# Deterministic and stochastic forces in community ecology: integrating competing paradigms in theory and observation

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**Abstract**:

An important goal in community ecology is to understand the interactions between multiple mechanisms – species differences and niche differentiation, stochasticity, environmental heterogeneity, and spatial processes – and their consequences to community structure. In this dissertation, I address three distinct issues within this general program. First, using a spatially explicit model, I compare assembly, structure, and invasibility of communities with varying levels of neutrality *versus* niche-differentiation. Communities' responses to invasions are determined by the extent of functional variation in the local species pool, predicting varying responses to inter-biome exchange and evolutionary diversification along the niche-neutral gradient. Second, I demonstrate statistical bias in the standard test for monoculture overyielding and develop a bootstrap correction algorithm. Correcting this bias is important to evaluating the relative importance of selection and complementarity effects to community processes. Finally, I analyze the extent to which species differences, dispersal, and stochasticity influence metacommunity dynamics in a long-term nitrogen addition experiment. I find that all three mechanisms are active in the study system, necessitating further development of metacommunity models.

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# Chapter 1: Introduction

A major theme in recent community ecology is the integration of multiple mechanisms into more comprehensive models of community functioning. The originally dichotomous debate between niche (Chase and Leibold 2003) and neutral (Hubbell 2001) processes, for example, has led to an increasing depth of models including stochastic and deterministic processes. Similarly, metacommunity (Holyoak et al. 2005) models extend the spatial and environmental processes of metapopulation models to include species interactions. A common result of these syntheses is a need for empirical results to determine the relative importance of each mechanism in natural communities, and the development of statistical tools to interpret these results.

In this dissertation, I present the results of three approaches to the central goal of integrating multiple mechanisms in community ecology and interpreting empirical results. I use different methods in each chapter, drawing on individual-based stochastic modeling, statistical theory, and empirical analysis.

*Species pool functional diversity and community structure and invasibility*
Neutral theory (Bell 2000, Hubbell 2001) describes a null model for ecology, in which species differences are assumed not to affect demographic processes. Species coexistence in a neutral community, rather than resulting from stabilizing forces (Chesson 2000), results from a balance between the emergence of new species through speciation and extinction of others through random demographic drift. Niche theory, on the other hand, describes communities in which differences in species' traits and environmental

characteristics determine coexistences. Between these alternatives of purely deterministic and purely neutral dynamics, communities may experience stochasticity in dispersal or establishment that reduces the role or pace of niche-differentiation without eliminating it. Similarly, species pools may vary in the degree of functional variation present, possibly containing multiple functional groups of species identical to each other, but distinct from each other group. Communities with these characteristics are neither purely neutral nor purely niche-differentiated, and so novel models are required to predict their dynamics.

Chapter 1 presents a spatially explicit, individual-based model of local community assembly from a regional species pool. We determine how functional diversity in the species pool affects the structure and invasibility of the assembled community by varying the number of functional groups in the metacommunity, simulating the assembly process, and then simulating invasion by species with novel functional traits. We also examine which community characteristics facilitate or impede coexistence of neutral species within the same functional group. The model provides insight into how niche and neutral processes interact to shape long-term community assembly and responses to the introduction of new species through ecological or evolutionary processes.

*Detecting transgressive overyielding*

The relationship between species richness and productivity is a key area of ecological research, involving questions of biogeography, metabolic ecology, and functional differentiation (Mittelbach et al. 2001). A key question in this area concerns the mechanisms by which characteristics of a community's component species determine the

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productivity of mixtures. Two ways that increasing diversity can lead to increasing productivity are the complementarity and selection effects. Complementarity describes when functional differences and distinct resource-use strategies between species allow an assemblage of species to capture more resources than monocultures, and thereby achieve a greater productivity. The selection effect occurs as a statistical effect when polyculture productivity is driven by the presence or absence of the most productive single species. When this occurs, more diverse mixtures are more likely to contain the productive species, and therefore more likely to have higher productivities than less diverse mixtures. Complementarity is a central prediction of many theories of coexistence derived from niche-differentiation, so its presence or absence in natural communities is an important signal of the importance of these mechanisms.

