

Dispersal and Species Diversity: A Meta-Analysis

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ABSTRACT: Species diversity in communities of interacting organisms is thought to be enhanced by dispersal, yet mechanisms predicting this have little to say about what effects differing rates of dispersal have on diversity and how dispersal affects diversity at larger spatial scales. I performed meta-analyses on 23 studies comprising 50 experiments that manipulated species migration and measured community richness or diversity to test three hypotheses: that dispersal increases local diversity; that this effect depends on the rate of dispersal, specifically, that local diversity should be maximized at intermediate dispersal rates or else linearly related to dispersal rate; and that regional diversity may be either unaffected or negatively impacted by dispersal because dispersal tends to homogenize local communities. I found that immigration increased local diversity. Further, in animal studies, diversity appears maximized at intermediate dispersal rates but not with plant studies; however, more standardized studies are needed. Finally, results are ambiguous as to what happens at larger scales, with studies finding either declines or no change in regional diversity with dispersal. Taken together, these results reveal that dispersal has a complex, spatially contingent relationship with patterns of species diversity.

Keywords: dispersal, metacommunity, meta-analysis, richness, spatial scale.

Dispersal as a community-structuring mechanism has a long and recurring history in ecology. For example, shortly after the turn of the past century, Volney Spalding, an early plant ecologist, showed that dispersal was an important factor structuring desert plant communities (Spalding 1909). Since then, dispersal has had continued success as a potential explanation for community and biogeog-

raphy patterns (e.g., Gleason 1917; MacArthur and Wilson 1967; Levins 1969; Levins and Culver 1971; Horn and MacArthur 1972; Brown and Kodric-Brown 1977; Hastings 1980; Terborgh and Faaborg 1980; Cornell 1985, 1993; Shmida and Wilson 1985; Cornell and Lawton 1992; Rees 1995; Chesson 2000). However, only recently have ecologists further developed explicit predictions about the role of dispersal in structuring communities (e.g., Mouquet and Loreau 2003; Leibold et al. 2004; Mouquet et al. 2006) and used controlled experiments to test how dispersal affects species diversity (e.g., Kneitel and Miller 2003; Cadotte 2006). To date, no one has quantified how important dispersal is across differing habitats and organisms.

Many ecologists now dichotomize ecological processes into those operating at local and regional spatial scales (e.g., Ricklefs 1987; Cornell and Lawton 1992; Cornell and Karlson 1997; cf. Levins and Lewontin 1985). Local processes generally describe species interactions at small spatial scales, especially competition, niche partitioning, and predation, which serve to limit the number of locally coexisting species (e.g., Grinnell 1917; Hutchinson 1957; Chase and Leibold 2003; Kneitel and Miller 2003). On the other hand, processes operating at regional scales refer to organisms moving among local communities, new species entering local communities from a species pool or over long temporal scales, and speciation, all of which likely enhance local species diversity (Ricklefs 1987; Hubbell 2001; Leibold et al. 2004).

However, increasing evidence from studies of species invasions reveals that local communities are not saturated, with diversity increasing as new species establish in extant communities (Simberloff 1981; Sax et al. 2002; Smith and Shurin 2006). Dispersal enhancing local diversity is certainly not a controversial concept (e.g., Loreau and Mouquet 1999), but how dispersal affects local communities has been shown to depend on a number of processes such as the species interactions present. For example, dispersal may potentially differentially affect communities primarily structured by competition compared with those structured by a generalist predator (Shurin and Allen 2001; Kneitel and Miller 2003). The presence of differing species interactions may reduce certainty in the prediction that dis-

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persal increases local diversity. Furthermore, experiments using laboratory systems to examine predator-prey interactions show that dispersal can increase either the persistence of species (Huffaker 1958; Holyoak and Lawler 1996; Holyoak 2000) or the risk of extinction (Burkey 1997; Holyoak 2000; Cadotte and Fukami 2005), depending on the nature and stability of the interactions.

Yet more basic than these contingencies is the fact that dispersal is often more than an all-or-nothing process: species vary in their dispersal abilities, and local communities vary in their levels of isolation and connectedness (MacArthur and Wilson 1967; Cottenie et al. 2003; Mouquet and Loreau 2003). While dispersal is generally thought to increase local coexistence, too high a dispersal rate can be detrimental to species coexistence; hence, dispersal rate may have nonlinear effects on diversity (fig. 1; Kneitel and Miller 2003; Mouquet and Loreau 2003). Mouquet and Loreau (2003) modeled competitive differences and stochastic extinctions to show that intermediate dispersal rates maintain the greatest local diversity (fig. 1). Mechanistically, too low a dispersal rate means that both stochastic extinctions and negative interactions cause local populations to become extinct without rescue, while at high rates, dominant competitors are introduced into all local communities. However, the models of Mouquet and Loreau (2003) assume that negative interactions ultimately limit coexistence, and others assume that such negative interactions imply an upper limit to the number of species that can coexist (e.g., Ricklefs 1987; Cornell and Lawton 1992; Cornell and Karlson 1997). Other authors question whether communities can be saturated, predicting that as the size of the regional species pool increases, immigration should increase local diversity (e.g., Hubbell 2001; Smith and Shurin 2006 and references therein; but see a discussion of spatial scale contingencies in Loreau 2000).

