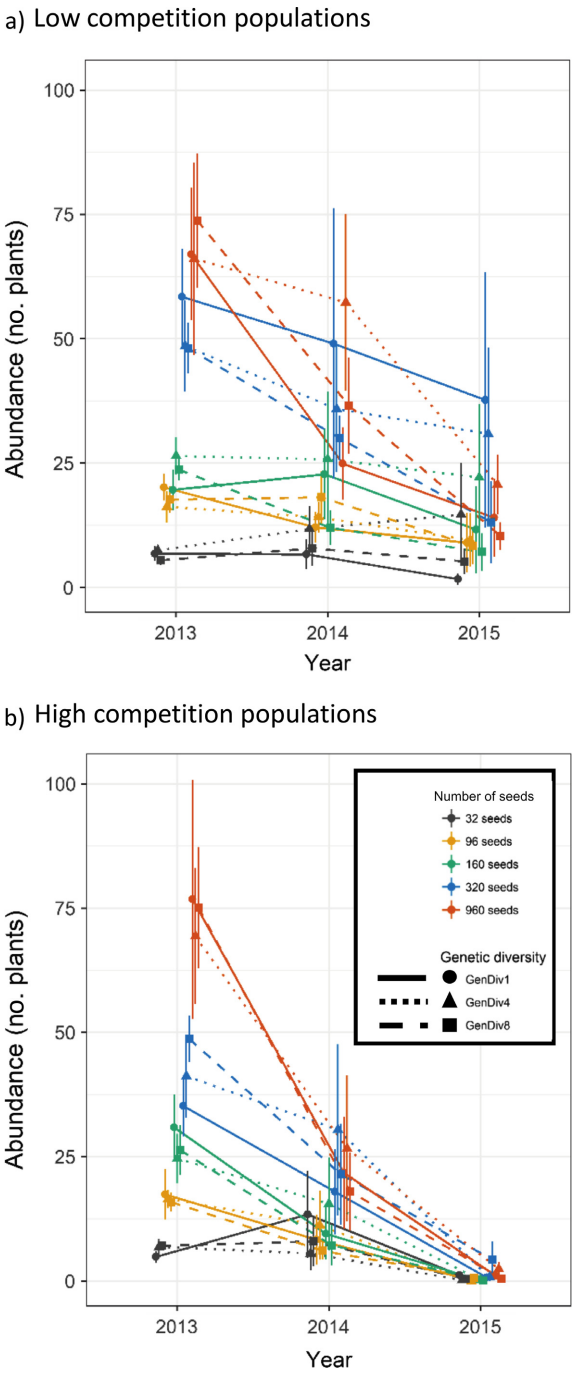

FIG. 2. Changes in *Arabidopsis* abundance over time in populations experiencing (a) low and (b) high competition. Abundance is reported as the number of reproductive individuals in a population. Note that data are omitted from one outlier plot in panel a (single-genotype, 160-seeds) that had 135 and 405 individuals in the second and third years, respectively (2.0 and 5.7 times greater abundances than the next largest value for that treatment combination, which increased mean abundance from 22.8 to 35.2 in 2014 and from 11.6 to 55.3 in 2015). Error bars represent 1 SE.

TABLE 2. Results from repeated-measures analysis on changes in *Arabidopsis* abundance over three years following seed additions.

Source	Parameter estimate	SE	χ^2	*P*
Low competition†				
Intercept	**3.052**	**0.660**	**22.06**	**<0.001**
Nutrients PC	**−2.927**	**1.475**	**4.06**	**0.044**
Seed number	**0.020**	**0.003**	**53.60**	**<0.001**
Genetic diversity	−0.006	0.102	0.003	0.953
Time	**−0.715**	**0.241**	**9.07**	**0.003**
SeedNum^2	**−0.00001**	**0.000003**	**25.98**	**<0.001**
SeedNum × Nutrients PC	**0.003**	**0.001**	**5.54**	**0.019**
GenDiv × Nutrients PC	**0.521**	**0.267**	**3.92**	**0.048**
Nutrients PC × Time	**2.116**	**0.581**	**13.67**	**<0.001**
SeedNum × Time	**−0.002**	**0.00035**	**27.30**	**<0.001**
GenDiv × Time	−0.012	0.041	0.08	0.775
GenDiv × Nutrients PC × Time	**−0.297**	**0.109**	**7.73**	**0.005**
High competition†				
Intercept	**4.36**	**0.406**	**117.61**	**<0.001**
Nutrients PC	**1.049**	**0.418**	**6.44**	**0.011**
Seed number	**0.014**	**0.002**	**55.10**	**<0.001**
Genetic diversity	−0.012	0.040	0.09	0.766
Time	**−1.606**	**0.136**	**143.01**	**<0.001**
SeedNum^2	**−0.000006**	**0.000002**	**14.59**	**<0.001**
SeedNum × Nutrients PC	**0.002**	**0.001**	**6.33**	**0.012**
SeedNum × Time	**−0.002**	**0.0003**	**68.45**	**<0.001**

Notes: Significant effects ($P < 0.05$) are shown in boldface type.

† Separate general linear models were run for low and high competition plots, with square-root-transformed abundance as the response ($n = 135$ for each analysis). Parameter estimates are reported in the transformed scale.