Unfortunately, detection of complementarity based on its strongest empirical evidence, when polycultures outperform the best monoculture (known as transgressive overyielding), can be difficult due to experimental design and statistical complications. In chapter 2, I discuss how the standard analyses of monoculture productivity have led to a bias against detecting transgressive overyielding and I develop methods to measure and correct for this bias in future tests. This analysis also suggests changes to experimental design when the goal is to determine maximal monoculture productivity.

*Local metacommunity processes: spatial dynamics in experimental fields*
Spatial dispersal processes are often considered in conservation design, analysis of species borders, and in theories of metapopulations and metacommunities. They are

rarely taken into account, however, in analysis of experiments testing other mechanisms. In chapter 3, I analyze data from two experiments from Cedar Creek Ecosystem Science Reserve (a nitrogen addition experiment and biodiversity experiment), and find that spatial processes within the experiments' boundaries significantly affect species' colonization and extinction rates. Due to the interactions of dispersal limitation and resource competition, each experimental grid acts as a small-scale stochastic metacommunity. The added insight from adopting the metacommunity perspective increases our understanding of experimental results, and could provide a valuable approach in analysis of other experiments with appropriate spatial structure.

# Chapter 2: Neutral species are excluded by functional differentiation in heterogeneous habitats

Current theory in community ecology attempts to understand interactions between deterministic niche-based processes and stochastic processes driven by dispersal and functional equivalence. We examined the consequences of variation in metacommunity functional diversity and dispersal limitation on local community assembly and structure in an individual-based simulation model with a heterogeneous environment. We found that functionally equivalent species were better able to persist when the metacommunity was limited to a small number of functional groups or under extreme propagule limitation. However, with increasing functional diversity in the metacommunity, neutral species were excluded at a rate significantly greater than chance. Because of the influence of long-time scale processes on metacommunity structure and composition, we analyzed our assembled communities' invasion resistance and stability under scenarios simulating biotic interchange and *in situ* speciation. In both scenarios, local communities with an initially higher functional diversity were both more resistant to invasion and suffered fewer post-invasion extinctions. Neutral species suffered the highest extinction rates under both scenarios. By examining the interaction between long-term niche and neutral processes in a metacommunity context, our analysis helps tie the predictions of these models to observed patterns of cross-realm invasions and species diversification. Our findings suggest that, in conditions with habitat or resource heterogeneity, both biotic interchange

and speciation eliminate neutral coexistence. Because it is unstable with

respect to these two fundamental processes, we do not expect neutrality to

be a common phenomenon in nature.

**Introduction**

While functional diversity is considered one of the major drivers of community assembly

and functioning (Tilman et al. 1997b, Hooper et al. 2005, Cadotte et al. 2011), recent

development of neutral theory has demonstrated that stochasticity and ecological

equivalence may also influence communities in important ways (Gravel et al. 2006, Adler

et al. 2007). Equivalence, the core assumption of neutral theory (Hubbell 2001), means

that species in ecological communities are demographically identical. This marks an

essential difference with traditional niche-based theories in community ecology, and

predictions of niche and neutral models are thus often contradictory. While niche theories

predict that functional trade-offs yield stable community composition, trait-environment

correlations, and predictable competitive outcomes (Higgins and Cain 2002, Chase and

Leibold 2003, Kneitel and Chase 2003), neutral theory predicts dynamic species

turnovers, trait-environment independence, and purely stochastic demographic processes,

and thus unpredictable species composition along gradients. Despite a growing number of

empirical and theoretical studies (Rosindell et al. 2011), key questions remain about the

compatibility and interactions between niche and neutral processes. In particular, models

are lacking that address whether neutrality can be a stable state of communities in

heterogeneous environments, or under the long-term processes of speciation and

migration.