Beyond dispersal effects on local community diversity is what happens at larger spatial scales. A number of authors have argued that dispersal among local communities serves to homogenize and therefore reduce among-habitat variation, or beta diversity (Loreau 2000; Mouquet and Loreau 2003; Cottenie and De Meester 2004). But how this reduction affects regional, or gamma, diversity is not clear (Loreau 2000; Kneitel and Chase 2004). The difficulty is that as dispersal increases local diversity, beta diversity decreases. Because we can view local and beta diversity as additive quantities, equaling regional diversity (Lande 1996; Veech et al. 2002), the relative change in regional diversity will depend on which diversity, local or beta, shows a greater response. Mouquet and Loreau (2003) show that at lower rates of migration, regional diversity remains unchanged as the loss in beta is offset by increases in local diversity (fig. 1). However, at higher rates of mi-

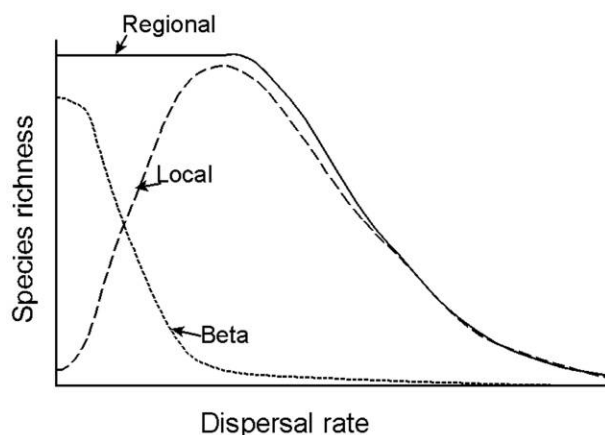


Figure 1: Hypothesized interaction between dispersal rate and species diversity at different spatial scales (adapted from Mouquet and Loreau 2003).

gration, losses in both local and beta diversity mean that regional diversity declines.

In this study, I used meta-analyses of published studies examining the following: (1) that the presence of dispersal increased local diversity (e.g., Shmida and Wilson 1985); or possibly (2) that this effect depended on rate of dispersal and that local diversity either (a) was maximized at some intermediate rate (Mouquet and Loreau 2003) or (b) increased with increasing dispersal rate; and, finally, (3) that regional diversity was either unaffected or negatively affected by dispersal (Mouquet and Loreau 2003).

Methods

I conducted meta-analyses on experimental studies that manipulated species dispersal and measured this effect on species richness or diversity. In June 2005, I searched two databases, Biological Abstracts (WebSPIRS 5, Ovid Technologies, New York) and Web of Science (Thompson Scientific, Stamford, CT), using various combinations of the following keywords: diversity, richness, local, regional, community, dispersal, immigration, and saturation. I used studies that manipulated immigration of individuals (either in a binary fashion or by rate), contained at least five species, and examined species for more than a single generation, in order to allow competitive interactions to occur. A total of 23 studies representing 50 experiments were included (table 1). These experiments represent a diverse array of organisms and study systems and, surprisingly, given how long immigration has been viewed as important for diversity, were all published within the past 10 years.

Despite recommendations from various authors (e.g., Gurevitch et al. [2000; 2001]), most studies used in this

Table 1: Articles used in this study

	Organisms	Dispersal treatment	Measure of diversity	Hypotheses tested	Used in rate analysis?
Brown and Fridley 2003	Plants	Seed sowing	Richness	Local (2)	No
Cadotte 2006	Protozoans	Open corridors	Richness	Local (2), regional (2)	No
Cadotte and Fukami 2005	Protozoans	Individuals moved among communities	Richness	Local (1), regional (1)	Yes
Cadotte et al. 2006	Protozoans	Individuals moved among communities	Richness	Local (6), regional (2)	Yes
Forbes and Chase 2002	Zooplankton	Connectivity among local communities	Richness	Local (1), regional (1)	Yes
Foster 2001	Plants	Seed sowing	Richness	Local (1)	No
Foster and Tilman 2003	Plants	Seed sowing	Richness	Local (1)	Yes
Foster et al. 2004	Plants	Seed sowing	Richness	Local (1)	No
Gehring et al. 2002	Soil fungus	Exclusion of mammal vectors	Richness	Local (1)	No
Gilbert et al. 1998	Arthropods	Patch connectivity	Richness	Local (1)	No
Gonzalez and Chaneton 2002	Arthropods	Patch connectivity	Richness	Local (1)	No
Gross et al. 2005	Plants	Seed sowing	Richness	Local (1)	Yes
Kellogg and Bridgman 2004	Plants	Seed sowing	Richness	Local (1)	Yes
Kneitel and Miller 2003	Protozoans	Individuals moved among communities	Richness	Local (2)	Yes
Matthiessen and Hillebrand 2006	Algae		Richness	Local (3), regional (2)	No
Mouquet et al. 2004	Plants	Seed rain exclusion	Diversity	Local (1)	Yes
Rantalainen et al. 2004	Arthropods	Patch connectivity	Richness	Local (3)	No
Shurin 2001	Zooplankton	Individuals moved among communities	Richness	Local (4)	No
Spencer and Warren 1996	Protozoans	Individuals moved among communities	Richness	Local (1)	No
Tilman 1997	Plants	Seed sowing	Richness	Local (1)	Yes
Warren 1996	Protozoans	Individuals moved among communities	Richness	Local (2), regional (2)	Yes
Xiong et al. 2003	Plants	Seed sowing	Richness	Local (1)	Yes
Zobel et al. 2000	Plants	Seed sowing	Richness	Local (1)	Yes

