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Source: *The American Naturalist*, Vol. 178, No. 4 (October 2011), pp. 464-477
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/10.1086/661900
Accessed: 28/08/2013 13:24

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VOL. 178, NO. 4 THE AMERICAN NATURALIST OCTOBER 2011

# Seed Supply, Recruitment, and Assembly: Quantifying Relative Seed and Establishment Limitation in a Plant Community Context

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*Submitted October 26, 2010; Accepted April 24, 2011; Electronically published August 24, 2011*

*Dryad data:* http://dx.doi.org/10.5061/dryad.9127.

ABSTRACT: There is a growing consensus that the relative constraints of seed limitation and establishment limitation in recruitment strongly influence abundance patterns in plant communities. Although these constraints have direct relevance to coexistence, most investigations utilize a seed addition approach that offers limited insight into these dynamics. Here we report the results of an assembly experiment with annual plant species from California grasslands to examine how propagule pool characteristics (dominant species abundance, functional diversity) influence establishment and seed limitation (density independence and density dependence across a gradient of seed supply) for each species, as well as how these constraints affect community diversity. Species were predominantly colimited by seed and establishment constraints, exhibiting saturating recruitment functions with increased seed supply. Consistent with competition-colonization trade-off predictions, recruitment constraints often depended on the degree of seed limitation of the competitive dominant, *Brassica nigra*; diversity was greatest in communities where *Brassica* was seed limited. Functional similarity within the propagule pool did not affect recruitment across a range of seed supply; likewise, functional diversity of the propagule pool was not related to community diversity. We conclude that seed limitation of the dominant species rather than niche similarity influences interspecific competition for safe sites and scales up to affect community-level diversity.

*Keywords:* seed addition, safe-site availability, density dependence, community assembly, niche overlap, competition-colonization trade-off.

## Introduction

Identifying mechanisms that determine the abundance of populations in plant and animal communities is a major question in ecology (Samuels and Drake 1997; Belyea and Lancaster 1999; Rees et al. 2001; Chase 2003). Seedling recruitment is an important determinant of plant population dynamics and community species richness (Tilman 1993; Weiher and Keddy 1999). In particular, there is growing consensus that the relative constraints of seed limitation and establishment limitation in recruitment strongly influence abundance patterns (Grubb 1977; Eriksson and Ehrlen 1992; Tilman 1997; Grime 2006; Emery et al. 2009). Populations can be described on a continuum from being seed limited, where the rate of seed supply is low relative to the availability of suitable microsites (or safe sites, after Harper 1977), to being establishment limited, where the rate of seed supply is sufficient to ensure that all suitable microsites are occupied and a combination of density-independent and density-dependent factors constrain recruitment.

Coexistence models differ in their predictions concerning how seed and establishment limitation influence interspecific interactions and scale up to influence diversity. For instance, if establishment were to follow a strict dominance hierarchy, coexistence would occur when the dominant species is largely seed limited; other species can establish in safe sites that the dominant species is not able to colonize because of a trade-off between competition and colonization (Shmida and Ellner 1984; Tilman 1994). Additionally, in niche overlap models, establishment limitation would be greatest among species that share similar safe-site requirements; coexistence would occur among species with low functional overlap, with diversity related to functional diversity in propagule pools (MacArthur and Levins 1967). Alternatively, in neutral-lottery models, recruitment is a function of a species' representation in the propagule pool; species share similar constraints on establishment (Chesson and Warner 1981).

Despite considerable theoretical work, tests of these pre-

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Am. Nat. 2011. Vol. 178, pp. 464–477. © 2011 by The University of Chicago. 0003-0147/2011/17804-52581$15.00. All rights reserved.
DOI: 10.1086/661900

dictions are surprisingly rare (Mouquet et al. 2004; Turnbull et al. 2004, 2005; Harrison et al. 2010), as it is difficult to quantify how variation in seed and establishment limitation among species affect interspecific interactions and ultimately influence community-level diversity. The most common approach to test whether populations are seed limited is to conduct seed addition experiments. While this method confirms the presence of seed limitation (Turnbull et al. 2000; Clark et al. 2007) and demonstrates that seed limitation can constrain diversity (Zobel et al. 2000; Foster et al. 2007; MacDougall et al. 2008; Myers and Harms 2009*b*), coexistence predictions rely on variation in the relative constraints of seed limitation and establishment limitation across populations. Only a handful of studies have described how the strength of seed and establishment limitation changes with multiple levels of seed input and thus are able to quantify the shape of a species recruitment function (Clark et al. 2007; Poulsen et al. 2007; Duncan et al. 2009; Munshaw and Lortie 2010). Moreover, no study has used this approach for multiple species to test how species interactions influence relative seed and establishment limitation, an important component of coexistence model predictions.

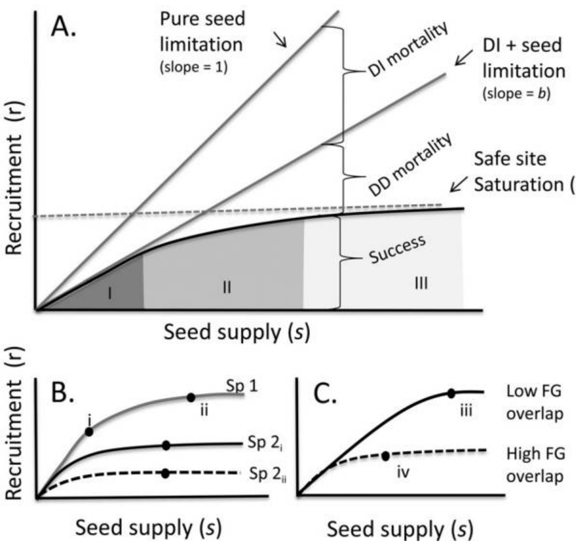

**Figure 1:** Interpretation of seed and establishment limitation based on recruitment functions (after Poulsen et al. 2007). *A*, Measurements of recruitment at several levels of seed supply allow the quantification of a recruitment function. A linear relationship with a slope of 1 would indicate pure seed limitation. Most often density-independent (DI) factors affect recruitment, reducing the slope of the relationship to $b$ (where $1 - b$ indicates DI mortality). A slope of 0 would indicate pure establishment limitation. A saturating recruitment function can be broken up into three regions: region I (slope $= b$), where a combination of seed and DI limits recruitment; region II, where intraspecific density dependence (DD) also arises (slope = between $b$ and 0), leading to colimitation by seed supply, DI, and DD factors; and region III, where seed supply saturates due to microsite limitation (when $s > n$, slope $= 0$ at $bn$), leading to limitation by DI and DD factors (pure establishment limitation). *B*, Example of how a competitive dominant may influence recruitment functions of other species in the community. At point *i*, species 1, the competitive dominant, is more seed limited than the less competitive species, species 2. However, it experiences less establishment limitation due to DI factors ($b_1 > b_2$). As species 1 shifts from being seed limited to purely establishment limited (from point *i* to point *ii*), species 2 is expected to experience more DI mortality, which is reflected in a reduction in $b$ as well as in the point where it reaches safe site saturation, $bn$. *C*, Example of how niche partitioning among functional groups (FGs) may decrease the intensity of interspecific competition and allow enhanced recruitment. DI factors are expected to be less intense (i.e., greater $b$) in communities where the propagule pool has low FG overlap (e.g., different safe-site requirements among species) than when there is higher overlap. Species would experience pure establishment limitation at lower levels of seed supply (point *iii* vs. point *iv*) in communities with higher overlap.

