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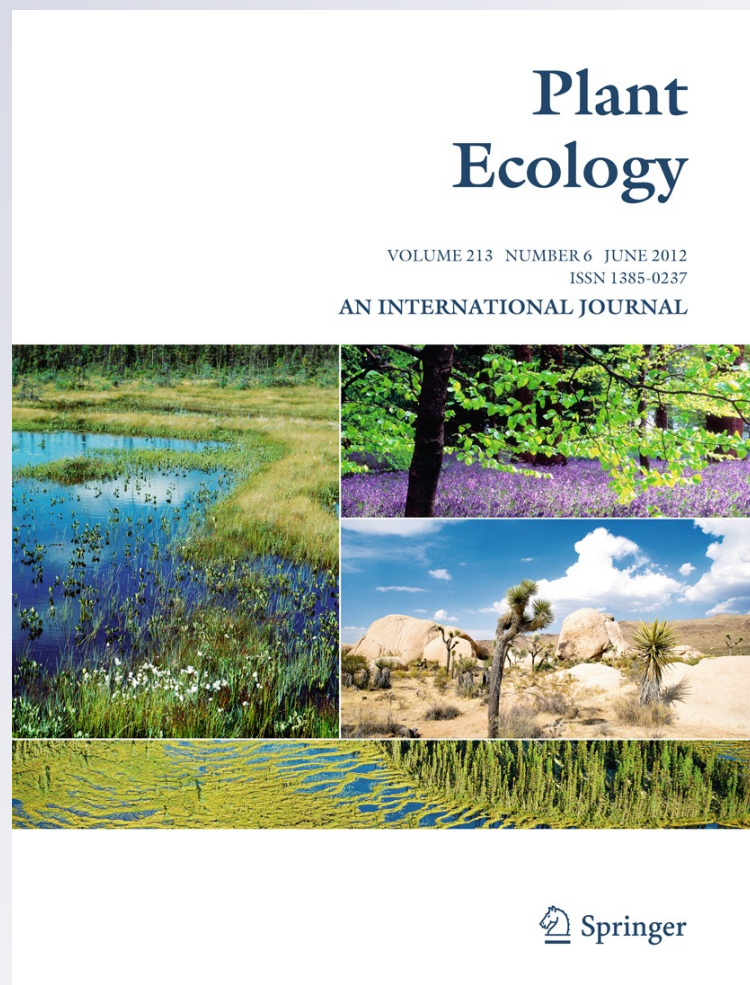## Stephen M. Hovick, Esra D. Gümüşer & Kenneth D. Whitney

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Community dominance patterns, not colonizer genetic diversity, drive colonization success in a test using grassland species

**Stephen M. Hovick · Esra D. Gümüşer ·
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Abstract Successful colonization and/or invasion depend on characteristics of the invaded community and of the colonizer itself. Although many studies have documented a negative relationship between invasibility and biodiversity, the importance of community evenness is rarely examined and thus poorly understood. However, colonizer characteristics, including population genetic diversity, can also be important determinants of colonization success. We conducted a greenhouse experiment to assess the relative importance of community evenness and colonizer population genetic diversity using the weed *Arabidopsis thaliana*. We added seeds of *A. thaliana* (varying genetic diversity while keeping propagule pressure constant) to four types of constructed plant communities: those dominated by legumes, grasses or forbs, or with equal abundances of all three functional groups. We selected community members from a large pool of species to avoid the confounding effects of species identity. We also assessed the success of multiple seedbank colonizers to assess generality in the effects of our evenness treatments. Equal-abundance communities were no better at suppressing colonization than communities dominated by a single functional group. Forb-dominated communities suppressed *A. thaliana* colonization better than grass-dominated communities and suppressed seedbank colonizers better than legume-dominated communities. Equal-abundance communities were similar to forb-dominated ones in their eventual composition and in their invasibility, suggesting that forbs drove colonizer suppression in that treatment rather than high evenness itself. Most of our forbs grew quickly, yielding productive forb-dominated communities; this points to the importance of growth and colonization phenology in our system. *A. thaliana* genetic diversity did not affect colonization success, perhaps because strong interspecific competition substantially limited *A. thaliana* seedling emergence.

Keywords Functional group · Population genetic diversity · Biological invasions · Community dominance/evenness · Invasion resistance · Colonization

Stephen M. Hovick and Esra D. Gümüşer contributed equally to this study.

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Introduction

A better understanding of plant colonization dynamics is necessary to identify potential invaders and the communities most threatened by invasion. In part, colonization or invasion success reflects characteristics of the recipient community with some communities

suppressing colonizers better than others (e.g., Crawley et al. 1999; Hector et al. 2001; Fargione and Tilman 2005; Emery and Gross 2007; Drenovsky and James 2010). Yet, colonization success also reflects key characteristics of colonizing species (e.g., growth rates and fecundity; Pyšek and Richardson 2007; van Kleunen et al. 2010) and their populations (e.g., propagule pressure, hybridization history, and population genetic diversity; Lockwood et al. 2005; Crawford and Whitney 2010; Hovick et al. 2012). Studies investigating the relative importance of the invaded community characteristics versus colonizer characteristics (i.e., invasibility versus invasiveness) may provide new insights regarding the determinants of successful colonization and invasion (Richardson et al. 2000).

Species diversity and invasibility are often negatively correlated (Hector et al. 2001; Herben et al. 2004; Tilman 2004; Fargione and Tilman 2005; Scherber et al. 2010). One common interpretation is that species-rich communities use a greater proportion of available resources, therefore reducing the niche space available to colonizers; however, Wardle (2001) argued that species richness effects may instead result from differences in species composition. Species-rich communities are more likely to contain a dominant species that exploits resources effectively, thus successful colonization may depend on species identity and not species richness per se. Nonetheless, most invasibility studies use richness as the sole metric of diversity. An information-rich alternative to species richness is evenness, which reflects species' relative abundances within a community. In plant communities, evenness can account for much more variation in proportional diversity (H') than does species richness (53 vs. 6 %; Stirling and Wilsey 2001), while also responding more rapidly to natural and anthropogenic perturbations (Chapin et al. 2000; Walker et al. 2006). Because communities with equal species richness can differ significantly in species' relative abundances, evenness may provide additional valuable information about species diversity effects on invasibility.