Note: The number in parentheses following hypotheses tested indicates the number of experiments.

analysis did not explicitly state mean values (\bar{x}) or a measure of variation such as standard deviation (s), so these values had to be extrapolated from figures using a program called DataThief II, version 1.1.0 (<http://www.nikhef.nl/~keeshu/datathief/>). The studies used here all included the sample size. In studies reporting multiple sampling dates, I used only the final sampling date in order to analyze outcomes over the most generations. Studies were classified into one or more of three groups: those comparing effects of the presence/absence of dispersal of individuals among communities or immigration into communities on local diversity (referred to as local studies), those that gave requisite information to calculate dispersal rate (rate studies), and those comparing the effects of dispersal on regional or metacommunity diversity (regional studies). Therefore, with the local and regional studies, dispersal

simply refers to individuals entering or moving among communities, while the rate studies refer to the standardized measure defined below.

It seems that hypotheses 1 and 2a are mutually exclusive when in reality they are not. Figure 2 shows that even when there is an underlying rate effect, the mean dispersal effect on local diversity will be larger than that of the no-dispersal control. Furthermore, whereas testing hypotheses 1 and 3 with existing studies was rather straightforward, the ability to examine hypothesis 2 was problematic because different studies variously defined dispersal rates. For example, most experiments used in this meta-analysis categorize treatments into, for example, high and low treatments, without any obvious standardization among studies.

In order to test hypothesis 2 adequately, one must stan-

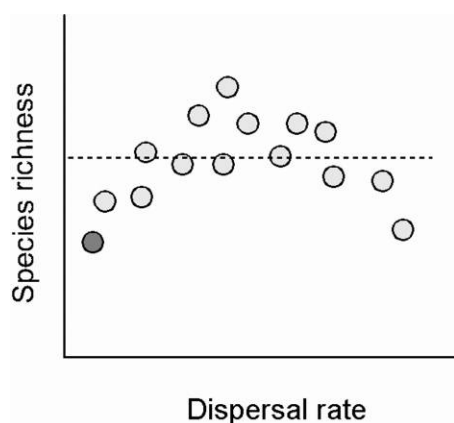


Figure 2: Dispersal enhances richness despite a rate effect. *Filled circle* = no-dispersal control; *open circles* = hypothesized rate effect; *dashed line* = mean of dispersal treatments.

standardize dispersal. A simple standardized rate of immigration (D) is the rate of immigration (i) per community resident density (ρ):

$$D = \frac{i}{\rho}, \quad (1)$$

where i is the number of individuals (n) per generation time (t) such that

$$D = \frac{(n/t)}{\rho}. \quad (2)$$

Here, ρ is a measure of the number of individuals per unit area (or volume). This type of standardization has the added benefit of allowing immigration rate to be analyzed in predictive regression models and permitting any study, even those that manipulate a single dispersal rate, so long as they provide the requisite information.

Some information required in equation (2) had to be determined from the primary and secondary literatures. For example, some of the plant-based studies gave a single species' proportion of total seed mass added, and so I had to find seed masses for the species used. Similarly, generation times needed to be located in the literature.

Experiments used to test the rate effect were divided into separate analyses, for animals and for plants. This was done because, first, plant and animal studies used very different measures of resident density, with plant studies using percentage cover and animal studies using an estimate of the numbers of individuals. Second, the unit of dispersal differed greatly. In animal studies, juveniles or adults were the units of dispersal, while in plant studies,

the units were seeds dispersed. These dispersal units have very different survivorships, resulting in animal studies dispersing tens to hundreds of individuals and plant studies dispersing thousands to tens of thousands of seeds.

Statistical Analyses

The approach was adapted from Gurevitch and Hedges (2001), and all the equations used are shown in the appendix. The basis of meta-analysis is to combine independent studies into some overall measure of effect size. In this case, the effect is of immigration on species diversity.