Species can be expected to differ in the relative degree of seed and establishment limitation they experience across a gradient of seed supply (Eriksson and Ehrlen 1992; Pywell et al. 2002; Tofts and Silvertown 2002; Zeiter et al. 2006); these differences should be reflected in their recruitment functions. For a given species population, pure seed limitation would occur if seed supply translates to seedling recruitment (i.e., a 1 : 1 relationship; fig. 1*A*); few studies, if any, have documented pure seed limitation. The number of suitable microsites can be influenced by how species respond to density-independent factors such as germination stimuli and stressors such as temperature, herbivory, and drought (Coomes and Grubb 2003; Baraloto et al. 2005); these factors should diminish the number of recruits per seed supply (i.e., a shallower slope; fig. 1*A*). For species that share potential safe sites with other species, density-independent limitation can be influenced by interspecific competition for suitable microsites (Turnbull et al. 2005; Myers and Harms 2009*a*); thus, increased interspecific competition should also contribute to a shallower slope of the recruitment function. Note that in this framework, "density dependence" refers to intraspecific density dependence and "density independence" includes factors relating to interspecific interactions. The region of density-independent establishment limitation combined with seed limitation can extend across the seed supply gradient (a linear function across the range tested) or, as seed supply increases, intraspecific density-dependent factors can further decrease microsite availability for a species, intensifying establishment limitation and causing curvature toward saturation (Herrera and Laterra 2009; from region I to region II in fig. 1*A*). At very high levels of seed supply, strong density dependence combined with density independence can cause populations to be solely establishment limited (a saturating function; region III in fig. 1A).

By viewing seed and establishment limitation as a continuum in community assembly, we provide one of the most direct tests to date of theoretical predictions concerning how dispersal and establishment constraints vary among species to influence species coexistence. On the basis of model predictions, in communities with a strict dominance hierarchy, dominant species should have relatively low density-independent mortality because of their superior ability to compete with other species for safe sites (i.e., have steep recruitment functions at low levels of seed supply; fig. 1*B*). In this case, coexistence should occur if there is a trade-off between competitive ability and colonization ability: when the dominant species is largely seed limited (e.g., at point *i*), it cannot exclude other, less seed-limited species from all safe sites (such as species 2 in fig. 1*B*; Tilman 1994; Turnbull et al. 2004). As seed supply of the dominant increases (e.g., to point *ii*), its establishment limitation should intensify and increase competitive effects on other species (e.g., increase density-independent mortality for species 2; fig. 1*B*). Alternatively, niche-based models predict that low overlap in safe-site requirements, relating to either environmental heterogeneity or resource partitioning, would decrease density-independent mortality (e.g., steeper slope; fig. 1*C*). In this case, coexistence should occur when the propagule pool is composed of functionally diverse species (Myers and Harms 2009*b*; Petermann et al. 2010). Finally, lottery models predict that all species share a recruitment function; establishment is largely a function of seed supply. In this case, coexistence would be maximized when seed supply rates of all species are equivalent (Mouquet et al. 2004).

Here we report the results of an assembly experiment aimed at simultaneously quantifying the recruitment functions of 12 annual plant species representative of annual grassland communities in California. In this community, seed size varies greatly, with many small-seeded species and a few large-seeded species (a common seed size distribution in plant communities; Westoby et al. 1992; Maranon and Grubb 1993; Rees 1995). Keeping total seed input constant, we created 135 experimental communities by manipulating the relative input of seed from each species, where the seed supply of any given species varied independently from the rest of the propagule pool. This approach allowed us to quantify the intensity of density independence, density dependence, and seed limitation over a large range of seed supply, as well as to examine how interspecific propagule pool characteristics (e.g., functional group overlap, abundance of dominant species) influenced these constraints. We test several predictions relating to how variation in these constraints influences coexistence. First, across a gradient of seed supply, species establishment limitation will increase as seed limitation of the dominant competitor decreases (dominance hierarchy prediction). In this case, diversity will be highest in communities where the competitive dominant is strongly seed limited. Second, species establishment limitation will increase with increased functional overlap in the propagule pool (niche overlap prediction); functional diversity in the propagule pool would lead to the greatest diversity in the established plant community. Alternatively, species will experience similar establishment limitations regardless of propagule pool composition (lottery model predictions); relative seed supply would govern establishment and diversity would be similar across communities.

## Material and Methods

### *Study Site and Species*

We conducted our study in a common garden at the arboretum of the University of California, Irvine, in Orange County, California (33°39′N, 117°51′W). Although we used 12 herbaceous annual species common to California grassland systems (table 1), two *Vulpia* species were combined because we were not able to consistently identify nonflowering individuals to species (thus, we refer to 11 species in our analysis although this section reflects 12). We refer to species by genus.

California grasslands are characterized by a Mediterranean climate, where the growing season occurs during the winter rainfall period and ends before summer (December through June). At our site, average annual rainfall is 325 mm, with average temperatures during the growing season ranging from 6.2° to 23°C (National Oceanic and Atmospheric Administration [NOAA], Laguna Beach Station; data from 1928 to 2006). In 2006, the year in which we conducted this experiment, the rainfall and temperatures were within the average range for that time period (NOAA, Laguna Beach Station).

### *Experimental Design*

To estimate recruitment functions for the species, we established experimental communities in which we varied the seed input of each species, ensuring a gradient of seed supply for each species as well as different propagule pool characteristics (e.g., functional group abundance, dominant species abundance) at a given seed supply rate. We added the same 12 species as seed to each experimental plot, with a consistent total seed input (10 g $m^{-2}$). This level of seed input ensured naturally realistic densities of adults at the community level. Our rationale for keeping total seed input mass constant was to keep overall density within a community relatively constant, as is often found in natural communities, and instead vary the relative densities of different species.

