REVIEW AND SYNTHESIS

Seed arrival, ecological filters, and plant species richness: a meta-analysis

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Abstract

Theoretical models predict that effects of dispersal on local biodiversity are influenced by the size and composition of the species pool, as well as ecological filters that limit local species membership. We tested these predictions by conducting a meta-analysis of 28 studies encompassing 62 experiments examining effects of propagule supply (seed arrival) on plant species richness under contrasting intensities of ecological filters (owing to disturbance and resource availability). Seed arrival increased local species richness in a wide range of communities (forest, grassland, montane, savanna, wetland), resulting in a positive mean effect size across experiments. Mean effect size was 70% higher in disturbed relative to undisturbed communities, suggesting that disturbance increases recruitment opportunities for immigrating species. In contrast, effect size was not significantly influenced by nutrient or water availability. Among seed-addition experiments, effect size was positively correlated with species and functional diversity within the pool of added seeds (species evenness and seed-size diversity), primarily in disturbed communities. Our analysis provides experimental support for the general hypothesis that species pools and local environmental heterogeneity interactively structure plant communities. We highlight empirical gaps that can be addressed by future experiments and discuss implications for community assembly, species coexistence, and the maintenance of biodiversity.

Keywords

Community assembly, disturbance, immigration, propagule supply, seed addition, seed dispersal, seed limitation, species coexistence, species diversity, species pool.

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INTRODUCTION

Dispersal plays a central role in a wide range of ecological processes, including community assembly, the maintenance of biodiversity, species coexistence, biological invasions, and ecosystem function (e.g., Chase 2003; Levine & Murrell 2003; Stachowicz & Tilman 2005; Zobel *et al.* 2006). One of the first models to invoke a direct role for dispersal as a key determinant of local biodiversity was MacArthur & Wilson's (1967) Theory of Island Biogeography. A fundamental prediction of this theory is that island species richness should be positively related to rates of immigration from mainland species pools. This seminal work set the stage for 'regional' hypotheses of community diversity, which postulate that local communities in species-rich regions should have higher diversity than communities in species-poor

regions (Ricklefs 1987; Taylor *et al.* 1990; Cornell & Lawton 1992; Eriksson 1993; Zobel 1997). These concepts helped to lay the foundation for the burgeoning field of metacommunity ecology (Leibold *et al.* 2004). In particular, neutral models of biodiversity have invoked a strong role for immigration as one of the main determinants of local biodiversity (Bell 2000; Hubbell 2001). In many of these models, local diversity is primarily controlled by immigration from the broader geographical species pool. In contrast, other models propose that 'ecological filters' imposed by local biotic and abiotic conditions influence dispersal-diversity relationships (e.g., Elton 1958; Grime 1979; Keddy 1992; Diaz *et al.* 1998; Huston 1999; Davis *et al.* 2000; Mouquet & Loreau 2003; Leibold *et al.* 2004). The extent to which these filters interact with species pools has implications for understanding community assembly

and biodiversity conservation in the face of habitat loss, fragmentation, and climate change.

Despite widespread interest in the role of dispersal in community assembly, we still lack a synthetic empirical understanding of how species pools and ecological filters interact to structure local biodiversity. To date, experimental tests of the role of propagule supply in natural communities have largely focused on terrestrial plants, with a concurrent growing number of experiments in animal and microbial communities (e.g., Cadotte 2006; Lee & Bruno 2009). In plant populations, there is strong evidence for propagule limitation (Eriksson & Ehrlen 1992; Turnbull *et al.* 2000; Moles & Westoby 2002; Clark *et al.* 2007). In a meta-analysis of 159 plant species, Clark *et al.* (2007) found that populations of most species examined were seed limited, especially in disturbed microsites. Although these patterns suggest an important role for propagule supply at the population level, they do not necessarily scale-up to predictable community-level consequences. For example, increased propagule supply could result in decreased or unchanged local diversity if immigrating species were to out-compete resident species for limiting space or resources. In contrast, propagule arrival could increase species diversity if immigrating species were to recruit into sites unoccupied by resident species or were to promote recruitment of other species. In a combined meta-analysis of nine plant and 28 animal experiments, Cadotte (2006) found support for the hypothesis that dispersal increases mean local diversity. Among plant studies, however, there was no relationship between local species diversity and dispersal, possibly owing to the small number of experiments used in the analysis and/or because only one predictor variable (dispersal rate) was examined. Collectively, these studies underscore the need to better understand the mechanistic consequences of propagule supply at the community level, especially the extent to which propagule arrival interacts with ecological filters to structure local biodiversity.