I employed a test for homogeneity of effects for the different treatments using Cochran's Q . If effects were found to be homogeneous, then a fixed-effects model for calculating the grand mean effects was used; otherwise, I used a mixed model (see appendix). I calculated the confidence interval (CI), and the standard approach to assessing significance is to see whether the CI intersects 0. However, I also used a nondirectional test, analogous to a χ^2 test, as an independent estimation of P values (see appendix). For all cases, I subtracted the mean control diversity from the treatment diversity; thus, a positive effect size implies that dispersal increases diversity.

The data compiled for hypothesis 2 included a continuous dependent variable (dispersal rate), so the standard meta-analytic approach had to be modified in this case. For each experiment included, I calculated a standardized dispersal effect as (treatment diversity – control diversity)/control diversity.

This dependent variable was regressed against the standardized immigration rate in both a linear and a nonlinear (quadratic) model. If both models revealed a significant relationship, they were compared using Akaike's Information Criterion (AIC). Because the dependent variable was standardized by the control, all regression models were constrained by an intercept of 0.

Criticisms of Meta-Analyses

Though an efficacious statistical tool, meta-analyses in ecology may be epistemologically problematic. One could view ecological processes as universal laws that transcend local vagaries of time and space, in which case meta-analyses are an appropriate tool for synthesizing results across experiments. However, if one subscribes to the idea that ecological patterns are driven by a multitude of spatially and temporally contingent processes or that many different processes can produce similar patterns, then meta-analyses falsely reify trends into a single hypothesis test (D. Simberloff, personal communication). If contingency and multiplicity of processes are important, ecol-

Table 2: Results of homogeneity tests for the fixed-effects model (Q_f) and the mixed-effects model (Q_m) if needed

Test	k	Q_f	Q_m
Local-binary	40	117.241*	50.890 NS
Regional	11	10.182 NS	...

Note: NS = nonsignificant.

* $P < .001$.

ologists should be primarily trying to understand how individual communities are structured rather than searching for general processes or laws that cannot predict or explain the workings of particular communities except at a very high level (Simberloff 2004).

Osenberg et al. (1999) critiqued the use of meta-analysis in ecology and called for the use of a variety of effect size metrics. However, Gurevitch et al. (2001) disagreed with Osenberg et al. (1999) and instead supported the use of a single mean effect size metric that can be universally understood by ecologists and argued that a lack of a standard makes evaluation of results difficult. Here, I use the standard approach advocated by Gurevitch et al. (2001).

Further, Murtaugh (2002) revealed that the data used in meta-analyses might be affected by journal quality. However, even if effect size increases with journal quality, that does not mean that a journal's quality caused the effect size (as would be interpreted from Murtaugh's use of regression); rather, this correlation could simply mean that more powerful experiments with more conclusive results are generally published in better journals. As long as researchers employing meta-analyses use studies from all recognized, peer-reviewed journals, then their analyses should represent an unbiased sample. Nevertheless, I regressed effect size on the log of ISI impact factor (Thompson Scientific). Effect size increased slightly with impact factor (slope = 2.1115), but this relationship was not significant ($P = .2317$).

Results

The studies used in this analysis represent a diverse range of organisms and dispersal treatments (table 1). The potential existed for these disparate experiments to exhibit diverse effects. I calculated standardized effect sizes for each study for hypotheses 1 and 3. Before interpreting the overall grand effect, I tested for homogeneity among studies and found that the local comparisons (hypothesis 1) had heterogeneous effects (table 2). For these comparisons, I used the mixed-effects model, and I used the fixed-effects model for the comparison among regional studies. It is important to note that the mixed model for the local studies was considered homogeneous, which means these stud-

ies did not need to be analyzed in smaller, more homogeneous groups (i.e., plants vs. animals).

Hypothesis 1: Dispersal Increases Local Diversity

Using a fixed model, I found that the studies comprising this comparison were heterogeneous, but they were homogeneous with the mixed model (see table 2), so the mixed model was used. Most experiments testing this hypothesis revealed a positive effect of dispersal on local diversity (fig. 3). In terms of confidence intervals, two experiments showed significantly negative responses, nine no response, and 29 a positive response. The grand effect was significantly positive (fig. 3; $\chi^2 = 113.870$, $df = 40$, $P < .0001$), meaning that the presence of dispersal strongly increased local diversity.