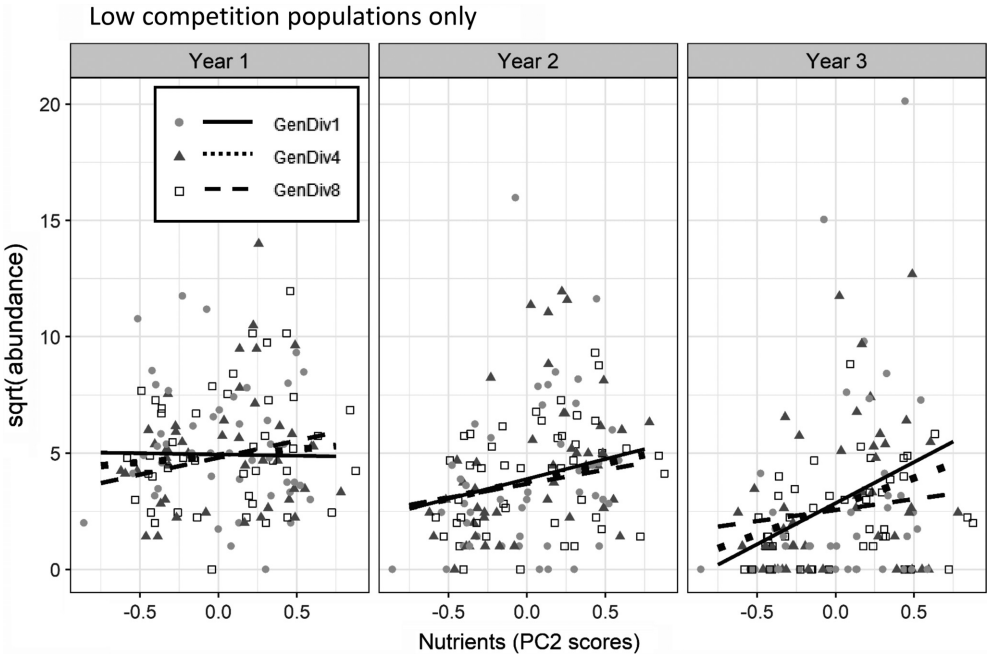

FIG. 3. Under low competition conditions, the relationship between soil nutrient availability and *Arabidopsis* abundance varied by genetic diversity (GenDiv) treatment and over time. Lines represent model parameter estimates, averaged over all effects of the seed number treatment (SeedNum); sqrt, square-root transformed.

TABLE 3. Results from hurdle models for *Arabidopsis* population persistence and abundances (for populations with at least one flowering individual) in the third year post-introduction.

	Population persistence				Flowering plant abundance†			
Source	Parameter estimate	SE	χ^2	*P*	Parameter estimate	SE	*Z*	*P*
Low competition								
Intercept	**−1.179**	**0.538**	**4.81**	**0.028**	**3.242**	**0.498**	**6.51**	**<0.001**
Nutrients PC	**1.235**	**0.560**	**4.86**	**0.027**	**1.895**	**0.529**	**3.58**	**<0.001**
Seed number	**0.010**	**0.003**	**8.58**	**0.003**	−0.00020	0.001	−0.37	0.711
Genetic diversity	*0.130*	*0.073*	*3.20*	*0.074*	**−0.186**	**0.067**	**−2.76**	**0.006**
SeedNum^2	**−0.00001**	**0.000003**	**5.56**	**0.018**	—	—	—	—
High competition								
Intercept	**−1.645**	**0.440**	**13.97**	**<0.001**	0.262	0.833	0.32	0.753
Nutrients PC	*1.16*	*0.601*	*3.75*	*0.053*	0.309	0.774	0.40	0.690
Seed number	**0.002**	**0.001**	**7.88**	**0.005**	0.0004	0.001	0.62	0.535
Genetic diversity	−0.052	0.075	0.48	0.49	−0.042	0.095	−0.44	0.661

Notes: Significant effects ($P < 0.05$) are shown in boldface type and marginally significant effects ($0.05 < P < 0.10$) in italic type.
† Sample sizes are 92 and 32, respectively, for low and high competition abundance analyses; —, not tested.

All 32 populations that persisted through the third generation under high competition were made up of very few individuals (mean = 3.8, median = 2, range: 1–33); our statistical models were therefore unable to explain variability in third-generation abundances (data not shown).

Tests for non-additive effects on abundance.—Under low competition conditions, negative non-additive effects for abundance were apparent only in the eight-genotype treatment plots, based on comparisons between observed data and expectations (Fig. 5; eight-genotype $t_{44} = 4.03$, $P < 0.001$; four-genotype $P = 0.636$; one-genotype $P = 0.402$). We note that two monocultures of genotype Se-0 outside the main experiment were outliers of similar magnitude relative to the outliers described above (with abundances of 564 and 289); excluding these plots resulted in expectations for one-genotype plots that were similar to the outlier-omitted observed data (Fig. 5 inset) and to the other GenDiv treatments ($P = 0.582$). Propagule pressure did not influence variation in the magnitude of non-additive effects, as evidenced by the lack of any variation in whether *t* tests among individual levels of the SeedNum treatment were significant or not (data not shown).

Performance variation among genotypes

The 25 genotypes we used differed significantly in post-introduction performance, based on abundances in monocultures in the third generation (including zero-abundance populations; $P < 0.001$; see Fig. 6 for pairwise comparisons). Two accessions (Se-0 and Pa-1) stood out as "good colonizers" while four stood out as particularly "poor" (Bur-0, Per-1, Lc-0 and Stw-0). As expected with increased sampling of the genotype pool, increasing genetic diversity increased the chances that at least one good colonizer had been randomly selected for inclusion; only 11% of founder populations in the single-genotype treatment had a good colonizer, compared to 33% of four-genotype and 44% of eight-genotype populations (with half of those eight-genotype plots receiving both good colonizer genotypes; see Appendix S1: Table S2). This pattern may be a key driver of our observation that increasing genetic diversity led to enhanced persistence under low competition conditions (Fig. 4b). However, also as expected, increased diversity also made it more likely that poor colonizer genotypes were selected; they comprised 22% of single-genotype founder populations but were included in 33% of four-genotype and 89% of eight-genotype populations (with one-quarter of those eight-genotype plots receiving either three or four poor colonizer genotypes; see Appendix S1: Table S2). This pattern would have effectively "diluted" any founding populations in the higher GenDiv treatments that included good colonizers by introducing those good genotypes at 25% or 12.5% the seeding rate compared to one-genotype populations (for four- or eight-genotype treatments, respectively), with the rest of the population composed of more poorly performing genotypes. Reduced persistence of key genotypes due to these reduced per-genotype seeding rates likely contributed to the greater genetic diversity losses we observed in initially higher diversity populations (Fig. 1) and may also have contributed to lower year three abundances for eight- and four-genotype populations relative to one-genotype populations (Fig. 5).