Ecological filtering occurs when biotic or abiotic factors limit the membership of species in a local community. Biotic filters, notably competition and predation, can influence effects of dispersal on local diversity in at least two important ways. First, increased immigration can reduce local diversity by introducing competitively dominant species or generalist predators into local sites or communities (Mouquet & Loreau 2003). Coexistence of competitively dominant and inferior species can occur, however, if competitively dominant species are dispersal limited (i.e., via 'competition-colonization trade-offs;' Tilman 1994), if competitively inferior species disperse short distances to take advantage of nearby sites before dominant species arrive ('spatial successional niches;' Bolker *et al.* 2003), or if rates of competitive exclusion are delayed owing to community-wide recruitment limitation (inferior species win sites by

forfeit; Hurtt & Pacala 1995). Second, increased immigration may have no effect on diversity if local communities are 'saturated' with species. Here, invasion of diverse local communities may be reduced because of more intense competition for limiting resources (Elton 1958).

Abiotic filters are hypothesized to impose strong constraints on local species membership. Classic examples include models of community diversity proposed by Grime (1979) and Huston (1999), in which the importance of species pools in structuring diversity is influenced by productivity. This 'shifting limitations hypothesis' (Foster *et al.* 2004) predicts that diversity is mostly limited by immigration from species pools at intermediate productivity, whereas establishment limitation imposed by competition for limiting resources becomes more important at high productivity. These concepts have given rise to the idea that community invasibility depends on the dynamics of resource availability (e.g., the 'fluctuating resource hypothesis;' Davis *et al.* 2000), in which invasion is more likely when processes such as disturbance increase space and resources for colonizing species. Disturbance can function both as an ecological filter (e.g., by directly removing resident species from local communities) or as a process that influences the intensity of other ecological filters (e.g., by altering limiting resources). In this way, locally patchy disturbance can promote coexistence of competing species by increasing 'niche dimensionality' within local communities (Harpole & Tilman 2007). In addition, the ability of species to exploit heterogeneity in resources may also depend on 'species pool dimensionality' (Questad & Foster 2008), i.e., the diversity of functional groups and traits present in the potential species pool. These ideas have led to the general hypothesis that 'species diversity will be greatest in communities with the most environmental heterogeneity, minimal dispersal limitation, and a functionally diverse species pool (Questad & Foster 2008).'

We present a meta-analysis that synthesizes results from 28 studies encompassing 62 experiments that explores how propagule supply (seed arrival) interacts with ecological filters to structure local plant species richness. We tested three main hypotheses. First, we tested whether seed arrival increases local species richness across experiments that did not manipulate the intensity of ecological filters. Second, we tested whether the effect of seed arrival on local species richness was positively related to species-pool diversity, measured in terms of both species diversity (richness and evenness) and functional diversity (functional group richness, evenness, and seed-size diversity) within the pool of species added to local communities in seed-addition experiments. Third, we tested the hypothesis that ecological filters influence the relationship between seed arrival and local species richness. For this hypothesis, we compared the effect of seed arrival under different intensities of ecological

filters (owing to disturbance, nutrient availability, or water availability) as well as relationships between local species richness and species-pool diversity in disturbed and undisturbed communities. We show that local species richness is generally limited by seed arrival across a wide range of plant communities. Moreover, we demonstrate that the strength of the positive relationship between seed arrival and species richness is enhanced by disturbance—a pervasive process that strongly influences ecological filters—as well as species and functional diversity within the pool of arriving seeds. We highlight some empirical gaps that can be addressed by future experiments and discuss the implications of our results for biodiversity theory.

MATERIALS AND METHODS

We searched the literature using Web of Science (Thompson Reuters) for experiments that manipulated seed arrival in communities and measured plant species richness and/or diversity. Our search included all studies published through December 2008 that contained the keywords 'seed addition,' 'seed sowing,' or 'seed augmentation,' in combination with the keywords 'richness' or 'diversity.' We used the following criteria to select studies for our meta-analysis: (1) sample sizes, means, and standard deviations (or standard errors) for species richness and/or diversity were reported in the paper or provided by the authors on request; (2) experiments contained a control treatment where seed arrival was not manipulated; and (3) the richness and identity of species used in the seed-arrival treatment was known. Most studies reported species richness, but very few reported species diversity or evenness. Therefore, we used species richness as the response variable in our meta-analysis.

We conducted our analysis in MetaWin version 2.0 (Rosenberg *et al.* 2000) using standard methods described in Gurevitch & Hedges (2001). Following Cadotte (2006), we first calculated an unbiased standardized effect size (Hedge's *d*) and variance for each experiment (Gurevitch & Hedges 2001). Hedge's *d* measures the mean difference in the response (species richness) between experimental and control treatments, standardized by the pooled standard deviation and adjusted for small sample size. Most studies did not report means and standard deviations (or standard errors) in the text or tables. For these studies, we used graphical software (DataThief III Version 1.5; http://datathief.org/) to extract these summary statistics from figures. Some studies used two levels of seed addition (control, addition), whereas others varied the number of species and/or seed densities added using several treatment levels (Table 1). For the latter studies, we used results from the treatment with the highest species richness and density of added seeds. Similarly, when studies used multiple treatment levels for an ecological filter (e.g., nutrient

addition), we used results from the highest treatment level. When results were reported for multiple sampling dates in a single paper or in separate papers, we used results from the most recent date or paper. To test hypothesis 1 (seed arrival increases local species richness), we used a mixed-effects model (Gurevitch & Hedges 2001) to calculate a combined mean effect size and 95% confidence interval (CI) for 32 experiments that did not manipulate the intensity of ecological filters. We rejected the null hypothesis if the 95% CI did not overlap zero.