Hypothesis 2: Nonlinear Effect of Dispersal Rate on Local Diversity

The animal and plant data had to be separated in order to test the hypothesis that there was a unimodal relationship between diversity and standardized dispersal rate. For the animal analysis (fig. 4), both the quadratic and linear models revealed a significant relationship between the standardized immigration rate and the treatment effect on diversity (quadratic model: $F = 5.771$, $df = 2, 16$, $P = .016$, $R^2 = 0.47$; linear model: $F = 11.307$, $df = 1, 16$, $P = .005$, $R^2 = 0.45$). Further, AIC indicated that the linear model better fit the data (linear model: AIC = 101.137; quadratic model: AIC = 119.017). However, it is

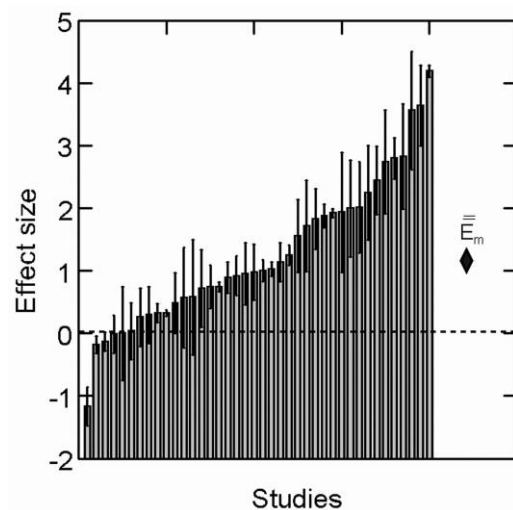


Figure 3: Standardized effect size of the studies used to test hypothesis 1 (local diversity). \bar{E} = grand mean effect size using the mixed model, m . Error bars represent the 95% confidence intervals.

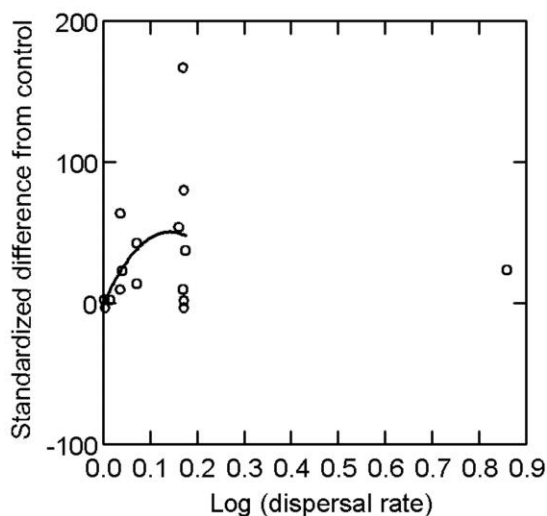


Figure 4: Effect of the standardized dispersal rate on the standardized diversity of treatment for animal experiments. The line represents the quadratic model, including all data points except the outlier.

clear from figure 4 and from regression diagnostics that there was an outlying data point with an extremely high dispersal rate. When this point was removed, the results indicated that the quadratic model was a significant predictor while the linear model was not ($F = 5.97$, $df = 2, 15$, $P = .013$, $R^2 = 0.46$ vs. $F = 3.085$, $df = 1, 15$, $P = .099$, $R^2 = 0.17$; fig. 4).

The results of the plant analyses revealed that neither quadratic nor linear models were significant predictors of treatment effects on diversity ($F = 0.35$, $df = 2, 6$, $P = .73$, $R^2 = 0.19$ and $F = 0.932$, $df = 1, 6$, $P = .389$, $R^2 = 0.19$, respectively). The plant data were represented by a small number of data points, with a lot of scatter at low dispersal rates (fig. 5). Further, an outlying data point with an extremely large dispersal rate was removed (not shown).

Hypothesis 3: Dispersal Decreases Regional Diversity

The fixed model was found to be homogeneous (see table 2) and so was appropriate. In six of the 11 studies comprising this comparison, dispersal negatively affected regional diversity (fig. 6). Four studies had a CI that overlapped with 0, indicating no effect, and one had a positive effect. The grand effect and its CI were well below 0, indicating a significant negative effect associated with dispersal. However, the result of the nondirectional test indicated nonsignificance ($\chi^2 = 14.653$, $df = 11$, $P = .1989$), revealing that this result needs to be carefully considered, especially in lieu of the small sample size, and

perhaps that meta-analyses in general need carefully to consider what is a significant result. The nondirectional test is a more conservative test and is less likely to find significance with small sample sizes and large variances.

Discussion

Individual studies exploring the effect of dispersal on patterns of species diversity may be influenced by various spatially and temporally dependent ecological processes (Zobel and Kalamees 2005). A meta-analysis can overcome these vagaries and highlight general effects of dispersal. I have shown that immigration had a strong positive effect on local diversity (hypothesis 1; fig. 3). This positive effect was apparent over a diverse assembly of study systems and organisms. If communities are available for colonization by new species, then larger-scale processes may be important for patterns of local diversity (Cornell and Lawton 1992). These results support the general notion that local communities are not necessarily saturated and that local species interactions may not limit future species invasions (e.g., Simberloff 1981; Sax et al. 2002; Smith and Shurin 2006). These diversity increases may not even be permanent, and without continued dispersal, diversity would decrease. Regardless, dispersal-dependent increases reveal that mechanisms such as mass effects (Shmida and Wilson 1985; Mouquet et al. 2006) can overcome negative interactions.