We varied seed supply by randomly assigning species to

**Table 1:** Influence of interspecific competitive environment on parameter estimates of recruitment functions for each species

| | | Low competitive environment | | | | High competitive environment | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Model | Fit | $b$ | $n$ | $r^2$ | Fit | $b$ | $n$ | $r^2$ | AIC$_{\mathrm{d}}$ |
| *Avena fatua* | None | Skellam | .110 | 44.5 | .04 | Same | | | | |
| *Brassica nigra* | None | Skellam | .253 | 733 | .43 | Same | | | | |
| *Bromus hordeaceus* | Dominant | Skellam | .098 | 1,285 | .48 | Skellam | .079 | 539 | .48 | 20.3 |
| *B. hordeaceus* | Niche | Skellam | .095 | 532 | .41 | Linear | .073 | ... | .57 | 21.4 |
| *Erodium cicutarium* | None | Skellam | .007 | 1,946 | .49 | Same | | | | |
| *Eschscholzia californica* | Dominant | Skellam | .032 | 2,285 | .63 | Skellam | .017 | 3,147 | .46 | 31.3 |
| *E. californica* | Niche | Skellam | .028 | 2,325 | .65 | Skellam | .025 | 827 | .22 | 19.2 |
| *Lasthenia californica* | None | Linear | .011 | ... | .55 | Same | | | | |
| *Lotus purshianus* | None | Linear | .004 | ... | .18 | Same | | | | |
| *Lupinus succulentus* | Dominant | Linear | .018 | ... | .45 | Skellam | .004 | 71.3 | .04 | 43.8 |
| *L. succulentus* | Niche | Skellam | .007 | 319 | .14 | Linear | .018 | ... | .44 | 18.1 |
| *Melilotus indicus* | Dominant | Linear | .047 | ... | .58 | Skellam | .062 | 490 | .38 | 29.9 |
| *M. indicus* | Niche | Skellam | .04 | 2,881 | .37 | Linear | .05 | ... | .64 | 12.8 |
| *M. indicus* | Niche[a] | Skellam | .06 | 1,336 | .42 | Linear | .05 | ... | .60 | 9.5 |
| *Vicia villosa* | Dominant | Linear | .034 | ... | .13 | Skellam | .28 | 2.5 | .014 | 5.64 |
| *Vulpia* species | None | Skellam | .025 | 1,154 | .08 | Same | | | | |

Note: See "Material and Methods" for a description of the models and model parameters in this table. We consider the intraspecific competitive environment in two ways: the degree to which the competitive dominant, *Brassica*, was seed limited (dominant model) and the amount of functional overlap in terms of growth form, on the basis of the seed supply of species in the same growth form (niche model). Two model fits are given when recruitment functions differed across these environments. We indicate "none" when one model best fit all subsets of data, likely indicating that species recruitment was affected by diffuse competition rather than specific characteristics of the competitive environment. The columns under "low competitive environment" indicate parameter estimates for the subset of the plots under low competitive conditions, either when *Brassica* was seed limited (when we added less than the estimated $n$, 733 seeds m$^{-2}$; dominant model) or when the propagule pool had low representation of other species of the same functional group (FG; when 25% of propagules were in the same FG; niche overlap model). The columns under "high competitive environment" indicate recruitment functions under conditions where interspecific competition would increase, either when *Brassica* was establishment limited (when we added >733 seeds) or when the propagule pool contained a high proportion of seeds of species (>25%) in the same FG; we list "same" when one model best fit both sets of data. If two models best describe the data set, AIC$_{\mathrm{d}}$ indicates the differences in the Akaike Information Criterion between the models. *Vulpia* species were combined in all analyses.

[a] While we examined two FGs, seed mass and growth form, seed mass groups affected recruitment functions only for *Melilotus*; these model results are given here.

12 seed input levels sampled from a log normal distribution: 0.09, 0.16, 0.24, 0.32, 0.39, 0.48, 0.60, 0.72, 0.93, 1.20, 1.64, and 3.23 g seeds added per square meter. A log normal distribution is a common species distribution in many communities (Rees 1995; Murray et al. 2005), and it is typical for seed banks in California annual grassland communities (R. Aicher and L. Larios, unpublished data). We chose to standardize mass instead of number of seeds, as small-seeded species tend to produce more seeds (Turnbull et al. 2005) and are more likely to have recruitment functions that saturate at higher seed input densities (Duncan et al. 2009). Standardizing by seed mass allowed us to cover a wide range of species seed input levels that also encompassed realistic ranges of species-specific seed input levels. For each species, we randomly selected nine plots (one-twelfth of the plots), in which it was sown as the most abundant species (3.23 g of seed). The abundances of the other 11 species were randomly drawn from log normal positions described above, with the constraint that each species appeared in each abundance rank at least once. In an additional 27 plots, we added an equal proportion of all species, again by mass (0.83 g m$^{-2}$). This design ensured that propagule pool characteristics varied independently from seed supply rate of any one given species.

Experimental communities were planted in 1-m$^2$ plots in a randomized block design consisting of three blocks, for a total of 135 plots. There were 0.5 × 0.5-m aisles surrounding all plots. To prepare the site for experimental planting, our first goal was to deplete the preexisting seed bank. To do this, we lightly tilled and then watered the site for 2 weeks to encourage germination from the seed bank (January 2006). We applied a systemic herbicide (Roundup, Monsanto, St. Louis, MO) 3 days after the last watering to kill all plants that had germinated.

On February 18, 2006, we seeded all plots by spreading the well-mixed seed mix uniformly by hand across each plot. Throughout the growing season, we weeded out all species that were not a part of the original 12-species mixture. The majority of species in our experimental plots were from the added seeds; weeding was not substantial. In one of the blocks, *Brassica* germinated from the seed bank. Because we wanted to control all seed sources, we weeded out *Brassica* individuals in this block to the average germination rate of *Brassica.* During peak biomass, from May 21 through June 1, 2006, we counted individual stems for all species in every plot to indicate each species' recruitment success. Because all species were nonclonal annuals, we could assume that each stem represented an individual.

### *Recruitment Functions*

We used the analytical framework developed by Duncan et al. (2009) to quantify recruitment functions for all species in the experiment. For each species, we asked how the number of seeds added to each plot $s$ relates to the number of individuals recruited $r$. We estimated that seed viability for the species was all >90% under standardized germination conditions in the laboratory; however, we were not able to assess germination success under field conditions for all species because of the difficulty in identifying individuals to species at a very early age.

Specifically, we fitted two recruitment functions for all species. First we used the Skellam function, where

$$r = bn(1 - e^{-s/n}). \tag{1}$$

As emphasized by Duncan et al. (2009), the parameters of the Skellam function have a direct biological interpretation: $n$ is the number of microsites and $b$ is the proportion of those microsites that are suitable for recruitment (reflecting density independence, which includes interspecific density dependence). When a large number of seeds is added (when $s > n$), the number of recruits saturates at $bn$, the number of suitable microsites (reflecting intraspecific density dependence). When a small number of seeds is added (when $s < n$), many suitable microsites are available and the number of recruits increases in proportion to the number of seeds added, and $r$ versus $s$ approximates a linear function with a slope equal to $b$:

$$r = bs. \tag{2}$$

We also fitted a more general recruitment function that included $\lambda$, a dispersion parameter, which assumes that seeds are aggregated within sites (Brannstrom and Sumpter 2005; Duncan et al. 2009), but this never had a better fit than the Skellam or linear functions.