We tested hypothesis 2 (local species richness is positively related to species and functional diversity within the pool of species added to local communities) using continuous, mixed-effects models (i.e., weighted regressions). For each of our five continuous measures of species-pool diversity (species richness, species evenness, functional group richness, functional group evenness, and seed-size diversity; see below), we tested whether the slope of the relationship between effect size and each variable was significantly different from zero based on *P*-values for the between-class homogeneity statistic Q_B (Gurevitch & Hedges 2001). For this analysis, we used data from 17 control experiments in studies that manipulated disturbance (i.e., undisturbed communities) to later compare to results from disturbed communities (see hypothesis 3 below). The results based on these 17 experiments were similar to results based on 29 experiments that did not manipulate ecological filters; for simplicity, we do not present the latter. We used the Dunn-Sidak method (Gotelli & Ellison 2004) to adjust the Type 1 error rate (α) based on five tests each for undisturbed (hypothesis 2) and disturbed (hypothesis 3, below) communities. However, we note that adjustments for multiple comparisons did not change the overall qualitative results. For significant regressions, we calculated the proportion of variation explained by the model (i.e., r^2) by dividing Q_B (heterogeneity explained by the model) by Q_T (total heterogeneity) (M.S. Rosenberg, personal communication).

For each species added as seed in each study, we extracted the seed mass, numbers of seeds added, and/or the total mass of seeds added. We excluded the one study conducted in a forest (Paine & Harms 2009) because the seed densities (24 seeds/m^2) and species added (all woody species) were considerably different than those added in the other studies, all of which were conducted in communities dominated by herbaceous species ($\geq$ 1950 seeds added/m^2) (Table 1). For many studies, we obtained seed mass data from the literature or the Royal Botanic Gardens Seed Information Database (Liu *et al.* 2008), which we then used to convert the total mass of seeds added for each species to numbers of seeds. To account for differences in plot size among studies, we standardized the number of seeds added per 1 m^2 (Table 1). For each experiment, we extracted the species richness of added seeds (Table 1) and calculated the

Table 1 Twenty-eight studies testing effects of seed arrival and its interaction with ecological filters on plant species richness

Study	Habitat	Location	Seed treatment*	N spp.†	N seeds/m²/year‡ Median	Total	N exp§	Ecological filter variables (N exp)¶
Brown & Fridley (2003)	Grassland	USA-NC	Density, sr	30	1777	53 333	1	
Dickson & Foster (2008)	Grassland	USA-KS	Addition	49	300	14 700	4	Disturbance (1) nutrient (1) water (1)
Eskelinen & Virtanen (2005)	Mountain	Finland	Addition	14	3200	44 800	2	Disturbance (1) predation
Foster & Dickson (2004)	Grassland	USA-KS	Addition	32	400	12 800	3	Disturbance (1) water (1)
Foster et al. (2004)	Grassland	USA-KS	Addition	34	400	13 600	2	Disturbance (1) productivity
Foster & Tilman (2003)	Savanna	USA-MN	Addition	23	274	43 317	1	
Fraser & Madson (2008)	Grassland	USA-OH	Addition	20	150	3000	1	Predation
Houseman & Gross (2006)	Grassland	USA-MI	sr	45	1600	122 700	1	Productivity
Kalamees & Zobel (2002)	Grassland	Estonia	Removal				1	Competition
Kellogg & Bridgham (2004)	Wetland	USA-IN	Addition	28			2	Disturbance (1) predation
Klanderud & Totland (2007)	Mountain	Norway	sr	27	3019	93 225	1	Temperature
Lord & Lee (2001)	Wetland	USA-NH	Addition	8			3	Disturbance (2)
MacDougall & Wilson (2007)	Grassland	Canada	Density	5	7500	37 500	4	Disturbance (2) nutrient (1) predation
Mouquet et al. (2004)	Grassland	France	Addition	8	2775	92 841	1	
Myers & Harms (in press)	Savanna	USA-LA	Addition	38	200	11 980	4	Disturbance/competition (2)
Myers & Harms (unpub. data)	Savanna	USA-LA	Addition	31	200	9300	3	Disturbance (1) water (1)
Paine & Harms (2009)	Rainforest	Peru	Density, sr	8	3	24	1	
Questad & Foster (2008)	Grassland	USA-KS	Addition	13	150	1950	2	Disturbance (1)
Reynolds et al. (2007)	Grassland	USA-MI	Addition	46	842	83 014	4	Disturbance (1) nutrient (1)
Russell & Roy (2008)	Grassland	USA-KS	Addition	18	320	5760	3	
Stein et al. (2008)	Grassland	Germany	Addition	60	300	14 800	1	Productivity
Stevens et al. (2004)	Grassland	USA-PA	Addition	30	1739	235 165	3	Disturbance (1) nutrient (1)
Suding & Gross (2006)	Grassland	USA-MI	Addition	22	935	63 017	2	Disturbance (1)
Tilman (1997)	Savanna	USA-MN	sr	54	2931	1 323 575	1	
Wilsey & Polley (2003)	Grassland	USA-TX	Addition	20	2111	80 971	4	Disturbance (2)
Xiong et al. (2003)	Wetland	UK	Addition	18	400	9600	4	Disturbance (2) water (1)
Zobel et al. (2005)	Grassland	Estonia	Addition	25	1040	26 000	1	
Zobel et al. (2000)	Grassland	Estonia	Addition	15	1500	22 500	2	Disturbance (1)