DISCUSSION

Our experiment highlights how resource availability and the time since introduction can mediate the independent roles played by propagule pressure and population genetic diversity in colonization success. Larger founder populations were more likely to persist over time, were better able to take advantage of abundant soil resources,

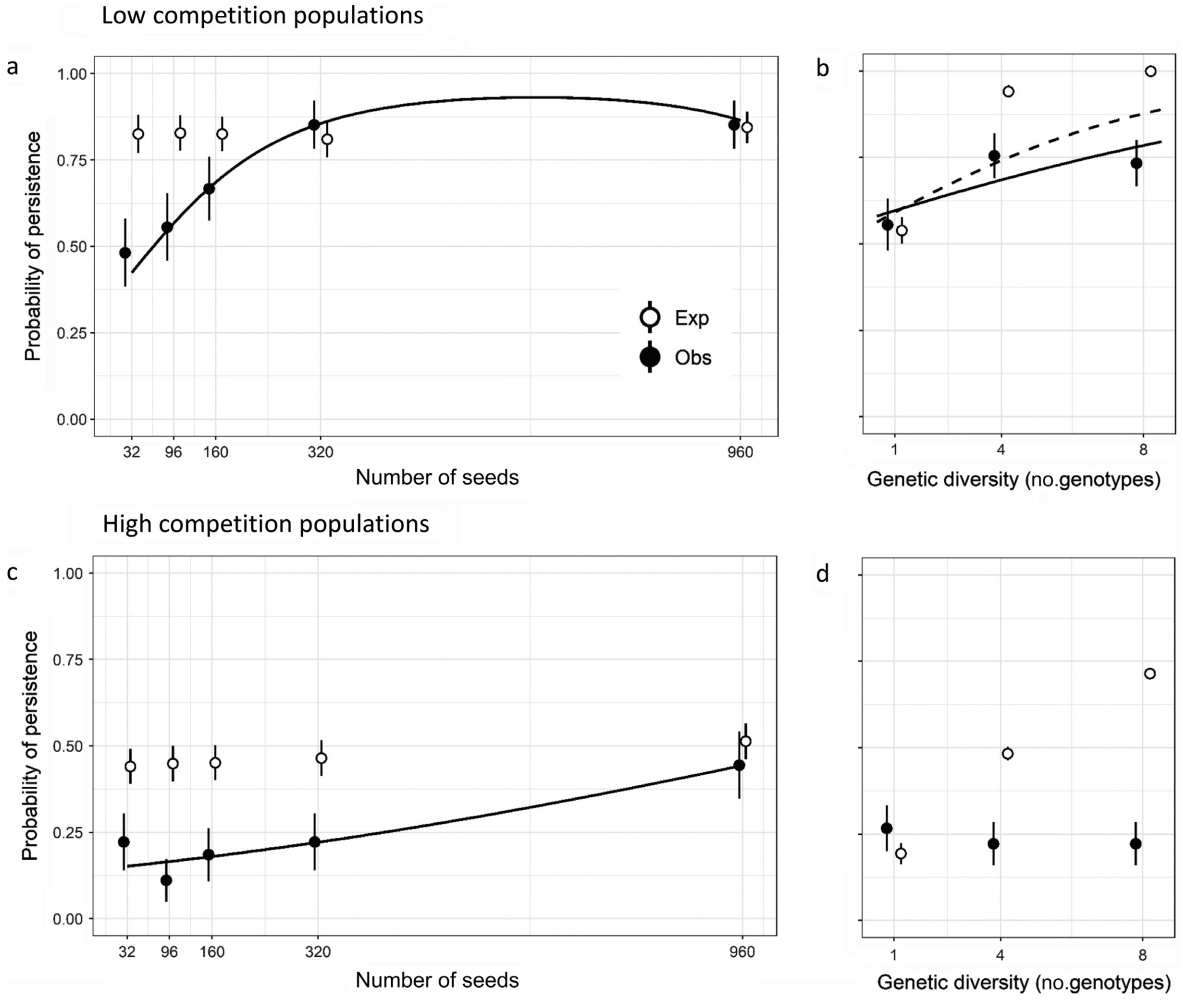

FIG. 4. Observed and expected relationships between the probability of *Arabidopsis* population persistence through the third generation and (a, c) SeedNum or (b, d) GenDiv. Observed means are shown as solid circles, and mean expectations based on monoculture data are shown as open circles. Data are shown separately for (a, b) low competition plots and (c, d) high competition plots. Predicted relationships from binomial GLM are plotted as a solid line in each case, although note that in panel b the relationship is marginally significant ($P = 0.074$) and in panel d it is nonsignificant. The dashed line in panel b indicates the predicted relationship between genetic diversity and persistence excluding plots in the upper 25th percentile of nutrient availability. Error bars represent 1 SE.

and retained genotypic diversity to a greater extent than smaller populations. However, in populations that persisted through the third generation, the effect of propagule pressure on third-generation population size was negligible, indicating a dampening of the effect of initial seed inputs. The effect of population genetic diversity was also contingent on local conditions and the time since introduction, with positive effects of increased diversity on persistence that were enhanced under low-nutrient conditions and over time (given a genetic diversity effect on persistence through year three but not year one). Both additive (sampling) effects and negative non-additivity contributed to the genetic diversity effects, with non-additive effects magnified under conditions of low propagule pressure and high biotic resistance.