On the basis of our measurements of $r$ (stem density) and $s$ (seed input) for each species in each experimental plot, we fitted these functions (eqq. [1] and [2]; as mentioned above, the *Vulpia* species were combined), using the SYSTAT nonlinear regression module (ver. 10.2; SYSTAT, Chicago, IL). We also fitted a recruitment function, irrespective of species, for the assembled communities (in this case, $r$ is total stem density and $s$ is total seed input) to assess the overall seed density effect on recruitment. We compared the fit of these recruitment functions with Akaike's Information Criterion (AIC; Akaike 1973). The estimated parameters indicate how species vary in the intensity of density-independent mortality ($1 - b$; this estimate includes postdispersal interspecific competitive effects and environmental stress as well as seed viability and germination constraints), intraspecific density-dependent mortality (approximated as increasing curvature of the recruitment function, $bn$), and the cessation of seed limitation (when $s > n$).

Our experimental assembly design allowed us to explore how the interspecific competitive environment may affect a species recruitment function. We describe the competitive environment in two ways: the degree to which the competitive dominant was seed limited (dominance hierarchy prediction) and the amount of functional overlap in the propagule pool (niche overlap prediction). For both types of analyses, we compared recruitment functions using AIC to determine whether the functions were different from each other or whether one global function best fitted the data.

First, in our experiment, *Brassica* was the clear competitive dominant species: in the plots that started with all species at the same seed mass, *Brassica* increased from 8% of the initial seed input to 52% of the adults. We tested whether the recruitment functions of the other species varied when *Brassica* was purely seed limited or just partially limited by available microsites (i.e., when $s < n$) and when *Brassica* was purely establishment limited (when $s > n$). To do this, we first determined that $n$ (the number of microsites) for *Brassica* was 733 (described above). Then we fitted recruitment functions for each of the other species for two subsets of our data set: in plots when seed input of *Brassica* was less than $n$ (we added less than 733 seeds to 60 plots) and when seed input of *Brassica* was greater than $n$ (we added more than 733 *Brassica* seeds in 75 of the experimental plots). Note that some of the plots were considered to be seed limited (when $s < n$), as *Brassica* was starting to experience some degree of establishment limitation (function was starting to curve; $s > bn$) but was not seed saturated.

Second, we base our test of functional overlap on two functional trait groupings that have been shown to reflect microsite requirements: growth form and seed mass. Three growth form groups (graminoids, forbs, and nitrogen-fixing forbs) were each represented by four species in our experiment (table A1). For seed mass groupings, we considered the three species with the most similar seed masses to that of a given species to be part of that species' seed mass functional group (table A1). We tested whether recruitment functions of each species changed on the basis of the seed supply representations of the other species in their same functional group. We described functional group overlap for each species as a proportion of the total propagule pool represented by others in the same functional groups: high overlap, >25% (2.5 g) of the propagule pool; low overlap, <25% (2.5 g) of the propagule pool. If functional group similarity did affect recruitment functions, then we described recruitment functions for these two subsets of our data set (similar to the analysis, above). Note that the competitive dominant, *Brassica*, was considered like any other species in the propagule pool; high forb and small-seed functional group representation necessarily often meant high representation of the competitive dominant.

### *Parameter Relationships with Species and Community Characteristics*

We tested how four characteristics—growth form, seed mass, fecundity, and population growth—may explain variation among density-independent effects, described by $b$, in a species recruitment function. Because several species had linear recruitment functions over the seed supply added, we could not calculate similar relationships for $bn$ and $n$. Seed mass was estimated by weighing groups of 50 seeds of each species. Fecundity was estimated on the basis of the ratio of adult stems to seeds produced. To quantify seed production, we collected all seeds throughout the growing season. We were able to do this for all species except the most abundant species, *Brassica*, for which we estimated seed production on the basis of correlation with biomass (seed production = 0.1275(*Brassica* biomass) + 63.72, $R^2 = 0.46$, $P < .0001$, $n = 45$). Population growth was assessed with an index based on the natural log of the ratio of the final seed production to the initial seed input. A large positive ratio indicated that the species increased in abundance; a large negative value indicated a strong decline in population abundance over the generation. In order to standardize the conditions on which these estimates were based, we calculated both fecundity and population growth estimates from the 27 "even" plots where all species were added equally by mass. We regressed each of these species mean characteristics against the recruitment function parameters $b$ to determine the importance of density-independent effects. We used a log transformation for the parameter estimates to meet the assumptions of normality. When different recruitment functions fit each competitive environment (i.e., when *Brassica* $s > n$ vs. $s < n$), we conducted separate analyses with each set of estimated parameters.

To extend the predictions of recruitment constraints to community diversity, we take two approaches. First, we tested our predictions regarding effects on diversity on the basis of two characteristics of the propagule pool, seed supply of the dominant species (*Brassica*) and functional diversity (functional group evenness, based on either growth form or seed size groupings). Richness was constant in all propagule pools. Evenness of the propagule pool was based on the seed added in each of the three growth forms to a plot. For each plot, we used the Shannon diversity index to describe changes in species diversity of the adult community. Other diversity indices (evenness, Simpson's) yielded similar results. Second, because we describe recruitment functions for all species in the assembled communities, we ask how recruitment parameters aggregated at the community level relate to species diversity at the community level. For each plot, we calculated the community-weighted mean (CWM) for parameter $b$ across all species using a mass-ratio approach (Grime 1998; Garnier et al. 2004):

$$\mathrm{CWM}_{bj} = \frac{\sum_{i=1}^{sp} b_i s_{ij}}{S_j}, \qquad (2)$$

where $s$ is the number of seeds added for a given species $i$ and $S$ is the total number of seeds added in plot $j$. As we hypothesized that parameters should vary on the basis of community context (e.g., whether the competitive dominant is seed limited, high functional group overlap), we used parameters on the basis of the best fit models (described previously) that reflect these differences. As variation in recruitment parameters could indicate trade-offs among species in recruitment strategies that could lead to increased diversity, we also calculated the coefficient of variation (the ratio of the standard deviation to the mean) of the community-weighted function. We did not conduct similar analyses with the number of safe sites, $n$, as it was not estimated for species with linear fits. Then, to assess the relationship between community-aggregated parameters or propagule pool characteristics and diversity of the established recruits, we fitted linear and nonlinear regression functions, using AIC criteria to choose the best fit model.

## Results

### *Recruitment Function*

Species recruitment was most often best fitted by Skellam functions, although several species also exhibited linear nonsaturating functions. Of the best fitted functions, most explained variability in adult recruitment reasonably well ($r^2 > 0.40$, $n = 135$), although some species had poor but still statistically significant fits (e.g., $r^2 = 0.04$ and 0.08

for *Avena* and *Vulpia*, respectively; table 1). The relationship for all species that was calculated using total seed density versus total stem density was also best fitted by a Skellam function, although the fit was relatively poor ($r^2 = 0.061$; not shown); all plots had seed input levels greater than the estimated $n$ of 4,800, indicating that all plots had an adequate level of seeds added to saturate recruitment.