One challenge in making predictions regarding evenness and invasibility is that, depending on the context, invasibility may be expected to peak in either high- or low-evenness communities. On one hand, theory suggests that high-evenness communities can result in greater resource drawdown, and thus greater productivity, reducing the probability of colonization (Nijs and Roy 2000); this is consistent with several

empirical findings (Wilsey and Polley 2002; Tracy and Sanderson 2004; Zavaleta and Hulvey 2007). On the other hand, if some optimal trait value exists for a site, low-evenness communities containing a dominant species that matches this optimum may have higher productivity and therefore decreased invasibility than high-evenness communities (Norberg et al. 2001); this pattern has also been confirmed experimentally (Emery and Gross 2007). Thus, previous attempts to study the relationship between invasibility and community evenness have produced conflicting results.

These discrepancies might be explained via species identity effects (Crawley et al. 1999; Emery and Gross 2007; Daneshgar and Jose 2009). Most experimental low-evenness communities confound dominant species identity with low-evenness treatments by not manipulating dominant species identity or not randomly selecting replicates of dominant species from a larger pool, clouding inferences regarding the role of evenness in suppressing colonization (but see Tracy and Sanderson 2004). Although experiments with species that commonly occur as community dominants do provide valuable system-specific inferences, a different approach is needed to identify more general patterns. We suggest that testing for general patterns requires assessing colonizer suppression in experimental communities that are assembled via random species selection and where evenness is manipulated at the level of the functional group to remove the confounding effects of species identity.

Functional groupings aggregate species that use and compete for resources similarly. Since resource availability is often central to understanding colonization and invasion dynamics, the number and identity of functional groups in a community may significantly affect invasibility (Roscher et al. 2009; Hooper and Dukes 2010). For instance, Arenas et al. (2006) found that functional group identity was more important than functional group richness in the ability of macroalgal communities to resist invasion. Similarly, Daneshgar and Jose (2009) found that grasses reduced invasion by the grass *Imperata cylindrica* more than shrubs or forbs, highlighting the importance of functional group identity for community invasibility. In other cases, increasing functional group richness reduces invasion success (Symstad 2000; Xu et al. 2004), but to our knowledge no studies have assessed the relationship between invasibility and functional diversity by manipulating functional group evenness. We

recognize that functional groupings have utility only to the extent that species within the group use resources similarly, and that functional group classifications have their limitations (Eviner 2004). Nevertheless, we anticipate that broad generalizations regarding community diversity and invasibility are more likely to result from experiments manipulating community composition above the species level, and functional groups provide a valuable tool for doing so.

Although community characteristics that affect invasibility are important determinants of colonization success, many colonizer characteristics, such as population genetic diversity, can also contribute. Introduced species often suffer decreased genetic diversity due to bottlenecks when few individuals from the native range successfully colonize (Tsutsui et al. 2000; Dlugosch and Parker 2008); but, for some invaders, multiple introduction events have led to increased genetic diversity (Hufbauer and Sforza 2008; Prentis et al. 2009; Pairon et al. 2010). Genetic diversity is often positively correlated with phenotypic diversity, and recent studies have shown that increased genetic diversity in plants may impact ecologically meaningful outcomes, including enhancements to arthropod species diversity, net primary productivity, invasion resistance, and ecosystem resilience (Wimp et al. 2004; Reusch et al. 2005; Crutsinger et al. 2006, 2008). Increased genetic diversity may also promote colonization success. For example, multiple introductions of the invasive grass *Phalaris arundinacea* have alleviated genetic bottlenecks, ultimately leading to increased genetic diversity and heritable phenotypic variation in its invasive range relative to its native range (Lavergne and Molofsky 2007). Most studies assessing the effect of multiple introductions on genetic diversity have emphasized similar long-term adaptive benefits, yet increased genetic diversity can also benefit populations within a single generation. This is possible because diverse populations have a greater chance of including "preadapted" genotypes (sampling effects) or combinations of genotypes that partition available niche space particularly well (complementarity) (e.g., Reusch et al. 2005; Crutsinger et al. 2008; Crawford and Whitney 2010). Thus, where multiple introductions occur, high genetic diversity may enhance colonization success within the first generation following introduction.

This experiment jointly examines characteristics of plant communities and colonizers that can affect colonization and invasion success. We conducted a greenhouse experiment using *Arabidopsis thaliana* as a model invasive species, manipulating functional group evenness in the invaded experimental communities and population genetic diversity in *A. thaliana*. For increased realism, we added field-collected soil to all treatments, which let us assess how functional group evenness affected colonization from a diverse seedbank in addition to colonization by *A. thaliana*. We assembled initial plant communities using a robust experimental design that avoids confounding species identity effects with evenness effects, addressing the following three questions:

1. Do community dominance patterns affect community invasibility?
2. Does increased colonizer population genetic diversity enhance colonization success?
3. How important are these factors relative to one another?

Materials and methods

Model invasive species

We chose *A. thaliana* (family Brassicaceae; hereafter *Arabidopsis*) as a model invasive species because of its weedy characteristics (sensu Baker 1974), including its short life cycle, high fecundity, and expansive geographical range (Mitchell-Olds 2001) and because of the availability of worldwide, natural accessions (Table 5 in Appendix). *Arabidopsis* is an established weed in Texas (Nesom 2009), and earlier studies have used it to study invasiveness (Bergelson 1994; Weltzin et al. 2003). Furthermore, previous work has shown that increasing population genetic diversity in *Arabidopsis* monocultures can enhance colonization success and population-level fitness (Crawford and Whitney 2010).

We manipulated *Arabidopsis* population genetic diversity by sowing 1, 4, or 8 genotypes per invaded community. We selected from a large pool of thirty genotypes (Table 5 in Appendix) to avoid the problems of increasing similarity among treatments as diversity increases and the non-independence of replicates within high-diversity treatments (Huston

and McBride 2002). We discarded replicate genotype selections if 4-genotype treatments had more than one genotype in common or if 8-genotype treatments had more than three genotypes in common. Jaccard's similarity was 0.08 within 4-genotype treatments, 0.13 within 8-genotype treatments, and 0.10 between 4- and 8-genotype treatments, falling below norms in recent studies (≈ 0.25 or less: Weltzin et al. 2003; Crawford and Whitney 2010). Across all treatments, we added 96 *Arabidopsis* seeds per community, divided equally among the number of genotypes.

Experimental plant communities

For our experimental communities, we purchased seeds of 72 species representing all species occurring in southeast Texas grasslands that are available commercially within the region (using distribution data from http://plants.usda.gov; see Table 6 in Appendix). We were able to germinate 9 of 30 forbs, 12 of 23 grasses, and 8 of 19 legumes in sufficient numbers to use in the experiment (Table 1), selecting species at random within each functional group so we could assess the effects of evenness on invasibility without the confounding effects of species identity.