Propagule pressure: a null model for predicting invasion success, but with limits

Propagule pressure is commonly correlated with population establishment (Lockwood et al. 2005, 2009, Simberloff 2009) and is widely considered to be a central determinant of invasion or colonization success (Colautti et al. 2006, Eschtruth and Battles 2011, Horvitz et al. 2017). In contrast, the idea that propagule pressure may vary predictably in importance based on local abiotic and biotic conditions is a recognized, but relatively under-unexplored, concept in invasion biology (D'Antonio et al. 2001, Rouget and Richardson 2003, Lockwood et al. 2005, Simberloff 2009, Houseman et al. 2014). Controlling for propagule inputs, a given

TABLE 4. Mean observed and expected probabilities of *Arabidopsis* population persistence through the third generation, calculated separately for all treatment combinations.

Comp	GenDiv	SeedNum	Observed	Expected	*t*	*P*
Low	1	32	0.33 (0.17)	0.52 (0.10)	1.35	0.214
Low	1	96	0.33 (0.17)	0.54 (0.09)	1.46	0.183
Low	1	160	0.56 (0.18)	0.55 (0.08)	0.05	0.964
Low	1	320	0.78 (0.15)	0.50 (0.09)	1.72	0.124
Low	1	960	0.78 (0.15)	0.59 (0.08)	1.31	0.226
Low	4	32	0.56 (0.18)	0.95 (0.03)	2.46	0.039
Low	4	96	0.67 (0.17)	0.95 (0.04)	1.58	0.154
Low	4	160	0.78 (0.15)	0.93 (0.06)	1.25	0.246
Low	4	320	0.89 (0.11)	0.93 (0.04)	0.35	0.739
Low	4	960	0.89 (0.11)	0.95 (0.03)	0.75	0.475
Low	8	32	0.56 (0.18)	0.9998 (0.0001)	2.53	0.035
Low	8	96	0.67 (0.17)	0.9997 (0.0002)	2.00	0.081
Low	8	160	0.67 (0.17)	0.9998 (0.0001)	2.00	0.081
Low	8	320	0.89 (0.11)	0.9999 (0.0001)	1.00	0.347
Low	8	960	0.89 (0.11)	0.9997 (0.0003)	1.00	0.348
High	1	32	0.22 (0.15)	0.16 (0.06)	0.41	0.69
High	1	96	0.22 (0.15)	0.17 (0.06)	0.49	0.639
High	1	160	0.22 (0.15)	0.17 (0.06)	0.31	0.766
High	1	320	0.22 (0.15)	0.19 (0.07)	0.26	0.804
High	1	960	0.44 (0.18)	0.27 (0.10)	1.42	0.193
High	4	32	0.22 (0.15)	0.46 (0.05)	1.61	0.147
High	**4**	**96**	**0.00 (0.00)**	**0.47 (0.05)**	**10.15**	**<0.001**
High	4	160	0.22 (0.15)	0.47 (0.04)	1.84	0.104
High	**4**	**320**	**0.11 (0.11)**	**0.48 (0.05)**	**3.59**	**0.007**
High	4	960	0.56 (0.18)	0.53 (0.05)	0.15	0.882
High	8	32	0.22 (0.15)	0.70 (0.03)	2.79	0.023
High	**8**	**96**	**0.11 (0.11)**	**0.71 (0.03)**	**5.60**	**<0.001**
High	**8**	**160**	**0.11 (0.11)**	**0.71 (0.03)**	**4.35**	**0.002**
High	8	320	0.33 (0.17)	0.72 (0.03)	2.39	0.044
High	8	960	0.33 (0.17)	0.74 (0.03)	2.58	0.033

Notes: Expected and observed values are means with SE in parentheses. *P* values are based on paired *t* tests comparing observed vs. expected differences; significant differences based on Bonferroni adjusted α_{crit} of 0.01 (accounting for five comparisons within each GenDiv treatment level) are shown in boldface text.

founder population should vary from being more propagule limited in benign conditions to establishment limited in stressful conditions (Thomsen et al. 2006, Clark et al. 2007, Duncan 2016). Thus, a fixed increase in propagule pressure should enhance colonization relatively more in less stressful conditions, e.g., where resources are plentiful. The effect of increasing propagule pressure in our experiment varied in accordance with these expectations; greater seed inputs led to the most dramatic increases in abundance where nutrient availability was the greatest and biotic resistance the weakest. This pattern holds in other systems as well (Thomsen et al. 2006, Houseman et al. 2014), supporting the general hypothesis that the importance of propagule pressure for population establishment will be positively associated with the degree to which local conditions are favorable for the colonizing species or population (D'Antonio et al. 2001).

It is just as important to highlight when increased propagule pressure *fails* to explain colonization success, since such results contradict prevailing expectations. Two common scenarios can lead to the decoupling of propagule pressure from colonization success: abiotic or biotic conditions (1) that impede colonization regardless of propagule inputs (e.g., are related to ecophysiological tolerances) or (2) that permit colonization regardless of propagule inputs (e.g., are related to low invasion resistance in a system). Both extremes are illustrated by data from a species of dung beetle intentionally introduced throughout Australia (Duncan 2016), where establishment success was unrelated to propagule pressure and instead driven entirely by environmental conditions (see also Nuñez et al. 2011, Sinclair and Arnott 2017). Although propagule pressure in our study was a key predictor of persistence through year three, abundance in those persisting populations was entirely unrelated to propagule pressure (Table 2), reflecting a clear distinction between the key factors contributing to population establishment (as judged by presence/absence) vs. post-establishment abundance and population growth.