Neutral theory was proposed in part as a null model for community ecology, and as such provides predictions resulting from a very simple description of ecological communities. While neutral theory may not be a true null model in the parameter-free statistical sense (Gotelli and McGill 2006), it does provide predictions about ecological communities following a highly reduced set of interactions. Deviations from these predictions in empirical studies indicate the importance of species distinctions to demographic processes, the role of habitat heterogeneity, or some non-uniform process for speciation in that community (Alonso et al. 2006). Some empirical papers have found examples of contradictions between neutral theory's assumptions and patterns observed in natural systems (McGill et al. 2006), and others have pointed out the difficulty of testing the theory's main predictions (key neutral model predictions are not significantly different from those produced by a number of other theories (McGill 2003)). On the other hand, theory shows that neutral and niche processes are not mutually exclusive (Leibold and McPeek 2006, Chase 2007, Mutshinda and O'Hara 2010), and recent empirical studies have taken an integrative, rather than dichotomous approach (Thompson and Townsend 2006, Stokes and Archer 2010).

An important step to resolving the tension between niche and neutral theories is to consider how their assumptions about processes on the timescales of individual establishment and mortality scale up to predictions about community assembly and stability on long time-scales. The local predictions of each theory are well understood. On short time-scales and at local spatial-scales, neutral and niche theories differ in their

assumptions about species interactions and competition for available sites for propagule establishment. Neutral theory assumes within community equivalence between species, which implies no relation between local environmental characteristics, species identity and species abundance. Niche theory, however, predicts species-environment correlations when the relevant environmental characteristic changes along an axis of intra-community niche-differentiation.

Two major drivers of long-term community assembly are biotic interchanges and evolutionary diversification. In both of these cases, theoretical predictions can be compared with historical patterns. Typically, major biological interchanges, such as the joining of North America and Asia across the Bering Land Bridge, have resulted in mutual gains in biodiversity, and little extinction in either realm (Tilman 2011). This pattern has been repeated in many other cross-invasions, as well as with more recent human-facilitated biological exchanges, as few anthropogenic invasions have resulted in outright extinction.

A second long-term process that should be considered is how robust each model is to evolutionary diversification of functional traits. Two bookend cases to consider are 1) rapid radiative events that typically follow mass-extinctions or the arrival of novel taxa to isolated islands (Schluter 2000) and 2) gradual generation of novel functional diversity through adaptation and diversification of local species (Coyne and Orr 2004).

In this paper we present the results of a community assembly model designed to address the roles of functional diversity and neutrality on community structure. This model extends the non-spatial assembly model of Tilman (2004) to a spatially explicit individual-based framework. Our model is based on several particular assumptions about competitive dynamics in ecological communities. First, we assume species face trade-offs between traits that confer competitive advantages in differing environmental conditions. In the present model, these trade-offs take the form of resource-ratio specialization, as in the traditional essential resource competition model of Tilman (1982), with species differing in their relative competitive abilities for two resources. Second, we include explicit spatial structure and dispersal of discrete propagules. Stochastic dispersal introduces propagule limitation, which provides opportunities for neutral coexistence by limiting potential competitive interactions. Third, we introduce neutrality in the form of multiple species that have identical functional traits in order to examine the conditions under which neutral coexistence might be favored or eliminated. Finally, we include local priority effects through a probabilistic establishment model in which propagules face a resource-dependent risk of mortality as they grow from seeds to adults resulting in stochastic founder effects in the assembly process.

We apply our model to several scenarios of community assembly. In the simplest, a habitat is colonized by a local metacommunity. In these simulations, we vary the relative degrees of functional diversity and equivalence in the species pool. In our second set of simulations we introduce ecological invasion or speciation by including species with novel traits. In all cases, we are interested in the resulting patterns of diversity and

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neutrality. In particular, we ask whether it is possible for a community of functionally equivalent species to resist invasion by species that differ, either due to independent evolutionary past (biotic interchange), or due to local evolutionary diversification.

## Model Description and Methods

*Competition and Dispersal*

Interspecific competition in our model is determined by species' abilities to compete for two essential resources. Resource-ratio theory predicts that the outcome of competition between two individuals depends on their R* values for each resource (the lowest level of that resource for which they are able to persist) and the rate of supply of those resources in the local patch. In our model, species' R* values for each resource (R*1 and R*2, respectively) are constrained to lie along a linear trade-off curve. Thus, each species is characterized by a single trade-off value, $t$, which specifies both R*1 and R*2 (R*1 = R*max * t and R*2 = R*max * (1-$t$) ). In this model, competition between $N$ individuals at a site yields up to two coexisting species, one with a resource ratio (RR) lower than the site's resource supply ratio, and one with a RR higher than the site's supply ratio. The closest fits from either side coexist if both are sufficiently similar to the local site.