*Addition, seed-addition experiment where species were added to plots at a single density; density, seed-addition experiment where species were added to plots at varying densities; sr, seed-addition experiment where species were added to plots at different levels of species richness; removal, flowers clipped around plots to reduce seed rain.

†Maximum number of species added in seed-addition experiments.

‡Median number of seeds/species and total number of seeds added in seed-addition experiments.

§Total number of experiments used in the meta-analysis.

¶Numbers in parentheses indicate the number of experiments used to test the ecological filter hypothesis (hypothesis 3); some filters and experiments could not be used because the requisite data were not available or because of low sample size. Ecological filter variables: disturbance, disturbance manipulated through reduction of total plant cover and/or litter and/or increased soil disturbance; disturbance/competition, disturbance manipulated by removing guilds of competitors; nutrient, fertilization; predation, predators excluded with cages; productivity, study conducted across a natural productivity gradient; temperature, temperature increased; water, irrigation, experimental drought, or natural water gradient.

species evenness of added seeds using Simpson's evenness (Magurran 2004). We quantified functional diversity in two ways. First, we calculated functional group richness and evenness for species grouped into six standard functional types: non-legume forbs, legume forbs, C_3 grasses, C_4 grasses, woody, and 'other graminoids' (sedges and rushes). Second, we calculated functional diversity of seed mass using FD_{var} (Mason et al. 2003). This index measures the

variation in a functional trait weighted by species' abundances, is unaffected by species richness in the sample, and ranges from 0 to 1 (Mason et al. 2003). We will refer to this measure generally as 'seed-size diversity.'

We tested hypothesis 3 (ecological filters influence the relationship between seed arrival and local species richness) in two ways. First, we used categorical, mixed-effects models to test for differences in mean effect size between control

and treatment groups within studies that manipulated the intensity of ecological filters (Table 1). We performed separate analyses for three ecological filter variables for which requisite data were available from ≥ 4 experiments: disturbance ($n = 19$–21), nutrient availability ($n = 4$), and water availability ($n = 4$). Our disturbance category includes experiments that manipulated microsite availability either directly (e.g., manual removal of biomass or litter) or indirectly (e.g., fire). Thus, we use disturbance in a broad sense as both an ecological filter, as well as a process that influences the intensity of other ecological filters. Second, we used the weighted regression methods described above to test for positive relationships between effect size and each of the five continuous measures of species-pool diversity in disturbed communities ($n = 18$ experiments with requisite data); we did not perform regressions for the other ecological filters due to small sample size.

We also examined four additional covariates that could influence effect sizes: (1) study length; (2) plot size; (3) local community richness (mean species richness in control plots); and (4) a potential source of publication bias (ISI journal impact factor; Web of Science). We tested the significance of each continuous variable using the weighted regression methods described above and data from experiments that did not manipulate an ecological filter ($n = 29$ with requisite data), undisturbed communities ($n = 17$), and disturbed communities ($n = 18$).

RESULTS

We found a total of 28 studies encompassing 62 experiments (Table 1). Twenty-seven of the studies increased seed arrival through experimental seed addition, whereas one study (Kalamees & Zobel 2002) reduced seed arrival by removing flowers. The median plot size used for experimental treatments was 1 m^2 (range = 0.002–9 m^2). Across seed-addition experiments, the median percentage of added species that were absent from ≥ 1 control (no seed addition) plot was 81% (range = 40–100%; $n = 20$ studies with available data). Thus, most seed-addition species were likely members of the broader (regional) species pool, although most studies also added members of the local species pool (species occurring naturally in control plots). The studies spanned a wide range of habitat types (forest, grassland, montane and alpine communities, savanna, and wetland), but most (64%) were conducted in grasslands. Of the 28 studies, 75% examined how seed arrival interacts with one or more ecological filters to influence local species diversity. The most common ecological filter variable examined was disturbance (17 studies), followed by nutrient availability (4), water availability (4), predation (4, 3 of which included requisite controls), productivity (3), and temperature (1).