Such differences in the effects of propagule pressure on establishment vs. post-establishment abundances are

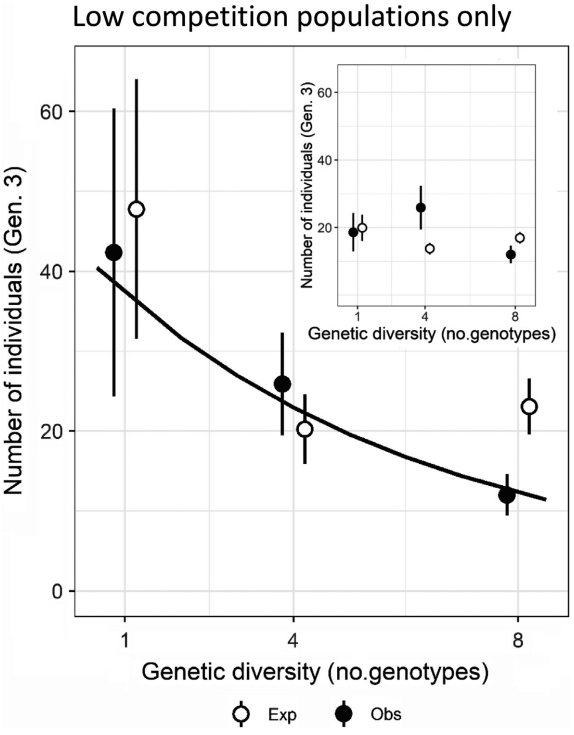

FIG. 5. Observed and expected *Arabidopsis* abundance in relation to genetic diversity in the subset of low competition populations that persisted through year three post-introduction. Observed means are shown as solid circles, and mean expectations based on monoculture data are shown as open circles. The predicted relationship from truncated negative binomial GAM is plotted as a solid line. Abundance declined with increasing genetic diversity (main figure), although this effect was not significant after excluding two outlier populations in the single-genotype treatment (inset; note that two outlier monocultures of the same genotype are also omitted in the inset, affecting expectations as well). In the highest diversity treatment only, observed abundance was significantly lower than expectations based on performance in monocultures. Error bars represent 1 SE.

intriguing, since these two key metrics of colonization success often respond similarly to propagule pressure. In one example, an observational study of three invasive tree species in South Africa found that distance from the putative invasion source (a proxy for propagule pressure) was associated with presence/absence patterns as well as percent cover (Rouget and Richardson 2003), although in all cases propagule pressure was a poorer indicator of abundance than of presence/absence. In a second example, two chrysomelid beetle species were experimentally introduced as biocontrol agents across a range of founder population sizes (Grevstad 1999, 2006). Here, propagule pressure was positively associated with both the likelihood of establishment and population growth rates (thus abundances) after three years (Grevstad 1999) as well as population persistence to year ten post-introduction (Grevstad 2006); unfortunately, abundance in year ten was not reported. Thus, for these two examples propagule pressure appears to have been similarly related to establishment and post-establishment abundances (see also Fauvergue et al. 2007, Burgess and Marshall 2011, Britton and Gozlan 2013, Estrada et al. 2016, Lange and Marshall 2016). Whether this pattern is general remains to be seen, but increased demographic stochasticity in small populations *should* yield a positive association between abundance and the likelihood of population persistence over time and thus a similar relationship between propagule pressure and both metrics (although see Memmott et al. 2005 for a contrary example).

Why then might we have found discordant associations between propagule pressure and persistence vs. abundance in the current study? The fact that abundances generally declined over time (Fig. 1) is evidence that most of our *Arabidopsis* populations were population sinks, perhaps explaining the lack of a correlation between propagule pressure and abundances in extant populations. As newly founded populations decline toward extinction, stochasticity may become a relatively more important driver of abundance than initial founder population size. Alternatively, with increased time post-introduction the positive effects of propagule pressure may simply become less important than limits imposed by local environmental conditions (Nuñez et al. 2011). In either case, discordant associations between propagule pressure and establishment vs. post-establishment abundances may result, complicating our ability to predict post-establishment metrics of population success.

Context-dependent effects of genetic diversity on colonization

Longer-term population persistence was enhanced by increasing genetic diversity: the effect was marginally significant with the full data set but significant when the highest nutrient plots were excluded, indicating that the benefits of increased genetic diversity were magnified with diminishing resource availability. To our knowledge, there are no previous reports from experiments that have manipulated genotype richness where genetic diversity effects depend on resource availability, but our findings are consistent with data from seagrass (*Zostera marina*) experiments and surveys that have documented stronger positive effects of genetic diversity after periods of stress (Hughes and Stachowicz 2004, 2009). Results from *Arabidopsis* and *Zostera* are also similar to those from Hufbauer et al. (2013), who manipulated genetic backgrounds (inbred to outbred) in colonizing whiteflies (*Bemisia tabaci*) and found that inbreeding depression limited population establishment, but only under stressful conditions (a novel food source). Thus, across these disparate systems we see a similar pattern: positive effects due to enhanced genetic diversity and negative effects due to reduced genetic diversity were both magnified under low-resource conditions. Interestingly, the lack of any such effects in an experiment with flour beetles