For six of the species, the competitive environment, described by either seed limitation of the competitive dominant or functional niche overlap, did not affect recruitment functions (table 1; fig. 2). Despite the lack of response to these factors, density-independent mortality was evident by the relatively low $b$ estimations: all were less than 0.05, with the exceptions of *Avena* ($b = 0.11$) and *Brassica* ($b = 0.25$). Density-independent mortality was likely a combination of abiotic constraints and diffuse competition. We found that the Skellam function fitted the data best in four of the six species (table 1; fig. 2), indicating that seed supply reached high enough levels to cause density dependence and safe-site saturation. For the two other species (the small-seeded forb *Lasthenia* and the large-seeded legume *Lotus)*, a nonsaturating linear model best fitted the data, indicating that seed supply rates were not high enough to overcome density-independent mortality ($1 - b$) and saturate safe sites.

For the other five species, recruitment functions differed when the competitive dominant, *Brassica*, was establishment limited. Three of the species (all legumes: *Lupinus*, *Melilotus*, and *Vicia*) shifted from linear to Skellam functions in the high competitive environment (when *Brassica* $s > n$; table 1; fig. 3). Saturating recruitment functions for two other species, *Bromus* and *Eschscholzia*, remained best fitted by the Skellam function but shifted because of the competitive environment. In all cases where the recruitment function changed, the proportion of suitable microsites for the species (parameter $b$) decreased in the more competitive environment.

Some of the species that responded to the competitive environment on the basis of *Brassica* seed limitation also responded to the degree to which their functional group was represented in the propagule pool (table 1; fig. 4). Similarity in growth form influenced the recruitment of four species; seed mass similarity influenced only one species (table 1). However, the recruitment function of only one of these species, *Eschscholzia*, shifted in the predicted direction, with a decrease in parameter values (particularly $n$, available microsites). With greater functional group

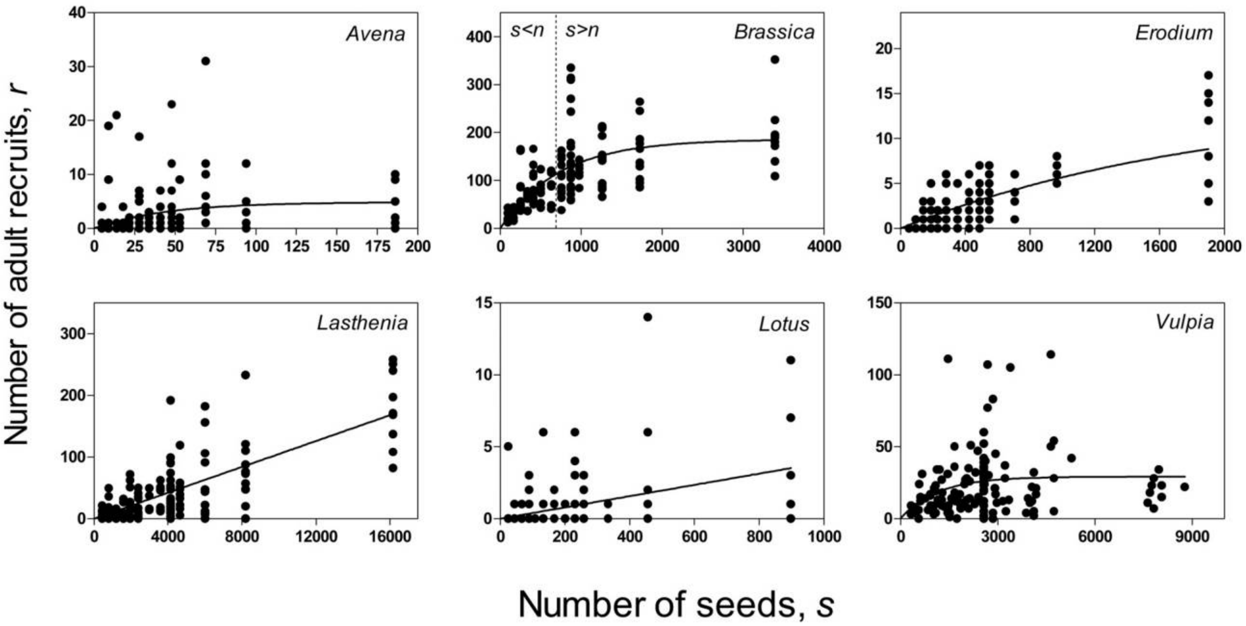

**Figure 2:** Recruitment functions for the six species in which recruitment was not affected by competitive environment (i.e., seed limitation of the competitive dominant *Brassica* or high seed supply of other species in their functional group). Each symbol represents the species recruitment in a plot on the basis of its seed input; other species' seed inputs varied, but total seed input and diversity of the propagule pool remained constant. See table 1 for parameter estimates for best fit models. The dotted vertical line in the *Brassica* panel indicates the point where the recruitment curve saturated and seed limitation ended (when $s > n$).

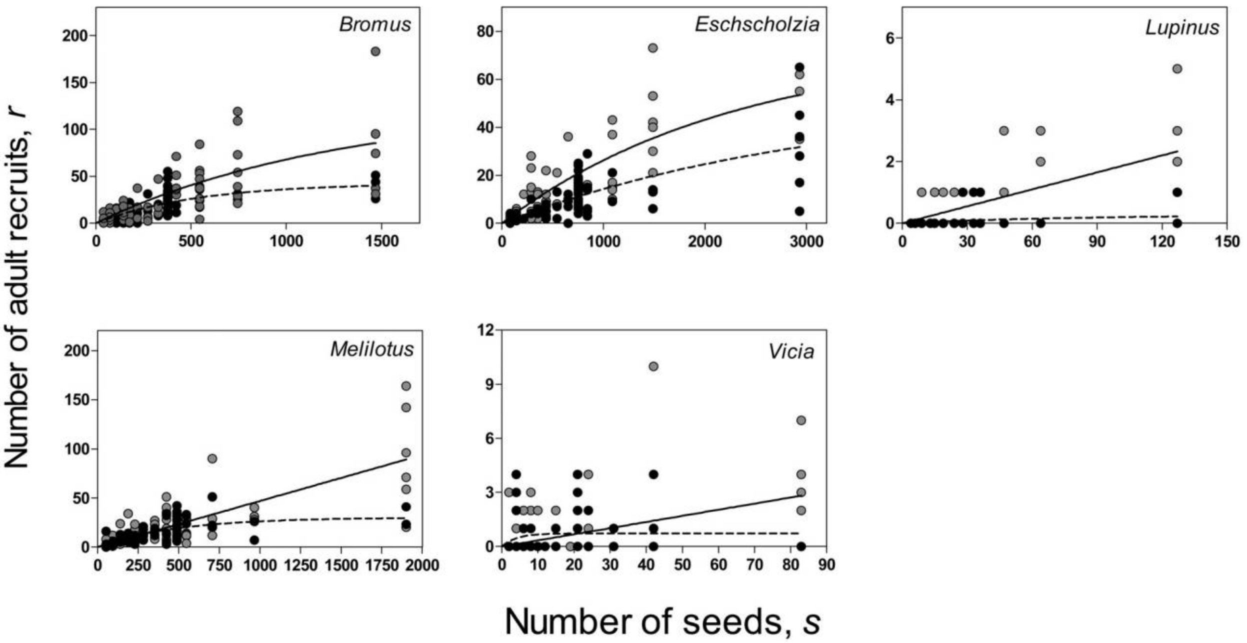

**Figure 3:** Recruitment functions of five species that were affected by the competitive environment described by the seed limitation of the competitive dominant, *Brassica*. We fitted functions to two subsets of data: plots where *Brassica* $s < n$, indicating seed limitation (gray symbols and solid lines), and plots where *Brassica* $s > n$, indicating establishment limitation (black symbols and dotted lines; see *Brassica* panel in figure 2, in which the dotted vertical line indicates establishment limitation and the cutoff point for the groupings). Table 1 lists recruitment function parameters.