Further, there is a potential nonlinear effect of dispersal rate on species diversity (fig. 4), qualitatively supporting the claims for this made by Mouquet and Loreau (2003).

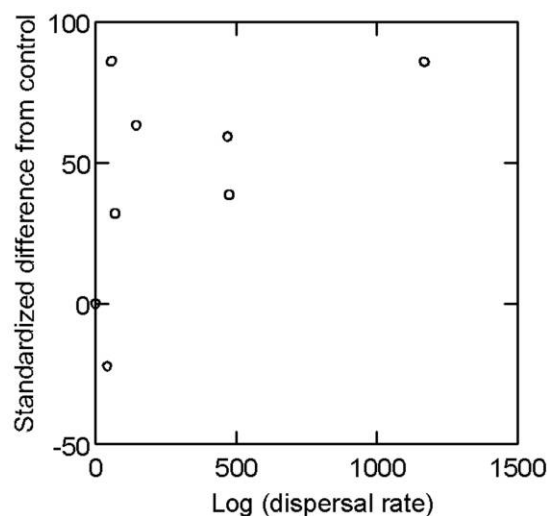


Figure 5: There was no effect of the standardized dispersal rate on the standardized diversity of treatment for plant experiments.

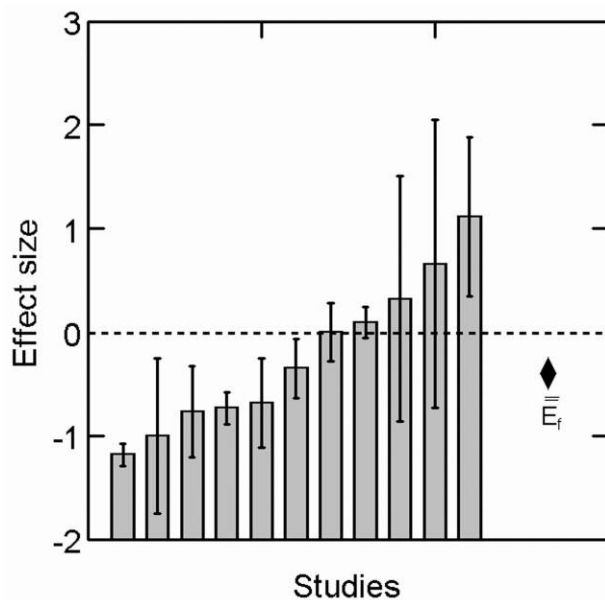


Figure 6: Standardized effect size of the studies used to test hypothesis 3 (regional diversity). \bar{E} = grand mean effect size using the fixed model, f . Error bars represent the 95% confidence intervals.

The results would have benefited from a greater sample size. The animal studies (fig. 4) were missing higher rate treatments, with the exception of the single outlier from Cadotte and Fukami (2005). In fact, several animal studies claimed to examine more than a single dispersal rate treatment, yet the different rates within a single study were surprisingly similar once entered into equation (2). The obvious conclusion from these results is that empirical studies need to conceptualize dispersal rate better to test hypotheses about the effect of dispersal rate on patterns of species diversity.

However, focusing on a single scale of organization can lead to erroneous conclusions about processes occurring at other scales. That local communities are not saturated does not necessarily lead to the conclusion that communities are under the control of regional processes. The processes defining patterns of local diversity may have different effects at larger spatial scales and vice versa (Huston 1999; Loreau 2000; Sax et al. 2002). Dispersal may increase local diversity, but dispersal will also likely affect beta, or among-community, diversity (Loreau 2000; Kneitel and Chase 2004). My analysis revealed that dispersal experiments often observe declines in regional diversity, at least more often than they observe increases (hypothesis 3), but again there is a dearth of studies testing this hypothesis, and there were certainly too few studies to examine the role of rate of migration on regional diversity. The likely

explanation for the decline is that by allowing increased numbers of individuals to move among local communities, beta diversity declines as these communities become increasingly homogenized. This homogenization means that dominant competitors or generalist predators have impacts in all local communities and likely structure the region in a monotonous fashion (e.g., Cadotte and Fukami 2005; Cadotte et al. 2006). Kneitel and Chase (2004) thought that if coexistence-promoting mechanisms are local in nature (resource use, environmental stress, predation, etc.), then local diversity should be high, and perhaps increasable, while beta diversity should be low. Kneitel and Chase (2004) were uncertain about what should happen to regional diversity, but the present results show that the magnitude of the increase in local diversity is not likely to be greater than declines in beta diversity, meaning that in the presence of dispersal, regional diversity will decline or remain unchanged compared with no-dispersal treatments. Therefore, species in dispersal treatments are either just as likely or more likely to become extinct as in no-dispersal treatments.