We established four community evenness treatments: legume-dominant, forb-dominant, grass-dominant, or equal abundance of the three functional groups. All communities comprised six plants of three species with one randomly selected species per functional group. Equal-abundance communities received two plants per functional group, while all other treatments received four plants from the dominant functional group and one plant from each of the two remaining functional groups. Within each of ten experimental blocks (Table 1), a single three-species community was used for all four community evenness treatments and all three genetic diversity treatments, yielding $n = 120$ pots total.

We established community evenness treatments in the greenhouse by transplanting 3- to 4-week-old plants on Oct 21, 2010 into pots (25.4-cm diameter) containing a mixture of 3.4 L Metro-Mix, 2 L sand, and 0.6 L field soil (sifted to remove rocks and roots). All transplants were approximately the same size at planting time. Field soil was collected from a pasture in Waller, TX (29°57.80′N, 95°55.17′W) dominated by grasses (e.g., *Paspalum notatum*, *Lolium perenne*, and *Cynodon dactylon*) and ruderal forbs (e.g., *Stellaria media*, *Conyza canadensis*, *Rumex* sp., *Plantago* sp., and *Oxalis* sp.). We stratified *Arabidopsis* seeds at 4 °C for 4 days; on November 1, we sowed them on the soil surface after mixing them with c. 20 mL of sand to ensure they were evenly distributed. Temperatures in the greenhouse fluctuated naturally between 60 and 80 °F. To minimize location effects, we re-randomized pot locations in the greenhouse three times. We terminated the experiment on April 12, 2011, when all but three *Arabidopsis* individuals had either died or reached reproductive maturity (99.8 % of emergents).

Data collection

We measured percent cover of all pots on November 16, December 16 and February 8 as a potential predictor of success by *Arabidopsis* and seedbank colonizers. We used a digital camera to take photographs 106 cm above the soil surface. We then

Table 1 Random assignments of forb, grass, and legume species to replicates (blocks)

Block	Forb	Grass	Legume
1	*Monarda citriodora*	*Buchloë dactyloides*	*Dalea candida*
2	*Portulaca oleracea*	*Tripsacum dactyloides*	*Desmanthus illinoensis*
3	*Phlox drummondii*	*Panicum virgatum*	*Indigofera miniata*
4	*Coreopsis tinctoria*	*Leptochloa dubia*	*Desmodium sessilifolium*
5	*Oenothera speciosa*	*Aristida purpurea*	*Lupinus texensis*
6	*Linum rigidum*	*Bouteloua curtipendula*	*Amorpha fruticosa*
7	*Lindheimera texana*	*Sorghastrum nutans*	*Vigna luteola*
8	*Gaillardia pulchella*	*Andropogon gerardii*	*Strophostyles helvola*
9	*Stellaria media*	*Panicum virgatum*	*Amorpha fruticosa*
10	*Monarda citriodora*	*Bouteloua curtipendula*	*Strophostyles helvola*

analyzed the percent area covered by vegetation by means of the green leaf algorithm in VegMeasure2 (Johnson et al. 2003).

We measured colonization success in *Arabidopsis* by tracking individual seedlings throughout the experiment to record seedling emergence and which of those seedlings survived to reproduce. We conducted eleven censuses: November 14, November 18, November 22, November 29, December 7, December 14, December 21, January 13, February 10, March 9, and April 6. At the experiment's termination all aboveground biomass was harvested, sorted to species and dried at 60 °C. Most of the communities were rootbound at experiment's end, making it impossible to separate belowground biomass to species. We quantified biomass of the species we had planted to assess treatment differences in productivity and to quantify actual relative abundances by the end of the experiment using biomass-based evenness. Seedbank colonizers were identified to morphospecies, and we used total colonizer biomass and colonizer species richness to quantify their colonization success. We also used per-morphospecies colonizer biomass to calculate Shannon-Wiener diversity (H'), but because it was highly correlated with species richness ($r = .81$, $p < .001$) and the results of all analyses were similar, we present data on richness only. One biomass sample was misplaced, thus $n = 119$ for analyses on seedbank colonization success.

Data analysis

For all analyses, we considered percent cover, colonizer genetic diversity, and community evenness treatments as fixed effects. We included block as a random effect to gauge the importance of community composition (i.e., variation among each randomly selected set of three species). For each analysis we first assessed whether to retain the random block effect using a likelihood-ratio test (Bolker et al. 2009). We dropped interaction terms (e.g., percent cover × community evenness) unless they were significant, thus they do not appear in most analyses. The probability of reproduction by *Arabidopsis* and species richness of seedbank colonizers were both analyzed by generalized linear models, specifying underlying binomial and Poisson distributions, respectively. To test whether colonizer suppression was significantly higher or lower in equal-abundance communities versus those dominated by a single functional group, we used planned contrasts. Seedling emergence and seedbank colonizer biomass were $\log_{10}$-transformed after adding one to improve normality of residuals, and analyses were conducted assuming an underlying normal distribution. All analyses were conducted using R v 2.13.1 (R Development Core Team 2011) with significance tests based on type 3 sums of squares (using package *car*). Throughout the text, we report mean ± 1 SE.

Results

Community evenness treatments

Community evenness treatments differed soon after planting with percent cover in early November significantly higher for forb-dominated communities than all other treatments (Table 2; $F_{3,116} = 9.53$, $p < .001$). These differences did not persist; percent cover rapidly increased and did not differ among community treatments in mid-December (61.3 % ± 1.4; $F_{3,116} = 0.89$, $p = .45$) or in early February (73.1 % ± 1.3;

Table 2 Means (SE) by community evenness treatments for percent cover (in November) and for community biomass, biomass-based evenness, and the proportion of community biomass made up of forbs (in April, when the experiment was harvested)

Community evenness	Percent cover (%)	Community biomass (g)	Biomass-based evenness	Proportion forb biomass
Equal-abundance	39.07 (3.7)b	52.90 (5.3)ab	0.35 (0.05)a	0.78 (0.05)ab
Forb-dominated	52.59 (4.7)a	61.85 (6.2)a	0.17 (0.04)b	0.86 (0.05)a
Grass-dominated	26.21 (2.5)b	52.60 (6.3)ab	0.29 (0.04)ab	0.78 (0.05)ab
Legume-dominated	34.07 (3.2)b	45.09 (4.9)b	0.39 (0.05)a	0.69 (0.06)b

Means with the same subscript letters do not differ significantly (based on Tukey post hoc tests). Sample sizes are 30 for each community evenness treatment, but for the equal-abundance treatments, $n = 29$ for biomass-based responses due to one misplaced sample. Note that initial, abundance-based evenness of the community evenness treatments were 1.0 for equal-abundance communities and 0.79 for all others; these evenness levels were maintained throughout the experiment

$F_{3,116} = 0.25$, $p = .86$). Despite this similarity in percent cover, by the end of the experiment in early April, total biomass of our communities was significantly higher in forb-dominated than legume-dominated pots (Table 2; $F_{3,116} = 9.0$, $p = .029$), and biomass-based evenness was lowest in pots that were numerically forb-dominated and highest in equal-abundance and legume-dominated communities (Table 2; $F_{3,116} = 4.3$, $p = .007$).