overlap, the recruitment functions of the three other species shifted from a Skellam saturating function to a linear function and parameter values increased, indicating a decreased intensity of interspecific interactions. Because *Eschscholzia* is the only species of the four in the same functional group as *Brassica* (both are forbs), these results are more consistent with the idea that increased *Brassica* constrains recruitment rather than functional similarity per se. The graminoid (*Bromus*) and nitrogen-fixing (*Lupinus*, *Melilotus*) species experienced decreased competitive intensity in communities with greater representations of their own functional groups (fig. 4). Given the strong evidence for competitive effects due to *Brassica* and little evidence of stronger effects within functional groups, we explored parameter relationships on the basis of model fits related to competitive dominance (table 1; fig. 3) for these species, rather than the niche overlap model in the sections below.

### *Parameter Relationships with Species and Community Characteristics*

Seed mass, growth form, and fecundity did not relate to estimates of *b*, the proportion of suitable sites. Species characterized by fast population growth, exhibiting large increases in abundance from the initial propagule pool to final seed production, had higher estimates for parameter *b*, the proportion of suitable sites ($r^2 = 0.47$, $P = .02$, $n = 11$ for low competitive environments when *Brassica* $s < n$; $r^2 = 0.49$, $P = .016$, $n = 11$ for high competitive environments when *Brassica* $s > n$). Seed mass of *Brassica*, the competitive dominant in this system, was the third smallest in the experiment (table A1), and the density-independent parameter of its recruitment function, *b*, was the highest among all species (table 1).

Community diversity was related to several aspects of the propagule pool and recruitment characteristics of the species. Consistent with the strong effects on recruitment functions (fig. 3), the seed input of *Brassica* was negatively related to diversity ($r^2 = 0.10$, $P < .001$, $n = 135$; fig. 5). Community-weighted parameter *b*, weighted by initial seed supply and aggregated among species, was also related to the diversity of the resulting communities. Propagule pools with large aggregated *b* (e.g., communities with a large proportion of individuals with high recruitment success per available microsite) were less likely to be diverse ($r^2 = 0.32$, $P < .001$, $n = 135$; fig. 5). Because *Brassica* had the greatest estimate of *b*, this pattern was consistent with the relationship with *Brassica* seed input, but it also reflects the response of other species with high *b* parameter

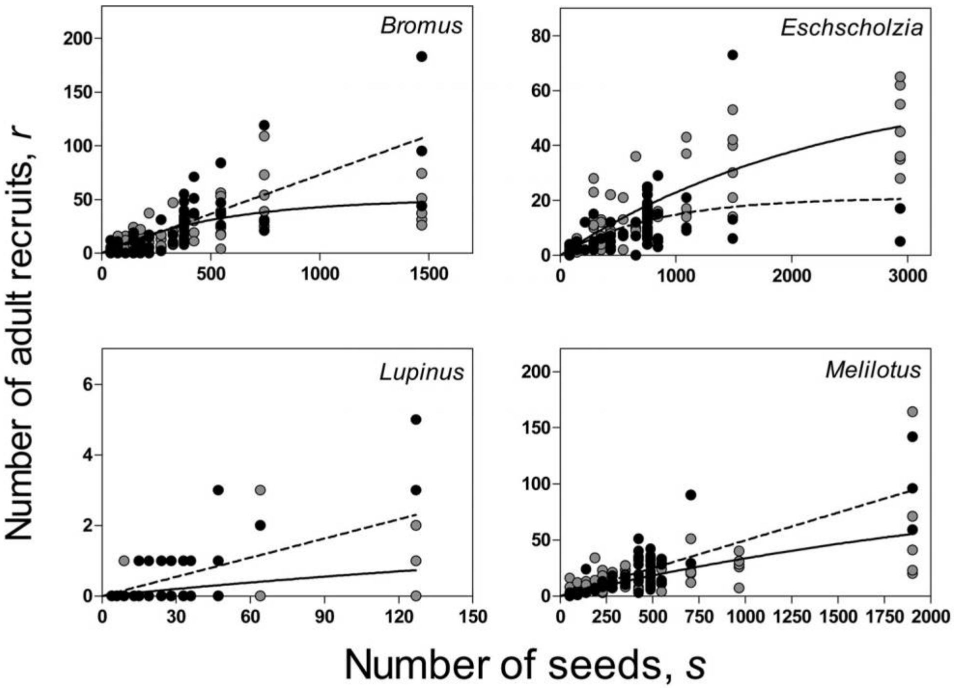

**Figure 4:** Recruitment functions of four species that were affected by the competitive environment described by the proportion of the propagule pool represented by species in the same functional group (graminoid, forb, or nitrogen-fixing forb). We fitted functions to two subsets of data: plots where the functional group representation was low (<25% of the propagule pool; gray symbols and solid lines), and plots where representation was high (>25%; black symbols and dotted lines). Table 1 lists recruitment function parameters. While we expect increased density-independent mortality (higher interspecific competition for safe sites) with higher functional group overlap, increased intensity of interspecific competition (lower $b$) occurred only for the one forb (*Eschscholzia*). The other species (the graminoid *Bromus* and nitrogen-fixing forbs *Lupinus* and *Melilotus*) experienced less interspecific competition when in similar functional group propagule pools; this pattern could reflect reduced competition with the forb *Brassica*, the competitive dominant.

estimates. In contrast, adult community diversity was not influenced by the functional group evenness of the propagule pool (fig. 5). Similarly, the variability in recruitment parameter $b$ within a community, which can indicate potential niche partitioning, was negatively related to diversity: when weighted $b$ values were very variable among species (high coefficient of variation), diversity was low ($r^2 = 0.09$, $P = .001$, $n = 135$).

## Discussion

The magnitude of seed limitation relative to establishment limitation is rarely considered in seed addition studies, but it is essential to test the questions of what factors limit the size or density of populations. In addition, these relationships can be fundamental to the understanding of community assembly and the resulting patterns of diversity, particularly in systems that depend heavily on species recruitment. Recruitment functions, describing the relationship between seed input and seedling or adult density, are a powerful means to describe the relationship between seed limitation and establishment limitation. Recruitment functions in our assembled communities indicated that species experienced a combination of seed limitation and establishment limitation and that the relative degree of seed and establishment limitation was influenced by species traits and the interspecific competitive environment. In particular, we find strong evidence of processes consistent with competition-colonization mechanisms, where seed limitation of the competitive dominant reduced interspecific establishment limitation in one-half of the other species in the community and was associated with increased community diversity.