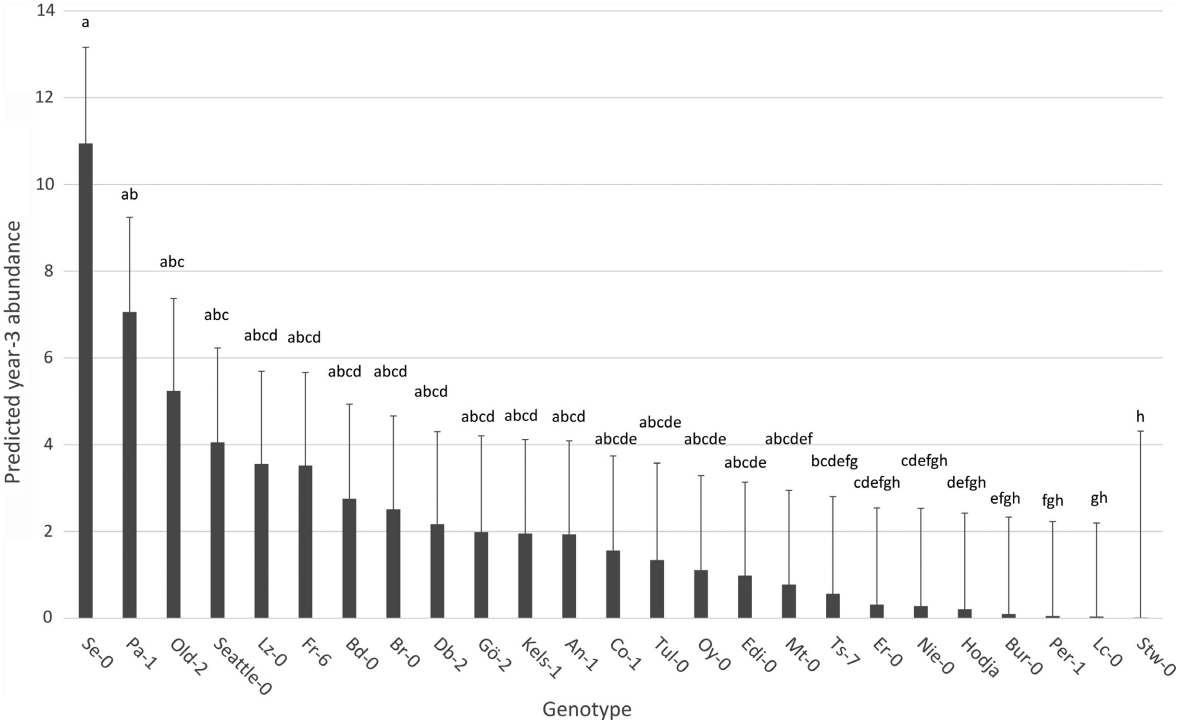

FIG. 6. Expected per-genotype *Arabidopsis* abundance in the third year post-introduction, from models accounting for the random effects of experimental treatments in monoculture plots. Genotype differences are based on Tukey post hoc tests; statistically similar genotypes ($\alpha_{crit} = 0.05$) are denoted with the same lower-case letter. Error bars represent 1 SE.

(*Tribolium castaneum*) varying in their genetic background (Szűcs et al. 2014) may also support the generalization, since the low-resource food in that experiment was only weakly stressful to the study species (Szűcs et al. 2014). Together, these observations suggest that population genetic characteristics may tend to have the greatest implications for colonization success under stressful conditions or resource limitation. We note that this pattern is directly in contrast with the effects of propagule pressure, which our study and others have found are magnified under low-stress conditions (see *Propagule pressure: a null model for predicting invasion success, but with limits*). Such information could be useful for prioritization and management of colonizing populations, either where colonization is desired (restoration, biological control) or unwanted (invasions).

Observed persistence in our mixed-genotype plots never exceeded expectations based on monoculture data, indicating that enhanced persistence in genotypic mixtures was not a result of niche complementarity or facilitation (i.e., positive non-additive mechanisms). Instead, we infer that sampling effects alone were responsible for enhanced persistence as genetic diversity increased and that the magnitude of these effects was strongest under low nutrient conditions. It would be interesting to determine whether this latter pattern holds in systems where complementarity is more pronounced than in our current study. If productivity is positively associated with the magnitude of complementarity effects, as has been reported in experiments manipulating diversity at the species level (Fridley 2002), then perhaps high levels of resource availability would also be associated with genetic diversity effects, albeit by a different mechanism than we observed here under low resource availability.

In our system, genetic diversity effects on persistence also strengthened over time, as evidenced by GenDiv effects on persistence through the third generation but not through the first. Enhanced genetic diversity effects over time are expected in manipulations of both inbreeding and genotypic richness. In the former, they are expected because of genetic recombination among sexually reproducing individuals, which facilitates adaptive evolution and/or masks deleterious alleles in previously inbred lines (Firestone and Jasieniuk 2013, Hufbauer et al. 2013, Szűcs et al. 2014). Because *Arabidopsis* is primarily selfing, we do not expect recombination to have played a major role in our study (only 7% of samples collected from genotypic mixture plots in the third generation were heterozygotes; see Appendix S1: Fig. S1). Instead, our results are better compared to studies in which genetic diversity treatments exclude the effects of sexual reproduction (usually single-generation studies with clones of a perennial species) by manipulating genotypic richness in experimental populations. Under these circumstances, the effects of genetic diversity may be enhanced over time if, for example,

genotype-specific increases or declines in relative abundance contribute to population-level stability despite changing environmental conditions, or if diverse populations harbor variation that becomes selected upon at some point in the future. In fact, when temporal patterns have been assessed, most such studies do report increases in genetic diversity effects over time (Martins and Jain 1979, Reusch et al. 2005, Drummond and Vellend 2012, Wang et al. 2012, but see Hughes and Stachowicz 2009). Notably, these patterns and mechanisms are analogous to those observed in biodiversity-ecosystem function studies, where benefits from increased *species* diversity also tend to increase over time (Cardinale et al. 2007). Overall, the prevailing message from a wide range of empirical work is that any effects of increased diversity, either within or among species, should become magnified over time. Assuming one is interested in longer-term outcomes, this message has critical implications, not only for how subsequent experiments are designed and interpreted but also for how these concepts are implemented in practice (e.g., in ecological restorations or in managing species invasions). For example, a finding that variation in genetic diversity has no immediate effect on population establishment (Hovick et al. 2012) may be uninformative regarding effects of genetic diversity that are realized over the longer term. We suspect future work will show that in most systems enhanced genetic diversity in a founder population will enhance colonization success, as long as those post-introduction populations are monitored for a sufficiently long period of time.