The relatively low biomass-based evenness values we observed at the end of the experiment reflect the fact that most forb species grew quickly to dominate their community treatments, regardless of initial abundances. The single exception to this pattern was that forbs were significantly less dominant (based on biomass) in legume- versus forb-dominated pots (Table 2; Kruskal–Wallis $\chi^2 = 11.3$, $p = 0.010$). Across our community treatments, pots with high percent cover in November had low biomass-based evenness in April (Pearson $r = -0.19$, $p = .043$).

Arabidopsis colonization success

Seedling emergence

Overall emergence of *Arabidopsis* seedlings was low with only 13.3 % of all sown seeds emerging (1,529 of 11,520), and population genetic diversity did not affect emergence (Table 3). *Arabidopsis* seedling emergence in equal-abundance communities did not differ from average seedling emergence across communities dominated by a single functional group (contrasts: $Z = 1.41$, $p = .160$). Emergence was reduced in equal-abundance and forb-dominated communities relative to grass-dominated ones (Table 3;

Fig. 1), and it varied by block, indicating a significant effect of community composition (Table 3; Fig. 4 in Appendix). Contrary to expectations, *Arabidopsis* emergence increased in pots with greater percent cover in November ($\beta = 0.006 \pm 0.002$), suggesting that even in our relatively benign greenhouse conditions, *Arabidopsis* seedlings may have experienced net facilitation (via 'nurse plant' effects) at the earliest stages of colonization.

Arabidopsis reproduction probabilities

Of our 120 experimental communities, 18 had at least one reproductive *Arabidopsis* individual during the course of the experiment. The probability of reproducing was unaffected by *Arabidopsis* population genetic diversity (Table 3). In comparison to the
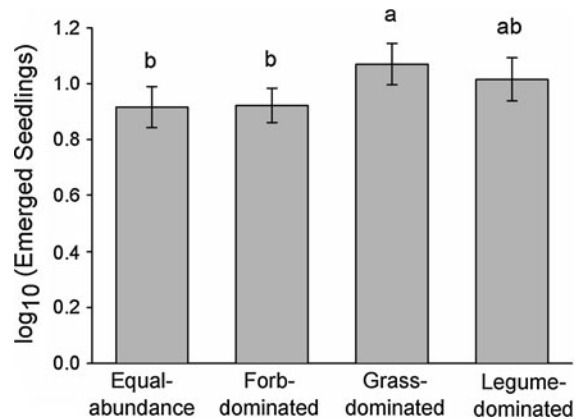

Fig. 1 Community evenness treatments significantly affected *Arabidopsis* seedling emergence. Treatments not sharing a letter have significantly different numbers of emergent seedlings (based on Tukey post hoc tests). *Error bars* ±1 SE

Table 3 Effects of community evenness treatments and genetic diversity on *Arabidopsis* colonization success (seedling emergence and the probability of reproduction)

Source	df	Emergence		Pr (reproduction)		
		χ^2	P	χ^2	F	P
Community evenness	3	12.24	0.007	–	4.94	0.003
Genetic diversity	2	0.87	0.648	–	0.30	0.743
November percent cover	1	9.87	0.002	–	47.07	<0.001
Block[a]	1	9.11	0.002	0.05	–	0.820

Significant effects of community composition on *Arabidopsis* colonization are indicated by a significant block term

[a] Significance of the random block effect was assessed by log-likelihood tests; when the fixed-effects model fit better, block was dropped from the final model

average response across communities dominated by a single functional group, the likelihood of *Arabidopsis* reproduction was only marginally lower in equal-abundance communities (contrasts: $Z = 1.87$, $p = .062$). The probability of reproducing did vary among community evenness treatments (Table 3); *Arabidopsis* reproduction was less likely in equal-abundance (3.3 % of 30 pots) versus legume-dominated communities (26.7 %), with forb- and grass-dominated communities showing intermediate probabilities (13.3 and 16.7 %, respectively). The probability of *Arabidopsis* reproduction was unaffected by community composition (the block effect) and was highest in pots that had low percent cover in November ($\beta = -0.09 \pm 0.02$; Table 3).

Seedbank colonizer success

Seedbank colonizer presence and biomass

Seedbank colonizers were present in 111 of 119 communities (93.3 %). Colonizer biomass in equal-abundance communities was marginally lower than biomass averaged across communities dominated by a single functional group (contrasts: $Z = 1.80$, $p = .071$). The combined biomass of all seedbank colonizers was significantly lower in forb-dominated than legume-dominated communities (Table 4; Fig. 2a). Colonizer biomass in equal-abundance and grass-dominated pots was intermediate, being marginally lower in equal-abundance communities than legume-dominated ones ($p = .065$) and marginally lower in forb-dominated than grass-dominated ones ($p = .096$, based on Tukey post hoc tests; see Fig. 2a). Colonizer biomass was not affected by November percent cover, and it was only marginally affected by community composition (Table 4; Fig. 4 in Appendix).

Seedbank colonizer richness

We identified 24 seedbank colonizer morphospecies with richness ranging from zero to eight in individual communities. Colonizer richness in equal-abundance communities did not differ from average richness across the other communities (contrasts: $Z = -0.23$, $p = .327$). Colonizer richness declined in response to increasing cover in November, but only in equal-abundance and forb-dominated communities (Figs. 2b, 3a; Table 4). Community composition also significantly affected colonizer richness (Table 4; Fig. 4 in Appendix).

To further explore the significant interaction between community evenness treatments and November cover, we conducted a similar analysis using the combined biomass of our planted species at the end of the experiment as a predictor instead of November cover. This analysis was meant to help assess the effect of observed differences in growth phenology among functional groups. Colonizer richness declined marginally in response to increasing community biomass, and this pattern did not differ across community treatments (Fig. 3b; community × biomass: $\chi^2 = 1.69$, $p = .64$; community: $\chi^2 = 0.07$, $p = .99$; biomass: $\chi^2 = 3.42$, $p = .064$; block: $\chi^2 = 171$, $p < .001$), suggesting that although colonizer richness responded differently to November cover across our community treatments, the richness response to community biomass later in the experiment was uniform.