## Hypothesis 1: seed arrival increases local species richness

Seed arrival significantly increased local species richness (Fig. 1a). Among all 62 experiments, 70% had significantly positive effect sizes (95% CI's did not overlap zero) and only one study had a significantly negative effect size. Among the 32 experiments that did not manipulate an ecological filter, the combined mean effect size was significantly positive (Fig. 1a).

## Hypothesis 2: local species richness is positively related to species-pool diversity

In undisturbed communities, the effect of seed arrival on local species richness was positively influenced by species evenness in the pool of species added in seed-addition experiments ($P = 0.0287$, $r^2 = 0.26$, $\alpha = 0.05$), but not species richness or functional diversity (richness, evenness, or seed-size diversity; $P \geq 0.220$) in the seed pool (Fig. 2, top panels; see Table S1 in Supporting Information). However, the significant relationship between effect size and species evenness became marginally non-significant after adjusting for multiple tests (adjusted α for five tests = 0.01). In summary, we found that local species richness was strongly limited by seed arrival and positively related to species evenness in the seed pool.

Hypothesis 3: ecological filters influence the seed arrival-species richness relationship

Seed arrival had a stronger positive effect on species richness in disturbed relative to undisturbed communities (Fig. 1b; see Table S1). Disturbance significantly increased the mean effect size by 73% (Fig. 1b; $P = 0.015$; $n = 19$–21 experiments). In contrast, nutrient addition decreased the
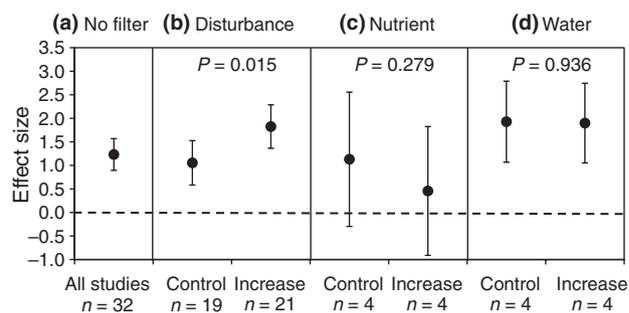
Figure 1 Mean effect size (Hedge's $d \pm$ 95% confidence interval) of seed arrival on local plant species richness (a) in experiments where ecological filters were not manipulated and in response to (b) disturbance, (c) nutrients, and (d) water availability. *P*-values from categorical, mixed-effects models testing for differences in mean effect sizes among control and treatment groups are shown in panels b–d (see Table S1 for homogeneity statistics).
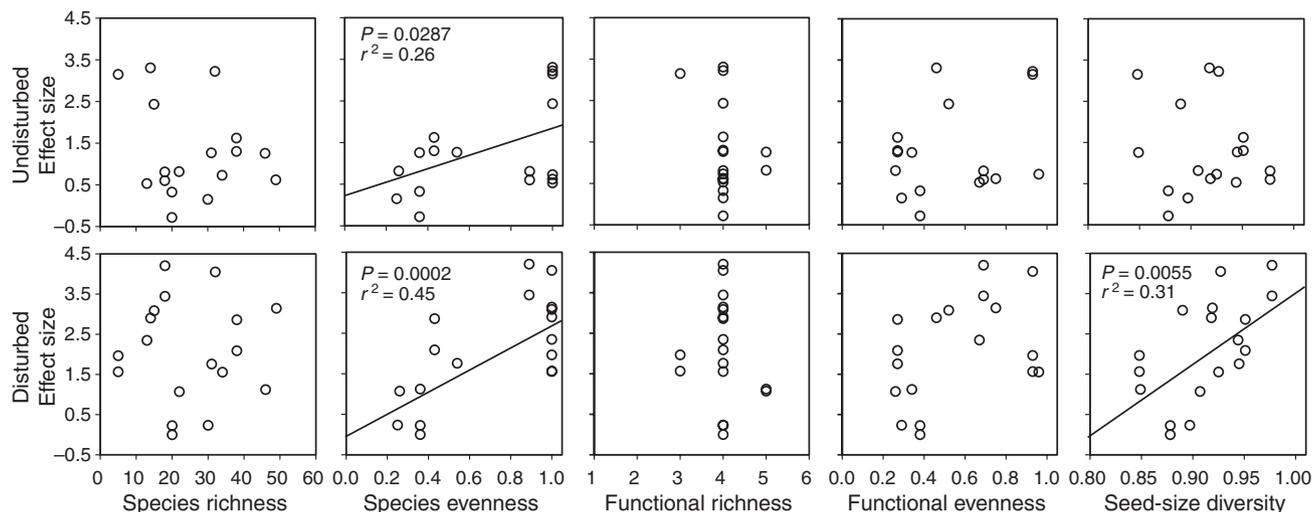
Figure 2 Relationship between effect size (Hedge's *d*) and the species richness, species evenness (Simpson's evenness), functional group richness, functional group evenness, and seed-size diversity (FD_{var}) of plant species added to local communities in seed-addition experiments. The relationships are plotted for 17 experiments in undisturbed communities (top) and 18 experiments in disturbed communities (bottom). Summary statistics from weighted regressions are shown for relationships with $P < 0.05$ (see Table S1 for homogeneity statistics).

mean effect size, but not significantly (Fig. 1c; $P = 0.279$; $n = 4$ studies). There was also no significant effect of water availability on mean effect size (Fig. 1d; $P = 0.936$; $n = 4$ studies).