Dispersal in the model occurs at local and regional scales: in each timestep, established adults disperse a fixed number of seeds to nearby sites (25 in the simulations discussed here), and a number of propagules from the metacommunity arrive as immigrants, randomly distributed across the entire habitat (1 for every 200 sites). Immigrant propagules are selected uniformly from the species in the metacommunity species pool.

We assume that local dispersal is limited in range, which prevents unnecessary

simulation of wasted propagules (those that land in unsuitable habitat).


*Probability of Establishment and stochastic competition*

Propagules landing on a site must survive a stochastic growth process from seed to

adulthood in order to compete for the site. We assume a constant mortality rate, $\mu$,

throughout the growing period, and that the time to adulthood, $t_A$, depends on the

species' stoichiometry (resource ratio), the ratio and level of available resources at the

site, and the adult:seedling biomass ratio (see Tilman (2004) for details). Because we

treat mortality as an exponential process, this yields a probability of survival to adulthood

$p_A = 1 - \exp(\mu t_A)$. Species' mortality rates are assumed to be identical, so our model does

not include any competition-colonization tradeoffs. This model produces a local

stochastic founder's effect, as seedlings landing in already-occupied sites experience

depleted resources, and therefore face a much greater risk of pre-competition mortality,

whether or not they are better suited to the site than the current occupant. Propagules that

survive to adulthood may displace or coexist with current occupants according to the

resource-ratio competition model.


Our dispersal and establishment model, though based on the pure dominance competition

resource-ratio model, is actually a weighted lottery model given the stochastic

establishment process (Sale 1977). The stochastic framework is appropriate for our

simulation for two reasons. First, individual-based models like this one are concerned

with the success or failure of individual propagules, for which stochastic effects are likely

to be quite prevalent. Second, competitive asymmetry between adults and seedlings for both soil resources and light creates local founder effects, which are better captured in a stochastic model. Our model preserves the dominance nature of resource ratio theory, because a better competitor that survives to adulthood will take over the site. In this way, an established adult will never lose its site to an inferior competitor, and will lose to a superior competitor only with a certain probability. However, the stochastic growth barrier means that any species landing at an empty site has a chance to become established, even if superior competitors also land there, so long as the superior competitors fail to survive to adulthood. This model reflects many observed assembly patterns, in which initial community composition is determined by chance establishments, and succession occurs over time as dominant competitors succeed in colonizing (Myers and Harms 2009).

*Habitat heterogeneity and resource dynamics*

When there are two limiting resources, as in our model, resource-ratio theory predicts coexistence of up to two species in a given site with its particular supply ratio. Thus, higher diversity only occurs in spatially heterogeneous landscapes composed of sites with many distinct supply ratios. In our model, habitat patches differ in their availability of the two essential resources, and, like species, are characterized by their position on a linear trade-off between supply of each resource. While a precise trade-off in resource supply is not realistic, this structure reflects the many instances of gradients in environmental variables (Silvertown 2004). Site resource-ratios follow a truncated Gaussian distribution (mean = 0.5, variance = 0.1667, and we redraw if the random value is < 0 or > 1), so that

more equal resource levels are more common. Sites are spatially arranged in a gradient with low R1, high R2 on one side of the habitat, and high R1, low R2 on the other side.

*Mortality*

Sites are vacated when their adult occupants die, which happens with a fixed probability, $m = 0.05$, during each timestep (note this is different from $\mu$, the mortality rate during growth from seedling to adult). Age-independent exponential mortality may not be realistic in most cases, but inclusion of a maximal individual lifespan or deterministic mortality does not change the qualitative results of our model. At the particular mortality rate we use, over 95% of individuals die within 60 timesteps. At the end of each timestep, each empty site's resource levels revert to the equilibrium supply point. This is analogous to resources with a continuous supply, such as water or soil nutrients. When occupied, however, the available resources are determined by the occupying species' consumption vector(s) and the supply point. (See appendix for the equilibrium resource level formula).