### Utility of Our Approach

We describe an experimental community assembly approach that can quantify population recruitment functions and their contribution to community diversity, addressing the needs highlighted by recent meta-analytical reviews (Clark et al. 2007; Poulsen et al. 2007). We expand on more typical seed addition studies by accounting for all

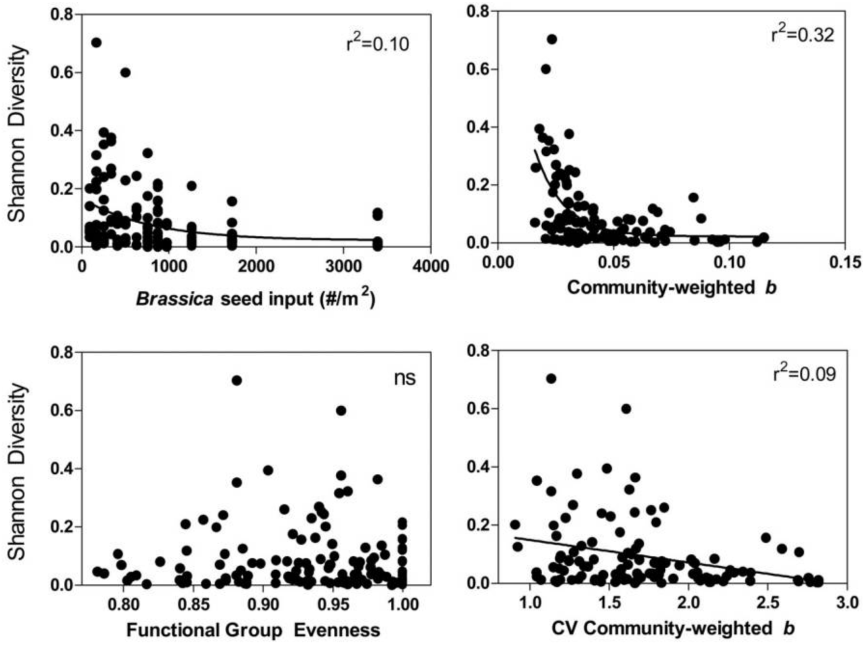

**Figure 5:** Relationships between propagule pool characteristics and diversity of the resulting adult community. On the basis of a strict competitive hierarchy, a competition-colonization trade-off would be indicated by a negative relationship between diversity and the propagule input of *Brassica*, the competitive dominant (*top left*), as well as a negative relationship between diversity and community-weighted *b* recruitment parameter (*top right*). Niche partitioning could also lead to increased diversity; however, diversity was not positivity related to functional group evenness (*bottom left*) and was negatively related to variation in recruitment parameter *b* in the propagule pool (*bottom right*). Significant relationships are indicated by solid lines.

sources of seed input, manipulating seed input at multiple levels, and addressing limitation at both very low and very high seed input levels (necessary to estimate density-independent mortality and seed saturation levels, respectively). Our approach also allows us to test predictions across many species and on community-level measures such as diversity.

Recruitment functions can take a variety of forms, ranging from linear functions of seed input to strongly nonlinear saturating functions (Duncan et al. 2009). Recent meta-analysis of seed addition experiments used the assumption of linear relationships (necessary when a study adds one level of seeds) to compare across experiments and species (Clark et al. 2007); a companion paper that focused on a small subset of experiments with multiple seed addition levels also found a preponderance of linear relationships (Poulsen et al. 2007). In our study, linear recruitment functions were the exception; nonlinear saturating functions best fitted recruitment relationships for most of the species, particularly under highly competitive conditions when *Brassica* was establishment limited. As argued by Poulsen et al. (2007) and Duncan et al. (2009), our results further emphasize that experiments that add one level of seed augmentation have limited value.

The nonlinear recruitment functions in our study were best fitted by Skellam functions. Poulsen et al. (2007) found that the Beverton-Holt function best fitted saturating functions, indicating the prevalence of high aggregation (when dispersion, $\lambda$, approaches 1; Duncan et al. 2009). In our experiment, the degree of aggregation was low, likely because we added seeds in a relatively uniform manner and attempted to avoid high degrees of spatial clumping at the start of the experiment. A random or uniform distribution of seeds, which we attempted to achieve in this study and which is a common goal in seed addition studies in general, may not recreate the highly aggregated nature of natural dispersal and should be a methodological consideration in recruitment studies.

Similar to other seed limitation studies, we found that a small fraction of seed recruits and survives the first growing season. For most species, the fraction was small at even very low levels of seed input (estimated by parameter $b$ when $s < n$), when one would expect seed limitation to be at its strongest. Our estimates of $b$ ranged from less than 1% to 25%, and it averaged less than 6%. Surprisingly, these estimates are lower than the 14% estimate of average seed limitation in the meta-analyses conducted by Clark et al. (2007), even though their estimate was based on ambient levels of seed inputs rather than very low densities. We estimated seed viability for all species to be greater than 90%, indicating that the low $b$ values are mostly influenced by postdispersal density-independent mortality such as environmental stress and interspecific competition for safe sites.

### *Linkages to Traits and Community Assembly*

Our results strongly support predictions of a strict dominance hierarchy, where a trade-off between competitive and colonization ability is necessary for coexistence (Tilman 1994; Turnbull et al. 1999, 2005; Mouquet et al. 2004; DiVittorio et al. 2007). For one-half of the species in the experiment, seed limitation of the competitive dominant species, *Brassica*, decreased density-independent mortality because of reductions in interspecific competition. We were also able to demonstrate that the shift from seed limitation to establishment limitation of the dominant species (based either on *Brassica* specifically or on species with high $b$ parameter estimates in general) reduced community diversity. Although we were not able to follow patterns over multiple generations, our results indicate that coexistence would be possible only in communities where the dominant species was seed limited. Thus, this study is one of the first community-level demonstrations to indicate that the competition-colonization trade-off can lead to coexistence.

We were unable to show the benefits of functional diversity through the reduction in interspecific competitive interactions in this experiment. We did not find evidence of increased seed or establishment limitation with increased niche overlap as described by functional group similarity. Niche overlap effects may have been weaker than competitive effects of the dominant species, as has also been observed in other experiments (Smith and Knapp 2003; Emery and Gross 2007). We designed our propagule pools so that species representation varied by growth form and seed mass. While this approach allowed us to introduce propagule pools that varied in functional group similarity, it did not test for effects related to complete loss of specific species or functional groups from the propagule pool. In addition, growth form and seed mass groupings may not have adequately described functional diversity related to safe-site requirements; however, other studies consistently find strong patterns on the basis of these groupings (Fargione et al. 2003; Hooper and Dukes 2004; Petermann et al. 2010).

Species strongly differed in their establishment limitation, even at similar seed supply rates. This pattern is inconsistent with lottery model predictions, and it suggests that the communities were strongly governed by competitive assembly processes. These results reflect assembly under relatively homogenous environments, both spatially and temporally. More variable environments might allow for increased variability in recruitment at a given safe site and might decrease more deterministic competitive pressures.