Discussion

In our experiment, characteristics of invaded communities were significantly more important determinants of colonization success than was genetic diversity of

Table 4 Effects of community evenness treatments on non-*Arabidopsis* seedbank colonizer success (total biomass and colonizer richness)

Source	df	Biomass		Richness	
		χ^2	P	χ^2	P
Community evenness	3	10.72	0.013	1.57	0.670
November percent cover	1	0.57	0.450	1.56	<0.001
Community × cover	3	–	–	9.62	0.020
Block[a]	1	3.00	0.080	171.0	<0.001

Significant effects of community composition on seedbank colonization are indicated by a significant block term

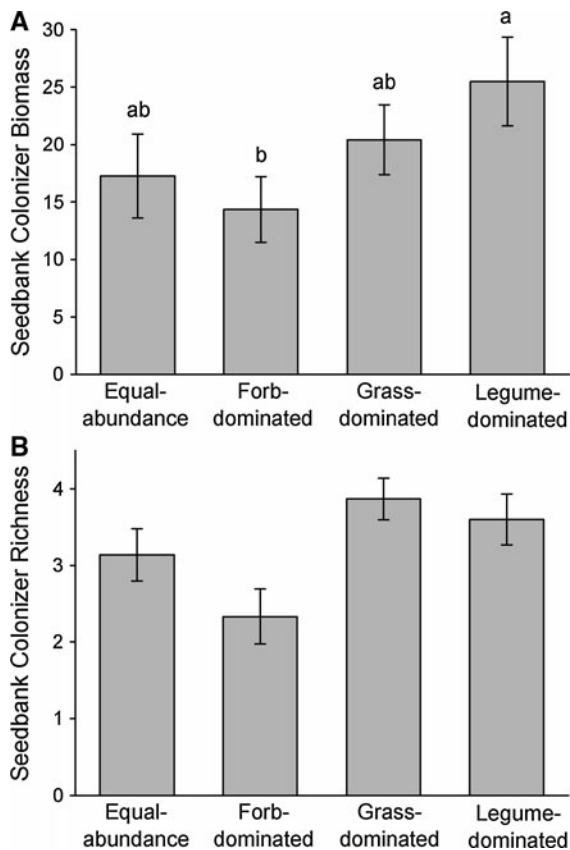[a] Significance of the random block effect was assessed by log-likelihood tests

Fig. 2 A Non-*Arabidopsis* seedbank colonizer biomass differed among community evenness treatments. Treatments not sharing a letter had significantly different amounts of colonizer biomass (based on Tukey post hoc tests). **B** Non-*Arabidopsis* seedbank colonizer richness did not differ among community evenness treatments. *Error bars* ±1 SE

the colonizer. Although suppression of both *Arabidopsis* and seedbank colonizers was greatest in forb-dominated and equal-abundance communities, high-evenness communities did not consistently suppress colonizers more than low-evenness communities. Our findings indicate that functional group differences, perhaps in growth phenology and plant architecture, were the ultimate drivers of invasibility in our system.

Effect of functional group evenness

Our equal-abundance treatments were among the best at suppressing colonization by both *Arabidopsis* and seedbank colonizers, in partial support of earlier findings (Wilsey and Polley 2002; Tracy and Sanderson 2004). However, contrary to the expectation that evenness and colonizer suppression will be positively

correlated, planned contrasts did not indicate consistently greater invasion in communities dominated by a single functional group relative to equal-abundance communities. In addition, our equal-abundance and forb-dominated communities were highly productive, producing similar proportions of forb biomass and having similar effects on colonization by *Arabidopsis* and seedbank colonizers. In this way, our results are not fully consistent with previous findings (Wilsey and Polley 2002; Tracy and Sanderson 2004), instead pointing to forbs as the most productive functional group and thus the one that most suppresses colonization.

Given that many of our grasses commonly occur as dominant species and that grasses in general are often highly competitive (D'Antonio and Vitousek 1992), we were surprised that our grass-dominated communities were highly invasible. Because *Arabidopsis* (a forb) was least successful in colonizing forb-dominated communities, our results may reflect an influence of limiting similarity (Strauss et al. 2006); however, our experiment was not designed to test this hypothesis explicitly (i.e., we did not also add legume and grass colonizers). Instead, our findings suggest that increased colonizer success in grass-dominated communities resulted from relatively slow growth by many of our grass species. Grass-dominated communities thus had less cover in November and were quickly overgrown by neighboring forbs, but not before *Arabidopsis* colonizers were able to establish themselves (see Table 2).

Functional group differences in growth phenology may have been a critical factor underlying differential colonizer suppression among our community treatments. Many of our forbs were relatively fast growing when compared to the legumes and grasses we planted, which led to forbs making up a large percentage of total community biomass by the end of the experiment in most of our treatments. Rapid growth by forbs may also explain why increased cover early in the experiment was associated with decreased seedbank colonizer richness only in equal-abundance and forb-dominated communities (Fig. 3a). Although equal-abundance pots received half the number of forbs that our forb-dominated pots did (two versus four), in many cases two mature plants were sufficient to usurp much of the space available within a single pot (E.D.G and S.M.H., personal observation). Because equal-abundance and forb-dominated