*Species Pool Functional Diversity*

The structure of our model allows us to combine neutrality and niche-differentiation in order to assess which factors allow coexistence of neutral species in a heterogeneous habitat and which encourage functional differentiation. By creating species pools in which multiple species share each resource-ratio trade-off value, we can run simulations in which neutral and niche processes operate simultaneously. In particular, interactions between identical species within functional groups are purely neutral, while those between species in different groups are a combination of stochastic and niche-driven.

With a single functional group, our model is a variation on Hubbell's neutral model. Key differences are that in our model, many sites may be unoccupied due to stochastic establishment, dispersal is limited in distance, and we assume a faster rate of immigration from the metacommunity. In most runs, we created a number of "functional groups", each containing 100 identical (neutral) species. By varying the number of functional groups, we can observe the dynamics of neutral and niche-differentiated species in communities with higher or lower degrees of neutrality relative to trait-differentiation. We call the number of functional groups (FGs) in the species pool the Species Pool Functional Diversity (SPFD). We experimented with other distributions of species, with either more or fewer species in each functional group, but obtained similar results.

### *Simulation experimental design*

Simulations were done in three sets of runs designed to investigate our model's predictions for different species pools and invasion scenarios.

(1): *Assembly and structure:* Our first goal was to examine the properties of local communities assembled from species pools with varying SPFDs. In particular, we were interested in whether neutral species would persist at levels predicted by neutral dynamics, or be excluded by increased niche differentiation. In these simulations, we varied the number of functional groups in the metacommunity from 1 to 256, capturing a wide range of neutral vs. niche-differentiated diversity in the initial composition. In each case, functional groups were assigned traits distributed evenly along the trade-off line.

(2): *Invasion resistance:* Second, we ran simulations to assess whether assemblages with varying degrees of neutrality were stable under ecological invasions or evolutionary diversification in the metacommunity. Simulations from (1) were altered by introducing new species with novel traits to the metacommunity after an initial local-assembly period (at $t$=10,000). Invaders' traits were chosen in different ways to simulate ecological and evolutionary cases. In the ecological case, species in the invading pool were created with traits drawn from a uniform distribution across the trade-off curve. In this context, we assume that independent evolutionary histories produced species with traits unrelated to the local community's. In contrast, in the evolutionary case, we wanted to assess the stability of neutral coexistence under local diversification of species. To that end, we conducted simulations in which the invading species' traits were drawn from normal distributions around the traits of the original species pools. In these simulations we varied the width of the normal curves to simulate different degrees of evolutionary trait lability. In all cases, the invaders accounted for 10% of the propagules added during the immigration phase of the simulation (90% were drawn from the pool of original species).

(3): *Dispersal limitation and species persistence:* We conducted a third set of simulations varying the number of propagules dispersed by adults in order to examine the effect of dispersal limitation on neutral coexistence and community structure and to test the model's sensitivity to this parameter. In these simulations, immigration from the metacommunity was also stopped after a fixed period of time. We observed how many species were lost after immigration cessation, allowing us to determine the relative frequency of 'core' versus 'transient' species in runs with more or less neutrality.

We used a 200x400 cell habitat with the environmental gradient along the longer axis in all simulations. Changes in the size of the habitat do result in different levels of diversity, as persistence time is directly related to population size in stochastic models like this, but do not affect our qualitative results. In particular, we found that relationships between functional diversity and species diversity, neutrality, and invasibility were robust to changes in habitat shape (100x800 and 400x200), as well as changes in area (141x283 and 283x566).

### *Measuring ecological neutrality*

In order to compare the results of our simulation to neutral expectations, we need a measure of neutrality for the simulation results and an estimate of the expected outcome under purely neutral dynamics. Despite increased interest in neutral theory, there is no single index to measure the degree of neutrality in a community. In a sense directly analogous to the genetic meaning, neutrality implies that species' demographics follow a purely random process in which species differences play no role in determining birth and death rates or competitive abilities. Accordingly, Gravel et al. (2006), used inter-run variance in species' realized abundances as a measurement of neutrality in their simulations. However, since our model involves a much larger species pool and large variance inherent to stochastic immigration and establishment, this measure was impractical to use in our case. Instead, we considered a newly established species to be neutral if it shared an identical resource-ratio trade-off with a currently established species. We measured the neutrality of an assembled community simply by counting the

number of neutral species. For example, if an assembled community contains 5 species with $t = 0.33$ and 8 with $t = 0.67$, we consider it to have $(5-1) + (8-1) = 11$ neutral species.