In disturbed communities, effect size was positively related to species evenness and seed-size diversity in the pool of species added in seed-addition experiments (Fig. 2, bottom panels; see Table S1). Moreover, the positive relationship between effect size and species evenness was stronger in disturbed ($P = 0.0002$, $r^2 = 0.45$) relative to undisturbed ($P = 0.0287$, $r^2 = 0.26$) communities (Fig. 2). This pattern was further supported by a negative relationship between effect size and the total density of seeds added/m^2/year in disturbed (weighted regression; $P = 0.0004$, $r^2 = 0.43$), but not undisturbed ($P = 0.1009$), communities. In contrast, there were no strong relationships between effect size and species richness ($P = 0.9553$), functional richness ($P = 0.5136$), or functional evenness ($P = 0.0779$) in the seed pool (Fig. 2, bottom panels). In summary, local species richness was more strongly limited by seed arrival in disturbed relative to undisturbed communities. In addition, effect size was more strongly related to species evenness, and only related to seed-size diversity, in disturbed communities.

Potential covariates influencing effect sizes

Across 29 experiments that did not manipulate an ecological filter, we found no relationship between effect size and study length ($P = 0.6600$), plot size ($P = 0.2859$), local community richness ($P = 0.6852$), or journal impact factor ($P = 0.8160$).

There were also no relationships between effect size and these variables in undisturbed or disturbed communities ($n = 17$–18 experiments, $P \geq 0.274$ in all regressions).

DISCUSSION

Propagule supply and local species richness

Our meta-analysis provides strong support for the hypothesis that local plant species richness is limited by seed arrival from local and regional species pools. We found that seed arrival significantly increased local species richness in a wide range of communities, including forest, grassland, savanna, wetland, and montane communities. All but one of the studies (Kalamees & Zobel 2002) manipulated seed arrival by experimentally adding seeds from local and/or regional species pools, suggesting an important influence for immigration from species pools in local community assembly. Enhancement of local diversity via immigration can be explained by a variety of mechanisms, including the presence of recruitment opportunities (available microsites) in unsaturated communities, satiation of seed and seedling predators (Turnbull *et al.* 2000), facilitation of immigrating species by resident species (Bruno *et al.* 2003), and reduction in local extinction owing to mass effects (Leibold *et al.* 2004). The importance of species pools in structuring local communities is widely recognized (Ricklefs 1987; Taylor *et al.* 1990; Cornell & Lawton 1992; Eriksson 1993; Zobel 1997; Leibold *et al.* 2004), but much of the empirical evidence comes from correlative studies of large- and small-scale diversity patterns (e.g., Ricklefs & Schluter 1993; Partel

et al. 1996; Caley & Schluter 1997). Even though it is not practical in most situations to manipulate regional species richness and observe the consequences for local species richness, the propagule-arrival experiments summarized here provide useful insights into what happens locally when immigration from, or the size of, species pools increase(s).

We found little evidence for negative effects of seed arrival on local species richness, a pattern inconsistent with competition-colonization trade-off models of species coexistence (e.g., Tilman 1994). A key assumption of these models is that arrival of dominant competitors results in competitive exclusion of resident species, thereby reducing local diversity. The absence of this pattern in our analysis may simply reflect that the duration of most experiments was too short to observe competitive exclusion. Alternatively, propagule arrival and competition may influence components of community structure other than species richness, such as species relative abundance (e.g., Mouquet *et al.* 2004). In our analysis, most studies only reported species richness, so we were unable to assess treatment effects on species relative abundance and evenness. We advocate that, when possible, future experimental studies decompose effects of propagule supply on species diversity into both species richness and evenness components. The lack of negative effects of immigration on species richness could also be attributed to species selection, i.e., dominant competitors may not have been added to local communities as seed-addition species, or were added at low enough densities to preclude strong competitive effects. This explanation seems less likely, however, given that positive relationships were generally observed within studies that manipulated levels of species richness in the seed-addition pool (Tilman 1997; Brown & Fridley 2003; Houseman & Gross 2006; Klanderud & Totland 2007) and the large numbers of species (median of 25 species) and seeds (median of >800 seeds/species/m^2) added.