Our results highlight not just the importance of genetic diversity for colonization success but more specifically the importance of genotypic *identity*. The fact that persistence benefits from increased genetic diversity (Fig. 4b) did not correspond to increased abundance in higher diversity populations (Fig. 5) may reflect dilution of performance by "good colonizer" genotypes (particularly Se-0) due to the prevalence of "poor colonizers" in high diversity populations (Appendix S1: Table S2). This pattern may also contribute to the negative non-additive effects that we observed primarily in our highest diversity populations. The importance of genotypic identity has been emphasized previously in other genetic diversity experiments (Vellend et al. 2010), as well as in natural systems. For example, although multiple haplotypes of the invasive grass *Phragmites australis* have been introduced from Europe to North America and can be found in the non-native range, most invasions are dominated by a single, highly successful haplotype (Saltonstall 2002). The implications of genotypic identity are clearly important, but particularly when sampling effects are more pronounced than complementarity they also represent a conundrum for testing whether increased genetic diversity enhances colonization: performance may be positively associated with increasingly diverse founder populations *on average*, but it is also possible for low diversity populations in a particular introduction event (or in our case, experiment) to by chance consist largely of high-performing genotypes. Explicitly accounting for these idiosyncrasies (i.e., how well the requirements of individual genotypes are matched to local environmental conditions) will be a key hurdle moving forward if we expect to make accurate predictions in other systems regarding the nature and magnitude of genetic diversity effects on colonization success.

The implicit relationship between propagule pressure and genetic diversity

Although we found no explicit statistical interactions between propagule pressure and genetic diversity on colonization success, the fact that increasing propagule pressure led to greater retention of genotypic richness over time indicates an important implicit relationship between these two factors. This positive association between propagule pressure and realized genotypic richness in the third generation occurred despite propagule pressure being unrelated to population sizes in that year. And, in high competition conditions where biological resistance was the greatest, realized genetic diversity in year three responded to variation in propagule pressure only (and not initial genetic diversity). Both observations highlight an increase in the likelihood of per-genotype persistence as an important mechanism by which propagule pressure influences establishment and/or persistence at the population level. We contend that this represents an underappreciated benefit from increasing propagule pressure in systems where individuals vary in traits affecting survival. Intraspecific trait variability has received an increased degree of attention by ecology researchers in recent years (Bolnick et al. 2011, Violle et al. 2012), and our data represent a novel dimension by which intraspecific variation and propagule pressure can jointly influence population dynamics.

Longer-term patterns of genotype retention, specifically, the fact that the relationship between founder population size and genotype retention through year three was better described as hump-shaped than simply saturating (Fig. 1c), highlight an unexpected potential effect of negative density dependence under extreme propagule pressure. Negative density dependence has been reported in large colonizing populations (Hedge et al. 2012, Warren et al. 2012, Barney et al. 2016), but such reports are generally limited to individual-level performance metrics (e.g., reduced per-capita fecundity). We observed similar reductions in per-capita fecundity in our experiment (data not shown), but additionally saw population-level declines coinciding with per-capita declines when propagule pressure was high. It seems plausible that the combined effect of poorly performing genotypes becoming relatively rare plus low per-capita reproduction across the population might lead to greater genotype loss over time when founder populations are particularly large.

Genetic diversity effects and the putative role of intraspecific density

We predicted that genetic diversity effects would be most likely in high-density conditions (i.e., significant interactions between genetic diversity and propagule size) in part because of niche differentiation (see also Cardinale et al. [2007] for analogous patterns with species diversity). If genotypes differ in traits related to their use of limiting resources, then increasing genetic diversity may lead to increases in resource uptake and thus population success, particularly where population density is relatively high and intraspecific individuals most likely to interact (Drummond and Vellend 2012, but see Cook-Patton et al. 2017). Such non-additive genetic diversity effects have previously been reported in *Arabidopsis:* in a greenhouse experiment, complementarity was observed to have contributed to increases in seedling emergence, flowering duration, population biomass and population fecundity with increased genetic diversity (Crawford and Whitney 2010). In our current experiment, strongly nonlinear patterns in colonization success indicate that populations at the upper end of our SeedNum treatments were not seed limited, and therefore, densities should have been high enough for *Arabidopsis* individuals to interact. Yet, despite our experimental populations reaching high enough densities that complementarity mechanisms *could* have affected colonization success, we found no evidence that they did so.