Given this measure of neutrality, we want to determine whether the output of any simulation differs significantly from what would be expected under neutral dynamics. In general, the expected number of neutral species in an assembled community depends on the size and functional diversity of the species pool and the diversity of the assembled local community. Under purely neutral dynamics, species traits are irrelevant to assembly, so species composition is completely random. To that end, we compared the observed number of neutral species with the number that would be expected if a community of equal total diversity were drawn randomly from the same metacommunity. We determined these expectations by conducting random assembly simulations for each SPFD and calculating the probability of $n$ neutral species at each diversity level. We conducted 10000 simulations for each SPFD level. We also used these expectations to calculate the cumulative probability of obtaining an observed number of neutral species or fewer under purely neutral assembly.

## Results

### *Assembly*

Our first set of simulations examined the properties of communities assembled from species pools with varying numbers of functional groups. We found differences in total and neutral diversity, proportion of core and transient species, and the probability of the resulting structure under neutral dynamics as a function on SPFD.

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*Diversity*

We found that total community diversity was, overall, strongly positively related to SPFD, and that the differences became more pronounced throughout the simulations (Fig 2.1 and 2.2 a.). All runs had in common a very rapid increase in diversity at the beginning of the simulation, as the initially empty habitat's high resource availability was favorable for propagule establishment. However, the runs quickly diverged, showing significant differences in diversity from $t=50$ on.

The runs fell into three qualitative categories with different post-boom behaviors. Those with 32 or fewer functional groups saw permanent declines in species diversity after $t=10000$, those with 64 FGs maintained a nearly constant diversity, and those with more than 64 continued to increase in diversity through the end of the simulations. Among those that lost species after the initial period, a linear fit of diversity against log-transformed SPFD explained just 2.1% of the variance, while the quadratic fit explained 72.2% (Fig 2.3), with the highest diversities achieved with 1 and 32 functional groups (29.3 and 35.3 species, respectively), and the lowest occurring with 8 FGs (15.7 species). The two increasing runs, 128 and 256 FGs, were not significantly different at any point in the simulations.

The interesting result that species diversity decreased between SPFDs of 1 and 8 is consistent with neutral dynamics occurring within each niche. At these diversities, each niche was large enough to support neutral species, so the entire population was

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effectively composed of 1, 2, 4, or 8 roughly equally sized neutral communities. High

diversity in neutral communities occurs due to a long tail of rare species, and decreasing

total population eliminates these quite rapidly. As a result, our model predicts higher

equilibrium diversity for a single population of size $N$ than $m$ populations of size $N/m$.

The relationship between SPFD and assembly diversity becomes positive once SPFD

passes the threshold at which most rare neutral species are eliminated. At this point, few

species coexist due to drift, so the dominant coexistence mechanism is niche

differentiation.


*Neutral Diversity*

Both total and proportional neutral diversity (Figs 2.1 and 2.2, b and c) declined with

increasing SPFD and as the runs went on, however, in no cases were neutral species

completely excluded. Even in the highest SPFD case, neutral species were able to

establish very small transient populations, maintaining an average of 2-3 neutral species

present at any time. These populations were very short lived, and did not increase to

fixation.


All runs except the 128 and 256 SPFD cases lost neutral species over time, with the

greatest portion of decrease occurring before $t$=10000. For all times, there was a negative

relation between SPFD and both neutrality measures, with the caveat that higher SPFD

runs bottomed out before the simulations were complete. Unlike total diversity, there

were no thresholds in neutral response to SPFD.

In contrast, our probability measure showed a very distinct threshold (Figs 2.1 and 2.2 d). For a given local community and SPFD, we estimated the probability that a truly neutral process would generate an equivalent community with the same total diversity and the same or fewer neutral species. By this measure, runs with 4 or fewer functional groups were indistinguishable from pure neutrality, while those with 24 or more had probabilities of essentially 0. The 8 FG case was in the middle of a sharp transition boundary, and ended the simulation with an equilibrium probability of approximately 0.4.