Species-pool diversity and ecological filters

We found that the effects of seed arrival and species-pool diversity on local species richness were positively influenced by three factors: (1) evenness of species in the seed pool; (2) disturbance; and (3) seed-size diversity in the seed pool. Positive effects of seed-pool evenness may reflect a reduction in both local extinctions caused by demographical stochasticity (fewer rare species in the pool) and competitive effects of dominant species or functional groups within the pool. Disturbance increased the mean effect size by 73%, and the positive effects of species evenness and seed-size diversity on local species richness were stronger in disturbed relative to undisturbed communities. These results strongly support the hypothesis that disturbance plays a key role in mediating effects of species pools on local community assembly.

To understand the mechanistic causes and consequences of these patterns, it is important to consider the timing of disturbance relative to the timing of seed arrival. In most of the experiments used in our analysis, disturbance was manipulated prior to seed-arrival treatments. These studies therefore demonstrate an important role for disturbance in reducing post-dispersal establishment limitation imposed by factors such as space limitation, competition for limiting resources, and low niche dimensionality in local communities. Disturbance also influences recruitment from the soil seed bank, which can potentially obscure effects of seed arrival on species richness. In most of the disturbance experiments summarized here, it is not possible to distinguish the relative importance of these mechanisms, although some studies have directly manipulated interspecific competition (Myers & Harms in press), seed bank recruitment (Kalamees & Zobel 2002), and niche dimensionality (Questad & Foster 2008).

The positive relationship between species richness and seed-size diversity in disturbed (but not undisturbed) communities supports the hypothesis that species diversity should be highest in communities with environmental heterogeneity and a functionally diverse species pool (Questad & Foster 2008). Questad & Foster (2008) experimentally tested this hypothesis by creating a functionally redundant and functionally complementary species pool and measuring their effects on local plant diversity in the presence and absence of spatio-temporal heterogeneity imposed by disturbance. They concluded that a combination of high species-pool dimensionality (higher functional diversity) and niche dimensionality (environmental heterogeneity) maintained species coexistence by facilitating species sorting in heterogeneous environments. Our general finding of a positive relationship between local species richness and seed-size diversity in disturbed communities is consistent with this idea, suggesting that coexistence via species sorting may be a widespread mechanism in plant community assembly. Seed size is widely recognized as a key functional component of plant ecological strategies linked to species' regeneration niches (Westoby *et al.* 2002). Higher variation in seed size in the potential species pool can therefore allow more species to exploit 'windows of opportunity' (Davis *et al.* 2000) created when disturbance increases environmental heterogeneity in local communities. Our analysis illustrates the utility of examining functional biodiversity in species pools as a continuous variable measured in terms of a single key trait. Extending this framework by examining multiple functional traits provides a promising avenue for future observational and experimental studies.

Our review highlights the need to better understand how additional ecological filters interact with seed arrival to structure biodiversity. Although a wide range of ecological

filters has been examined (related to disturbance, nutrient availability, water availability, competition, predation, productivity, temperature; Table 1), the small number of experiments available for most ecological filters limits our ability to draw general conclusions. The lack of effects of nutrient or water availability observed in our analysis probably reflected small sample size ($n = 4$ experiments). In contrast, these abiotic filters could have both positive and negative effects on seed and seedling recruitment, resulting in no net effect on species richness. Of the three studies that examined effects of productivity and seed arrival on local species richness (Foster *et al.* 2004 [see also Foster 2001]; Houseman & Gross 2006; Stein *et al.* 2008), all demonstrated an interaction between the two factors, whereby positive effects of seed arrival declined at high productivity. These studies provide support for the shifting limitations hypothesis (Foster *et al.* 2004) based on the models of Grime (1979) and Huston (1999). Finally, we second the call by Turnbull *et al.* (2000) for more experiments addressing the interactive effects of natural enemies (e.g., seed predators) and seed limitation on plant populations and their community-level consequences. In the studies we examined, some natural enemies positively affected recruitment of dispersing species by reducing plant biomass and competition (Eskelinen & Virtanen 2005), whereas others negatively affected dispersing species via seed predation (Fraser & Madson 2008). Future experiments that disentangle effects of natural enemies can help to clarify the conditions under which propagule arrival influences biodiversity.

Where do we go from here? Limitations and empirical gaps

Natural levels of seed rain

An important limitation of most current seed-addition experiments is that natural levels of seed rain are not reported or unknown (Turnbull *et al.* 2000; Clark *et al.* 2007). To our knowledge, the highest level of seed rain reported for grasslands is 19 700 seeds/m^2/year (North-American tall-grass prairie; Rabinowitz & Rapp 1980), and numbers are known to vary widely among communities (e.g., 3820–10 000 seeds/m^2/year in European grasslands; Jakobsson *et al.* 2006; Poschlod & Jordon 1992 in Zobel *et al.* 2000). Among the studies included in our review, 50% used total seed densities that exceeded 20 000 seeds/m^2/year and 39% used densities exceeding 40 000 seeds/m^2/year, i.e., more than double the seed rain reported by Rabinowitz & Rapp (1980). High seed densities are useful when the goal of the experiment is to saturate most microsites with seeds or if seed viability is especially low, although seed viability data are infrequently reported. However, adding seeds at densities that occur well outside natural levels of seed rain can result in an overestimate of

the importance of species pools in limiting observed local diversity. In addition, most studies added seeds in a single dispersal event, thereby removing interspecific differences in the timing of dispersal, a process that can have important influences on community assembly. Although studies of natural seed rain may require significant investments in time, resources, and the selection of appropriate seed traps (e.g., Chabrerie & Alard 2005), they will greatly improve both the design and interpretation of seed-addition experiments.