These scale-dependent results have important conservation implications because the perspective of conservation managers in regard to migration depends on their scale of concern. For example, if managers are interested in maintaining maximal diversity over a fragmented landscape, then perhaps restricting, or at least not enhancing, dispersal would best ensure regional diversity. However, if the concern is a single local community, then enhancing immigration may be the best option. There is a long-running debate in conservation ecology as to the benefit of using corridors to link habitats (e.g., Noss 1987; Simberloff and Cox 1987). I would argue, on the basis of the current results, that this is a debate about the scale of effects rather than the nature of effects.

Limitations on Interpretation

The studies in this meta-analysis may not be adequate to draw firm conclusions about how dispersal interacts with species diversity at different spatial scales. I have four main concerns.

First, most of the studies either used homogeneous local conditions or failed to measure microenvironmental conditions. Metacommunity theory predicts that heterogeneity among local communities can have important consequences on species diversity (Mouquet et al. 2006). Heterogeneity should enhance the relative importance of mass effects, as heterogeneity likely results in spatial variation in a species' growth rate. Mouquet et al. (2006) showed that when heterogeneity is measured as resource supply rate differences among local communities, richness is maximized at intermediate levels of heterogeneity. Es-

entially, little or no heterogeneity results in regional domination by species best adapted to resource supply rates. While at high heterogeneity levels, local patches are inhabited exclusively by species adapted to local supply rates. In the intermediate case, large populations are able to subsidize slowly declining populations (e.g., mass effects). More than a mechanism for local coexistence, environmental heterogeneity can potentially drive diversity patterns at different spatial scales such that heterogeneity can be seen as a diversifying, or beta-increasing, processes (Cottenie and De Meester 2004), which would maintain greater regional diversity. This is an important criticism because when heterogeneity is not explicitly measured or addressed, a researcher's ability to interpret tests of hypotheses can be affected, as processes that can potentially enhance or reduce diversity may be in operation. Only two studies included local environmental differences (Kneitel and Miller 2003; Cadotte et al. 2006). For example, Cadotte et al. (2006) manipulated resource availability in local communities of aquatic protozoans and metazoans and found that low-resource communities showed a greater benefit from dispersal, presumably because extinction risks were higher in the absence of dispersal. Unfortunately, a couple of further studies that adequately included natural variation by using natural ponds had to be excluded because of the lack of a no-dispersal control. Cohen and Shurin (2003) examined the effect that distance gradients (as dispersal rate surrogate) had on pond diversity and concluded that distance had a strong effect on colonization and potentially on species diversity. Similarly, in a natural pond survey using distance as a dispersal surrogate, Chase and Ryberg (2004) showed that a region with closer ponds (higher dispersal rate) had lower regional diversity.

A second issue is the nature of the dispersal treatments. Most studies simply introduced set amounts of propagules without any explicit consideration for species-specific attributes. The natural movement of individuals influences patterns of species coexistence through a number of possible mechanisms: an evolutionarily derived competition-colonization trade-off (Levins and Culver 1971; Hastings 1980; Yu and Wilson 2001; Amarasekare 2003; Kneitel and Chase 2004), source-sink dynamics (Brown and Kodric-Brown 1977), or mass effects (Shmida and Wilson 1985; Kunin 1998). By removing a set amount of the community, or introducing a set number of propagules, studies are using a density-dependent dispersal probability that is antithetic to potential competition-colonization trade-offs, which require inferior competitors (lower abundance) to be superior dispersers. The drawback of incorporating natural dispersal abilities is that dispersal is less tractable. However, one study (Mouquet et al. 2004) explicitly manipulated dispersal to test potential competition-colonization

trade-offs in plant communities. They had dispersal scenarios in which dispersal was positively, negatively, or not correlated with competitive ability, and they showed that allowing for competition-colonization trade-offs enhanced coexistence and occupancy patterns for poor competitors.

Third, specific ecological interactions may change how dispersal impacts patterns of coexistence. For example, predation is thought to have profound effects on dispersal-mediated patterns of diversity (Shurin and Allen 2001). Kneitel and Miller (2003) and Cadotte et al. (2006) reveal that the presence of a predator can undo any positive effect of dispersal. However, Shurin (2001) showed that predation could offer openings for colonizers and in fact appears to enhance diversity increases through dispersal. Besides predation, variation in competitors could also impact the dispersal effect on diversity. For example, Cadotte (2006) showed that in competitively structured communities, variation in initial species assembly could result in supporting or rejecting the Mouquet-Loreau hypothesis, revealing the importance of community history.