Why is there a discrepancy between the greenhouse and field results? Perhaps the greenhouse experiment was more likely than our field experiment to pick up genetic diversity effects because there was less noise in the system, for example if environmental variability among plots in the field drowned out relatively weak diversity effects. However, the field experiment was likely a much more stressful environment for *Arabidopsis* than the greenhouse, which might be expected to offset this pattern by enhancing any effects of genetic diversity (Hughes and Stachowicz 2004, 2009, Reusch et al. 2005). Discrepancies may alternatively relate to genotypic identity, as different sets of genotypes were used in the two experiments. However, we think that the key to contrasting outcomes between studies is a fundamental difference in realized intraspecific densities. Crawford and Whitney (2010) sowed their *Arabidopsis* populations without interspecific competition at starting densities of 0.05 or 0.10 seeds/cm and observed very high recruitment rates and very large plant sizes (K. D. Whitney, *personal observation*). Densities in that previous study would be equivalent to 125 or 250 plants in our 50 × 50 cm field plots, values that we only observed in 9 out of 270 plots in the first year of our main experiment (and only 4 out of 270 in year three). Therefore, intraspecific competition may not have been strong enough for our populations to exhibit performance differences via genotypic niche differentiation as in Crawford and Whitney (2010). Hovick et al. (2012) made a similar argument to explain the lack of any genetic diversity effect in a separate *Arabidopsis* greenhouse experiment that had low intraspecific and high interspecific densities, leaving few opportunities for niche partitioning to occur. We think these patterns may indicate the existence of a higher threshold for complementarity effects than exists for negative density dependence in colonization success and perhaps population performance more generally. We know of no studies that have explicitly compared these density thresholds, but given the importance of intraspecific interactions in high-density populations (including native foundation species and introduced invasive species) we suggest this may be a worthwhile area of study.

Contrasting experimental design choices when testing for genetic diversity effects on colonization: simulated bottlenecks, admixture, or inbreeding

By randomly selecting independent sets of genotypes from a large pool for each of our genetic diversity treatments, ours is a conservative test for how variation in genetic diversity generally can affect colonization. This approach contrasts sharply with an alternative design that is commonly used for assessing genetic diversity effects, in which low diversity populations are composed of nested subsets of genotypes from high diversity treatments (Drummond and Vellend 2012). We contend that the nested design provides a test of genetic diversity within just one specific context: population bottlenecks. Although understanding population dynamics following a bottleneck is often critical for understanding variation in colonization success (Nei et al. 1975), founder events need not coincide with a bottleneck. This is particularly true in the context of biological invasions, where introductions may move individuals in such high numbers that even rare genotypes from the native range are introduced and diversity is similar in the non-native range (Dlugosch and Parker 2008) or where multiple source populations from across the native range are sampled and admixed populations in the nonnative range may be even more diverse than native populations (Kolbe et al. 2007, Lavergne and Molofsky 2007). Both experimental designs are valid and represent scenarios that are common during colonization, but we argue that it is critically important to be clear about the scope and limitations inherent in either approach (i.e., that the nested design tests hypotheses specifically about bottlenecks and not genetic diversity more broadly).

Our approach for manipulating genetic diversity permits tests of genetic diversity effects more broadly, but the admixture design we used does come with some practical challenges. The fact that genotypes used in our low diversity populations are not a subset of the genotypes used in high diversity populations introduces a substantial degree of noise to our system. For example, our best colonizer (Se-0) was relatively common in the single-genotype treatment (comprising 11% of all

replicates) but less so in the higher-diversity treatments (occurring in 6% of four-genotype treatments and 4% of eight-genotype treatments; see Appendix S1: Table S2), leading to apparent abundance declines with increasing genetic diversity. Such variability in composition, coupled with high variation in colonization ability among genotypes (Fig. 6), and thus, founding populations adds to the inherent variability expected in studying a process as stochastic as colonization. Given the conservative nature of our design, we therefore suggest that our results may indicate that variation in genetic diversity could play an even greater role during population establishment in natural populations than we have observed here.

We briefly highlight a third experimental design that has been used to investigate the effects of genetic diversity on colonization dynamics. In contrast with designs that emphasize the benefits that may accrue from admixture, this third approach emphasizes the costs associated with inbreeding (see Discussion in Hufbauer et al. 2013). These studies (Firestone and Jasieniuk 2013, Hufbauer et al. 2013, Wootton and Pfister 2013, Szűcs et al. 2014) are grounded in past work on the conservation genetics of rare species, often manipulating the extent to which founder populations are inbred (a severe form of population bottleneck) and thus representing the other end of a "genetic diversity spectrum," in comparison to admixture manipulations. This approach is particularly relevant for small founder populations that are expected to experience inbreeding depression (e.g., obligate outcrossers and species that historically occurred in large source populations), and it has been used effectively in experiments investigating the genetic and demographic effects of propagule pressure variation. In a few cases, these experiments have been designed to explicitly compare inbred and admixed populations, usually reporting stronger negative effects due to inbreeding than any positive effects due to admixture (Hufbauer et al. 2013, Szűcs et al. 2014, 2017, but see Wootton and Pfister 2013, who found no effect of their genetic diversity treatments). We note that the scenario involving highly inbred founder populations may be somewhat less relevant for biological invasions and colonization more generally because of the widespread association between uniparental reproduction and colonization and/or invasion propensity (Razanajatovo et al. 2016, Grossenbacher et al. 2017), due to the fact that such species may be less prone to inbreeding depression (Busch 2005). Future efforts at synthesizing studies on genetic diversity effects would yield valuable insights by integrating findings from experiments manipulating genetic diversity via inbreeding (and less severe population bottlenecks) as well as via admixture, accounting for a study's relative position along the spectrum of manipulated genetic diversity.

Conclusion

In most non-experimental systems, both genetic diversity and propagule pressure in a founding population are unknown, because observations are limited to the strains that persist over time and their post-establishment abundances. Given the critical role of founder populations for colonization and longer-term persistence in both basic and applied (e.g., biocontrol, invasions, and agriculture) settings, experiments like ours are fundamental for understanding the roles of these key population characteristics. Yet, it is clearly not sufficient to know simply that colonization can be enhanced by increasing the number and genetic diversity of colonizers. Our study draws attention to important context-dependencies involving time, resources and competition that influence the importance of propagule pressure and genetic diversity for colonization success. Future work should continue exploring these limits in a range of model and non-model systems if we are to fully understand the implications of these deceptively simple founder population characteristics.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1368/full

Data Availability

Data are available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.t80r9c1