Fig. 3 Community evenness treatments differed in how they suppressed non-*Arabidopsis* seedbank colonizer richness. Seedbank colonizer richness **a** declined with increasing November cover only in equal-abundance and forb-dominated communities (a significant community × cover interaction), but **b** declined with increasing April biomass in all community types
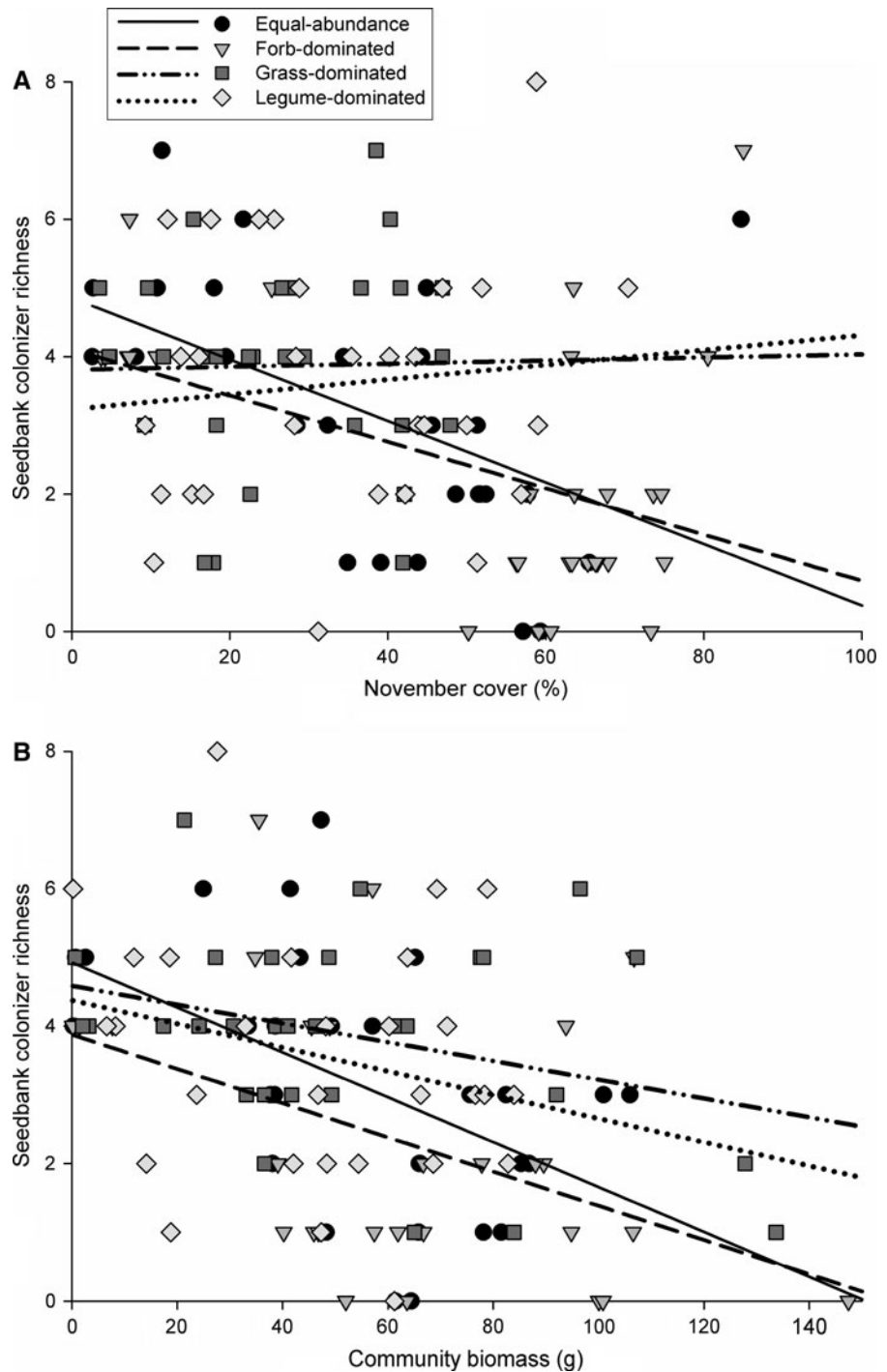
communities both experienced rapid canopy closure and biomass accumulation, colonizer seedlings had shorter windows of opportunity early in the experiment to emerge from the soil in those treatments. In field settings, similar dynamics could limit invasion success in communities with an abundance of fast-growing species although this will also depend on the timing of propagule arrival. The importance of timing

for colonization success (invasion phenology) has gained substantial attention recently (DeFalco et al. 2007; Wolkovich and Cleland 2011; Wainwright et al. 2012) and even minor differences in the timing of growth among invaded communities may be particularly important for colonizers at the earliest life history stages.

In addition to phenological differences, functional group differences in plant architecture could have contributed to our findings. For grass- and legume-dominated treatments, mean cover in November was lower than in forb-dominated treatments, and even the pots with relatively high percent cover seemed not to suppress seedbank colonization substantially. This latter pattern may reflect the fact that our largest grasses and legumes distributed much of their biomass vertically, whereas many of our forbs either produced large rosettes (e.g., *Rudbeckia hirta* and *Coreopsis tinctoria*), or spread by creeping growth that was relatively close to the soil (e.g., *Portulaca oleracea* and *Monarda citriodora*). Thus, in pots dominated by forbs (including equal-abundance treatments), light availability at the soil surface was probably more limiting than it was in grass- and legume-dominated treatments, even when estimates of percent cover were similar.

Insights from the evenness manipulations

Our method of manipulating evenness has two main strengths over the approaches that are commonly used to address hypotheses regarding invasion resistance and colonizer suppression. First, by assembling replicate communities at random from a large species pool, we avoid confounding the effect of community dominance (low evenness) with identity of the dominant species. The identities of species comprising a given community do matter, as shown by significant block effects in our analyses and similar results elsewhere (e.g., Symstad 2000; Emery and Gross 2007). And, although confounding the effects of species identity with effects of evenness may not change predictions in systems that are often dominated by the same species (e.g., aspen in northern forests), our approach should yield inferences that apply across grasslands where different species dominate in different local communities. Second, by holding species richness constant across our community treatments, we were able to focus only on the role of relative

abundance in our experimental system. Species richness is an important determinant of invasibility (Tilman 2004; Fargione and Tilman 2005; Scherber et al. 2010); however, if relative abundances are much more variable than species richness (Stirling and Wilsey 2001), then a deeper understanding of invasibility may ultimately require a deeper understanding of community evenness.

Although our greenhouse experiment lacks the realism of a field-based study, community composition in our treatments does resemble grasslands in the early stages of secondary succession, which can experience a similar degree of dominance by forbs (Collins and Adams 1983; Huberty et al. 1998). In these transitional communities, grasses increase in abundance and often dominate within only a few years. Our findings thus suggest that although colonization success may be limited in early-successional, forb-dominated communities, temporal changes in grassland community composition may provide invasion opportunities for newly arriving colonizers and those already present in the seedbank, perhaps via altered patterns of resource availability (Tilman 2004).