Finally, dispersal (as used in this study) is quite ambiguous. The studies used to test the first two hypotheses include either immigrants arriving from outside the local species pool or individuals moving among local communities within the local pool. Species pool effects can have important consequences for patterns of local diversity (Zobel 1997; Chase 2003). The first immigration type (from beyond the local pool) is often used in studies examining plant communities and provides greater tractability, as novel species are easy to enumerate. The second type (within pool) may be more realistic and explicitly draws links among spatial scales. This type of migration is an essential component of metacommunity dynamics. Metacommunities are sets of local discrete communities that interact via migration (Wilson 1992; Leibold et al. 2004). The studies used to test the regional diversity hypothesis used the within-pool method and are explicit examinations of metacommunity dynamics. These studies reveal that patterns of metacommunity diversity are a balance between local diversity enhancement and regional diversity limitation (see Holt 1993; Cottenie and De Meester 2004), and these patterns are likely mediated by dispersal rate (Mouquet and Loreau 2003).

Conclusion

The dispersal of individuals into and among local communities is thought to affect local diversity through a number of mechanisms. However, these mechanisms often do not explicitly predict what would happen to diversity if dispersal rates varied, nor do they predict effects at larger spatial scales. The results of this study show that dispersal

increases local diversity while simultaneously decreasing regional diversity in the majority of experiments. This pattern reveals that processes at an intermediate scale may be the best avenue to understanding how community diversity is structured. Further, I offer tentative support to the Mouquet-Loreau hypothesis that dispersal rate has a nonlinear effect on diversity. However, more studies that use standardized dispersal rates are needed. Future experiments should explicitly address spatial heterogeneity, the role of species differences such as in competition-colonization trade-offs, the role of specific ecological interactions, and where immigrants come from.

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APPENDIX

Meta-Analysis Methodology and Statistical Tests

Much of what follows in this appendix is adapted from Gurevitch and Hedges (2001). For the i th study, I computed an unbiased standardized mean difference (referred to as Hedges's d):

$$d_i = \frac{\bar{x}_i^e - \bar{x}_i^c}{s_i} J,$$

where \bar{x} is the mean diversity value of the experimental treatment (e) and the control (c) and s_i is the pooled standard deviation and J the correction term for small sample bias. The pooled standard deviation is calculated as

$$s_i = \sqrt{\frac{(N_i^e - 1)(s_i^e)^2 + (N_i^c - 1)(s_i^c)^2}{N_i^e + N_i^c - 2}},$$

where N is the sample size of the treatment (e) and control (c) for the i th study. The correction, J , is calculated as

$$J = 1 - \frac{3}{4(N_i^e + N_i^c - 2) - 1},$$

and as $N \rightarrow \infty$, $J \rightarrow 1$. I also calculated a sampling variance for the i th study:

$$v_i = \frac{N_i^e + N_i^c}{N_i^e N_i^c} + \frac{d^2}{2(N_i^e + N_i^c)},$$

which in turn allows for the calculation of the study confidence interval (CI),

$$CI_i = \frac{d_i \pm t_{\alpha/2, N-1} \sqrt{v_i}}{\sqrt{N_i^e + N_i^c}},$$

so that individual studies with significant treatment effects will have a mean effect (d) and a CI that does not overlap with 0.

Fixed-Effects Model

A standardized measure from k studies is combined into a grand mean effect:

$$\bar{E} = \frac{\sum_{i=1}^k w_i d_i}{\sum_{i=1}^k w_i},$$

where $w_i = 1/v_i$. The variance of this grand mean,

$$\bar{v}_E = \frac{1}{\sum_{i=1}^k w_i},$$

allows the calculation the grand mean confidence interval.

An important assumption is that the studies used in the meta-analyses have homogeneous responses to the treatments. I used Cochran's Q test,

$$Q = \sum w_i (d_i - \bar{E})^2,$$

which is analogous to the within-class variation in an ANOVA test. This Q statistic has a χ_{k-1}^2 distribution. If I failed to detect significance, then I used the fixed-effects model; otherwise, I used a mixed-effects model for describing the grand mean effects.

Mixed-Effects Model

The general calculations for the mixed-effects model are basically the same, except the variances are adjusted. For the grand mean effect,

$$\bar{E}^* = \frac{\sum_{i=1}^k w_i^* d_i}{\sum_{i=1}^k w_i^*},$$

where $w_i^* = 1/v_i^*$. The variance of this grand mean,

$$v_E^* = \frac{1}{\sum_{i=1}^k w_i^*},$$

allows the calculation of the grand mean CI. The difference here is that v_i^* is calculated differently. Here

$$v_i^* = v_i + \hat{\sigma}_{\text{pooled}}^2,$$

where

$$\hat{\sigma}_{\text{pooled}}^2 = \frac{Q - (k - 1)}{c_i},$$

and the constant, c_i is

$$c_i = \sum_{i=1}^k w_i - \frac{\sum_{i=1}^k w_i^2}{\sum_{i=1}^k w_i}.$$

For both the fixed and the mixed models, beyond examining the CI, I used a nondirectional test, analogous to a χ^2 test:

$$\chi_k^2 = \sum_{i=1}^k w_i d_i^2,$$

which gives a significance value to the grand mean departure from 0.

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