The role of dispersal in species coexistence vs. diversity limitation

The relative roles of dispersal in limiting vs. maintaining community diversity has received little attention, but has important implications for understanding community assembly, species coexistence, and biodiversity patterns at multiple scales (Vandvik & Goldberg 2005, 2006). Vandvik & Goldberg (2005, 2006) suggested an approach that partitions diversity into components that are independent of, maintained by, or limited by dispersal. This distinction is important, because it helps to clarify differences in the way dispersal has been conceptualized in the literature, e.g., in spatial models of species coexistence (Amarasekare 2003; Levine & Murrell 2003) vs. models based on dispersal limitation from regional species pools (e.g., MacArthur & Wilson 1967; Hubbell 2001). In this context, the seed-addition experiments used in our analysis generally provide insight into the extent to which community diversity is limited by dispersal (i.e., immigration; Vandvik & Goldberg 2005). In contrast, seed-arrival experiments that directly manipulate seed shadows are better suited towards understanding how dispersal maintains species coexistence (Stoll & Prati 2001; Levine & Murrell 2003). The utility of these complementary approaches does not necessarily reflect processes operating at different spatial scales. For example, metacommunity models predict that arrival of dominant competitors from the regional species pool reduces local diversity (Leibold *et al.* 2004). To resolve the general question of how dispersal facilitates species coexistence and limits diversity, we need better empirical data on several fronts, including the extent to which dispersal limitation differs among species (Clark 2009), interspecific trade-offs between dispersal ability and other ecological traits (Levine & Murrell 2003), functional mechanisms influencing interspecific responses to ecological filters, and how stochasticity in propagule arrival influences community assembly (Chase 2003; Turnbull *et al.* 2008).

CONCLUSIONS

Our review of experimental studies indicates that local plant species richness is generally limited by propagule supply, and that the consequences of propagule arrival for local diversity can be strongly influenced by ecological filters, such as those mediated by disturbance. Three important implications

emerge from our meta-analysis. First, current experimental studies in plant communities suggest a fundamental role for species pools in local community assembly, species coexistence, and biodiversity. Positive effects of species pools on local biodiversity suggest that many communities are unsaturated with species and open to invasion by both native and exotic species. At the same time, propagule supply imposes a strong limit to local diversity that can potentially have cascading effects on community stability (e.g., increased local extinctions) and ecosystem function (e.g., changes to primary productivity; Zobel *et al.* 2006; Lee & Bruno 2009). Second, a comprehensive understanding of the role of dispersal-based processes in community ecology will require synthetic approaches that explore how dispersal and environmental heterogeneity interact to structure communities. Theoretical and empirical contributions in this area will become increasingly important in the face of global environmental change owing to rapid habitat loss, fragmentation, and climate change. Finally, we need more empirical studies that test the mechanisms proposed to explain dispersal-diversity patterns, including the importance of functional trait diversity in local and regional species pools. The experimental studies reviewed here provide a useful framework from which we can build and expand on to help reconcile many outstanding questions in community ecology.

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SUPPORTING INFORMATION

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Table S1 Homogeneity statistics and *P*-values from categorical and continuous mixed-effects models.

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Table S1. Homogeneity statistics and *P*-values from categorical and continuous mixed-effects models. The results are summarized in Fig. 1 (categorical models) and Fig. 2 (continuous models). df = degrees of freedom, Q_B = between-class homogeneity, Q_W = within-class homogeneity, *P* = level of significance for Q_B (*P*-values <0.05 are shown in bold).

Variable	df_{total}	Q_B	Q_W	*P*
Categorical				
Disturbance	39	5.96	48.51	**0.0145**
Nutrient	7	1.17	6.97	0.2785
Water	7	0.03	6.42	0.8420
Continuous: No disturbance				
Species richness	16	0.83	20.80	0.3621
Species evenness	16	4.78	18.12	**0.0287**
Functional richness	16	1.50	19.74	0.2201
Functional evenness	16	1.12	18.97	0.2887
Seed size diversity	16	0.21	21.02	0.6431
Continuous: Disturbance				
Species richness	17	0.003	19.14	0.9553
Species evenness	17	13.27	16.00	**0.0002**
Functional richness	17	0.42	18.85	0.5136
Functional evenness	17	3.10	16.74	0.0779
Seed size diversity	17	7.68	17.03	**0.0055**