Effect of colonizer genetic diversity

Population genetic diversity did not affect colonization success in our *Arabidopsis* populations (see also Vellend et al. 2010; Craig et al. 2011), particularly relative to the strong effects of our community evenness treatment. Our findings contrast with previous experiments that reported significant genetic diversity effects in populations of *Solidago altissima* (Crutsinger et al. 2008), *Zostera marina* (Reusch et al. 2005), and *Populus* spp. (Wimp et al. 2004). One key difference is that, in contrast to *Arabidopsis*, these species are all community dominants which naturally achieve high densities and relative abundances during which intraspecific interactions may be much more important than interspecific ones (Whitham et al. 2006). Similarly, a previous greenhouse experiment with *Arabidopsis* used monoculture populations that therefore experienced only intraspecific interactions (Crawford and Whitney 2010), and it also found significant genetic diversity effects on colonization and establishment success. In contrast, in our study, we added *Arabidopsis* to communities with relatively large, fast-growing plants, and its low seedling emergence and high pre-flowering mortality led to

low *Arabidopsis* relative abundances. Owing to these high levels of interspecific relative to intraspecific interactions, our experimental design may have been unlikely to uncover effects of genetic diversity on colonization success, particularly in a ruderal species such as *Arabidopsis* that is most likely to be successful in disturbed, open habitats. Thus, we predict that increased colonizer genetic diversity is most likely to enhance the short-term establishment success of introduced species when the relative strength of interspecific interactions is reduced (e.g., via natural or anthropogenic disturbance) and when colonizers are introduced at high densities.

Conclusions

Forb-dominated communities developed higher percent cover than grass- and legume-dominated communities early in the experiment, resulting in stronger negative effects on colonization by both *Arabidopsis* and seedbank colonizers. Equal-abundance communities were similar in composition and invasibility to forb-dominated communities, but our analyses strongly suggest that dominance by forbs was more important for suppressing colonization than was increased evenness. The significant effects of community composition we found highlight the importance of species-specific variation in suppressing colonizers; however, our experimental design also makes it possible to infer how functional groups differ in invasibility, thereby maximizing generality in our understanding of biological invasions. Further investigations of invasion phenology relative to the growth phenology of dominant species may yield additional insights regarding the dynamics underlying successful invasions. In contrast to the importance of these community characteristics, *Arabidopsis'* population genetic diversity did not affect colonization success, perhaps reflecting the low intraspecific densities and therefore relatively weak intraspecific interactions *Arabidopsis* would have experienced in our experiment.

Appendix

See Tables 5, 6 and Fig. 4.

Table 5 *Arabidopsis thaliana* accessions used as the source pool for genetic diversity treatments

ABRC stock number	Name	Country
CS6643	Burren	Ireland
CS6660	Canary Islands	Spain
CS6673	Columbia	USA
CS6674	Catania	Italy
CS6736	Hilversum	Netherlands
CS6792	Mühlen	Poland
CS6805	Nossen	Germany
CS6839	Poppelsdorf	Germany
CS6850	Rschew	Russia
CS6857	San Feliu	Spain
CS6874	Tsu	Japan
CS6889	Wilna	Russia
CS6891	Wassilewskija	Russia
CS6897	Wü	Germany
CS6902	Zurich	Switzerland
CS6669	Coimbra	Portugal
CS28198	Cape Verde Islands	Cape Verdi
CS6699	Espoo	Finland
CS6799	Martuba	Libya
CS28578	New Zealand	New Zealand
CS6751	Kashmir	India
CS6680	Dijon	France
CS6811	Neuweilnau	Germany
CS6927	Rschew	Russia
CS6846	Raksice	Czech
CS6849	Richmond	Canada
CS6872	Tossa de Mar	Spain
CS6877	Turk Lake	Republic USA
CS6884	Vancouver	Canada
CS8142	Hartford	USA

Source Arabidopsis Biological Resource Center, Columbus, OH, USA

Table 6 Original set of species obtained for the experimental community evenness treatments

Species	Family	Functional group	Source	Pre-treatment	Seed germ[a]	Plug survival[a]	Used in exp
Coreopsis tinctoria	Asteraceae	Forb	Native American Seed	Stratification	H	M	Yes
Gaillardia pulchella	Asteraceae	Forb	Native American Seed	None	M	M	Yes
Lindheimera texana	Asteraceae	Forb	Native American Seed	None	H	H	Yes
Linum rigidum	Linaceae	Forb	Native American Seed	None	H	M	Yes
Monarda citriodora	Lamiaceae	Forb	Native American Seed	Stratification	H	H	Yes
Oenothera speciosa	Onagraceae	Forb	Native American Seed	Stratification	H	M	Yes
Phlox drummondii	Polemoniaceae	Forb	Native American Seed	Stratification	H	H	Yes
Portulaca oleracea	Portulacaceae	Forb	Native American Seed	None	H	H	Yes
Stellaria media	Caryophyllaceae	Forb	Sand Mountain Herbs	None	M	M	Yes
Agalinis heterophylla	Scrophulariaceae	Forb	Native American Seed	None	L	L	No
Amblyolepis setigera	Asteraceae	Forb	Native American Seed	None	M	L	No
Argemone albiflora	Papaveraceae	Forb	Native American Seed	Stratification	L	L	No
Callirhoe involucrata	Malvaceae	Forb	Native American Seed	Stratification	L	L	No
Centaurea americana	Asteraceae	Forb	Native American Seed	Scarification	L	L	No
Corydalis curvisiliqua	Fumariaceae	Forb	Native American Seed	Stratification	L	L	No
Dracopis amplexicaulis	Asteraceae	Forb	Native American Seed	None	H	M	No
Eryngium leavenworthii	Apiaceae	Forb	Native American Seed	Hot water bath; Stratification	L	L	No
Helianthus annuus	Asteraceae	Forb	Collected in wild	Stratification; Dark	M	M	No
Liatris pycnostachya	Asteraceae	Forb	Native American Seed	Stratification	L	L	No
Machaeranthera tanacetifolia	Asteraceae	Forb	Native American Seed	Stratification	L	L	No
Polanisia dodecandra	Capparaceae	Forb	Native American Seed	None	L	L	No
Proboscidea louisianica	Pedaliaceae	Forb	Native American Seed	Stratification; Scarification	L	L	No
Rudbeckia hirta	Asteraceae	Forb	Native American Seed	None	M	M	No
Thelesperma filifolium	Asteraceae	Forb	Native American Seed	Stratification	L	L	No
Verbesina enceliodes	Asteraceae	Forb	Native American Seed	None	L	L	No
Andropogon gerardii	Poaceae	Grass	Native American Seed	None	M	M	Yes
Aristida purpurea	Poaceae	Grass	Native American Seed	None	H	H	Yes
Bouteloua curtipendula	Poaceae	Grass	Native American Seed	None	H	M	Yes
Buchloe dactyloides	Poaceae	Grass	Native American Seed	None	M	M	Yes
Leptochloa dubia	Poaceae	Grass	Native American Seed	None	H	M	Yes