Functional traits, particularly seed mass and growth form, did not explain variability in recruitment functions across species or in community assembly dynamics. Tests of predictions relating to competition-colonization trade-offs in a strict dominance hierarchy are often based on seed size: large-seeded species have been found to exclude small-seeded species when they colonize the same microsite (Rees 1995; Turnbull et al. 1999), and they better tolerate conditions such as drought, shade, and herbivory (Westoby et al. 1996; Moles and Westoby 2004; Turnbull et al. 2005; Peco et al. 2009). In this study, the dominant species, *Brassica*, had the highest percentage of seed recruiting at low-density seed inputs, 25%, which was undoubtedly related to its ability to dominate the community. Instead of seed mass, competitive ability was reflected in low density-independent mortality (high $b$ values) and higher population growth rates. Likewise, niche predictions usually relate functional overlap to such traits as seed size or growth form (Rees 1995; Mouillot et al. 2007; Petermann et al. 2010), assuming that species with more similar traits would compete more for resources. Functional overlap in traits may become more important in communities without such a strong competitive hierarchy, as we found here.

Compared with the strong species-specific effects related to the limitations of the dominant species, our aim was to keep total seed input (irrespective of species) at saturating levels. At these saturating levels, we accordingly found little effect of total seed supply on overall recruitment. Because we manipulated the initial seed input of all species simultaneously, the higher variation in the composition of neighboring species may have allowed us to identify the large signature of interspecific density dependence. Strong species-specific effects make intuitive sense given the expectation that a microsite may be suitable for multiple species; however, recruitment functions have focused mostly on intraspecific density dependence rather than interspecific effects (Duncan et al. 2009). We also found that five species responded more to diffuse competition than to specific propagule pool characteristics, and most species exhibited intraspecific density dependence at high levels of seed input. We expect that if we had included manipulations of overall seed input levels similar to that found in a disturbance treatment, we would have also detected large influences on diversity (Foster 2001; Myers and Harms 2009*a*; Harrison et al. 2010).

### *Important Considerations*

While our community assembly approach yields important insights compared with typical seed addition studies, there are also several ways in which our interpretation differs from that of typical seed addition studies. Most notably, we quantified recruitment functions in the absence of ambient seed input. While this approach allowed us to more precisely control all seed inputs for a population, it is important to emphasize that we quantified the entire continuum from seed to establishment limitation rather than the specific case at ambient seed input. Thus, it is necessary to know where a natural population sits on a recruitment function in order to be able to characterize the degree of seed limitation. For instance, although we show that seed limitation of the dominant species is related to increased coexistence, we expect that *Brassica* should be a good colonizer, as it is small seeded, with high fecundity. The question remains how frequently seed limitation of this species occurs in natural field settings.

Most work on recruitment has focused on short-lived species; this study continues this focus. Because we assembled a community composed of annual species, we were able to run the experiment for one generation for all species and base our recruitment parameters on adult establishment. While assembling a community composed of annual species is appropriate for California grasslands (Shaw et al. 2002; Hobbs et al. 2007; Peco et al. 2009) and other types of communities (Turnbull et al. 2004; Emery et al. 2009), many plant communities have a greater range of life histories. These cases would require evaluation of seedling recruitment and/or monitoring over a longer period of time to assess how seedling recruitment patterns influence adult community structure.

Ensuring that seed addition studies are comparable across species is difficult because of expected trade-offs associated with seed mass and fecundity. In this study we held seed mass rather than seed number constant at the plot level. As is common in plant communities, the seed mass of our species varied to such a degree that if we standardized by seed number, we would have added over 600 g $m^{-2}$ of seed of the largest-seeded species in some plots. By controlling for seed mass, our experimental plots received differing seed densities; however, overall seed density was always in the range sufficient to saturate microsites and cause density-dependent establishment limitation. Even with our approach to adjust by mass and allow seed densities to vary, we did not identify points of seed saturation for two species, a possible indication that we needed to add more seeds for these species. Interestingly, for one of these species, *Lasthenia*, the smallest-seeded species in the experiment, the recruitment function remained linear even at the highest seed input level (17,000 seeds $m^{-2}$). We also did not identify saturation in some of the legumes, particularly when *Brassica* seed input was low (it was striking that all four legumes had linear recruitment functions under these conditions). This trend of nonsaturation for legumes in low competitive conditions appeared irrespective of seed size.

### *Conclusions*

By using an assembly approach to simultaneously quantify recruitment functions, we continued the recent extension of recruitment limitation framework (Clark et al. 2007; Poulsen et al. 2007; Duncan et al. 2009) to include multispecies experimental communities. Most seed addition studies find populations to be strongly seed limited and, often to a lesser degree, establishment limited (Zeiter et al. 2006; Clark et al. 2007; Myers and Harms 2009*a*; Oster et al. 2009). By quantifying recruitment functions for a community of annual plants, we show that species have different recruitment constraints ranging from strong seed limitation across all seed input levels, to sensitivity to density-independent mortality at even low seed input levels, to different saturation points of microsite availability at high seed input levels. Additionally, we use this approach to directly demonstrate the predictions of the competition-colonization theory of coexistence, showing that the limitations of dominant species can affect recruitment constraints for other species and that these differential limitations scale up to affect diversity of the assembled communities.

## Acknowledgments

This work was funded by grants from the University of California, Irvine, Newkirk Center for Science and Society and the National Science Foundation (NSF). We acknowledge fellowship support from the Graduate Assistance in Areas of National Need (U.S. Dept. of Education) program (to R.J.A.) and from the NSF Graduate Research Fellowship Program (to L.L.). We thank M. Aicher, M. Doan, D. Leong, C. Lessin, M. Purifoy, and R. Winkelman for help in the laboratory and field. We also thank S. Rodriguez-Buritica and two anonymous reviewers for helpful comments on earlier drafts of this manuscript.

# APPENDIX

## Supplemental Table

**Table A1:** Twelve annual herbaceous species used in this experiment

| Species | Growth form | Seed mass (g per seed) |
|---|---|---|
| *Avena fatua* | Graminoid | .017 |
| *Brassica nigra* | Forb | .00095 |
| *Bromus hordeaceus* | Graminoid | .0022 |
| *Erodium cicutarium* | Forb | .0017 |
| *Eschscholzia californica* | Forb | .0012 |
| *Lasthenia californica* | Forb | .00020 |
| *Lotus purshianus* | Nitrogen-fixing forb | .0036 |
| *Lupinus succulentus* | Nitrogen-fixing forb | .026 |
| *Melilotus indicus* | Nitrogen-fixing forb | .0017 |
| *Vicia villosa* | Nitrogen-fixing forb | .039 |
| *Vulpia* species[a] | Graminoid | .00087 |

Note: Nomenclature after Hickman (1993). These species are all common in California grasslands.

[a] *Vulpia microstachys* (seed mass, 0.0013 g) and *Vulpia octoflora* (seed mass, 0.00043 g) were combined and analyzed as *Vulpia* for all analyses; we provide average seed mass between the species here.

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