Table 6 continued

Species	Family	Functional group	Source	Pre-treatment	Seed germ[a]	Plug survival[a]	Used in exp
Panicum virgatum	Poaceae	Grass	Native American Seed	None	M	M	Yes
Sorghastrum nutans	Poaceae	Grass	Native American Seed	None	M	M	Yes
Tripsacum dactyloides	Poaceae	Grass	Native American Seed	None	M	M	Yes
Andropogon glomeratus	Poaceae	Grass	Native American Seed	Stratification	L	L	No
Bothriochloa barbinodis	Poaceae	Grass	Native American Seed	Stratification	M	L	No
Chasmanthium latifolium	Poaceae	Grass	Native American Seed	None	L	L	No
Elymus canadensis	Poaceae	Grass	Native American Seed	None	L	L	No
Eragrostis trichodes	Poaceae	Grass	Native American Seed	Stratification	L	L	No
Eriochloa sericea	Poaceae	Grass	Native American Seed	Stratification	M	M	No
Hesperostipa neomexicana	Poaceae	Grass	Native American Seed	Stratification	L	L	No
Hilaria belangeri	Poaceae	Grass	Native American Seed	None	M	L	No
Pascopyrum smithii	Poaceae	Grass	Native American Seed	None	L	L	No
Pleuraphis jamesii	Poaceae	Grass	Native American Seed	None	H	M	No
Schizachyrium scoparium	Poaceae	Grass	Native American Seed	None	L	L	No
Secale cereale	Poaceae	Grass	Native American Seed	Stratification	H	H	No
Setaria macrostachya	Poaceae	Grass	Native American Seed	Stratification	L	L	No
Sporobolus cryptandrus	Poaceae	Grass	Native American Seed	Stratification	H	L	No
Tridens flavus	Poaceae	Grass	Native American Seed	Stratification	M	M	No
Amorpha fruticosa	Fabaceae	Legume	Everwilde Farms	Stratification	H	H	Yes
Dalea candida	Fabaceae	Legume	Native American Seed	None	H	M	Yes
Desmanthus illinoensis	Fabaceae	Legume	Native American Seed	Stratification	H	H	Yes
Desmodium sessilifolium	Fabaceae	Legume	Everwilde Farms	None	M	M	Yes
Indigofera miniata	Fabaceae	Legume	USDA-ARS GRIN	Stratification	M	M	Yes
Lupinus texensis	Fabaceae	Legume	Native American Seed	Scarification	H	M	Yes
Strophostyles helvola	Fabaceae	Legume	USDA-ARS GRIN	Stratification; Scarification	H	H	Yes
Vigna luteola	Fabaceae	Legume	USDA-ARS GRIN	Scarification	H	H	Yes
Amorpha canescens	Fabaceae	Legume	Wildflower Farm	Stratification	L	L	No
Astragalus canadensis	Fabaceae	Legume	Native American Seed	Stratification	L	L	No
Astragalus leptocarpus	Fabaceae	Legume	USDA-ARS GRIN	Stratification	M	L	No
Baptisia alba	Fabaceae	Legume	Everwilde Farms	Stratification	L	L	No
Cassia roemeriana	Fabaceae	Legume	Native American Seed	Stratification	L	L	No
Centrosema fasciculata	Fabaceae	Legume	Butterfly Ginger (ebay purchase)	Stratification	L	L	No

Table 6 continued

Species	Family	Functional group	Source	Pre-treatment	Seed germ[a]	Plug survival[a]	Used in exp
Chamaecrista fasciculata	Fabaceae	Legume	Everwilde Farms	None	L	L	No
Dalea purpurea	Fabaceae	Legume	Native American Seed	None	M	M	No
Mimosa nutallii	Fabaceae	Legume	Speciality Perennials	Hot water bath	M	M	No
Sesbania vesicaria	Fabaceae	Legume	www.onaleeseeds.com	Scarification	M	M	No
Trifolium carolinianum	Fabaceae	Legume	USDA-ARS GRIN	Stratification	M	L	No

Species were only used in the experiment if germination and plug survival post-transplanting yielded enough plants to be used in a full experimental block

[a] Qualitative assessments of seed germination and plug survival (L low, M medium, H high)
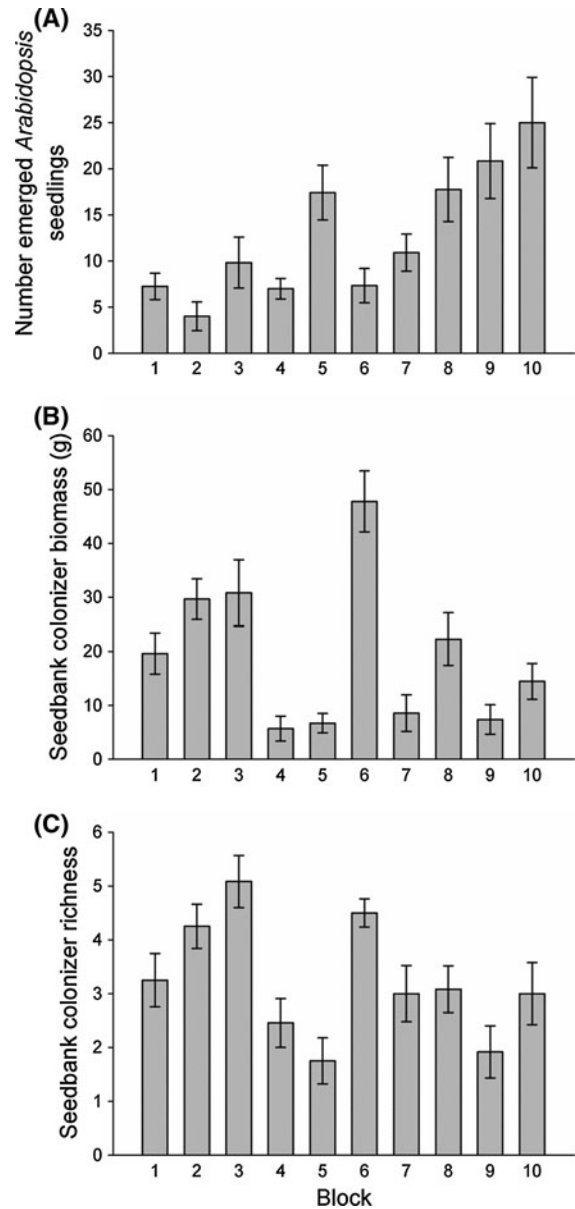

Fig. 4 Colonizer success varied in response to community composition (significant block effects), based on **a** *Arabidopsis* emergence, **b** non-*Arabidopsis* seedbank colonizer biomass and **c** non-*Arabidopsis* seedbank colonizer richness. *Error bars* ±1 SE

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