### *Functional diversification*

We simulated invasion by species with novel traits by expanding the pool of species from which invading propagules were drawn. We performed two variations of these diversification simulations. In the first scenario, the invading species' traits were uniformly distributed along the trade-off curve. Cases of biological exchange between previously separated realms would be likely to exhibit similar independence of native and invader trade-off values due to relatively distinct evolutionary histories. In the second scenario, the invading species' traits were drawn from normal distributions of given variances around the trait values of the original functional groups. This constraint could be considered more representative of invasion through evolutionary diversification as novel species' traits would exhibit strong correlation with existing traits.

*Ecological Invasion*

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In our first diversification scenario, we introduced species with new traits beginning at $t$=10,000. Novel species constituted 10% of the propagules arriving from the metacommunity.

In all runs, inclusion of novel species either increased diversity above that observed in non-invasion runs (SPFD <= 64), or had no effect on final diversity (SPFD >= 128) (Fig 2.4a). In runs with SPFD <= 16, introduction of novel species caused a very rapid increase in diversity, causing these cases to converge with the 64 and 128 FG runs. The 32 FG run was an interesting case in which the introduction of new species did not induce a rapid increase in diversity, resulting in the lowest total diversity of all SPFDs.

Functional diversification caused neutrality to drop to almost zero by $t$=50000 across all SPFDs, regardless of the number of neutral species present before the invasion (Fig 2.4). Again, 32 FGs was an interesting case, showing the slowest decline of neutral species, though also converging on zero.

The total number of species able to establish from the invading pool was significantly related to SPFD. In simulations with high SPFD values (>=64), species from the original pool accounted for at least 80% of final diversity. On the other hand, in simulations with <16 FGs, the original pool accounted for <20% of final diversity. The severe species loss in low SPFD runs occurs because invading niche-differentiated species reduce the habitat available to the native functional groups. As mentioned above, the neutral diversity in a niche is highly sensitive to the total size of that niche, and in these scenarios, the resulting

decrease in niche size is sufficient to cause many rarer neutral species to go extinct. Additionally, these cases have relatively low pre-invasion diversities, so are able to support a greater number of novel species.

*Evolutionary diversification*

Invasions with restricted traits were similar to the uniform invasions with higher values for evolutionary variance, but were quite different for small widths (Fig 2.5). Simulations were run with 8 initial functional groups, in a factorial design varying number of propagules per adult and the evolutionary width. All propagule numbers showed a similar pattern across evolutionary widths. Both narrow and wide variances led to significant exclusion of the original neutral species, but there is a critical threshold for W below which total diversity is limited to a constant value. For values of W above this threshold, diversity increases over time following the invasion, though for the ranges of W covered, never achieves the pre-invasion diversity. The exact value of the threshold depends on the number of propagules.

Below the threshold, the typical invasion pattern is for invading species further on the tails of the evolutionary distribution to displace those more similar to the original species, leading to a pair of dominant species in each niche accompanied by a number of transient species. Above the threshold, the evolutionary kernel is wide enough to permit coexistence of multiple evolved species, as the distance between them is larger than the stable limiting similarity threshold.

***Propagule output, dispersal limitation, and community stability***

Our third set of simulations was aimed at understanding the interaction of niche competition and dispersal limitation on general community stability and the ecological robustness of neutrality. We varied the number of viable propagules dispersed by mature adults in each run, producing different levels of dispersal limitation between simulations. Interestingly, total diversity had a U-shaped response to dispersal ability, achieving its highest values for 1 and 64 propagules, and its minimum at 8. (Fig 2.6) This pattern resulted from two counteracting processes – increasing dispersal ability reduced the number of neutral species able to coexist, while increasing the total number of species able to successfully establish.

We chose two dispersal levels for which to investigate the compositional stability of the assembled communities. In these simulations, we assembled communities for 500,000 timesteps, and then allowed these communities to continue for another 500,000 timesteps without immigration from the metacommunity. We used 1 and 16 propagules per adult, as these two levels produce communities of nearly equal diversity. We found that, after immigration ceased, the 16-propagule communities lost, on average, a single species, while the 1 propagule communities lost half of their species (40) before stabilizing.

Low dispersal rates mean that, balanced with a constant mortality, more sites are left unoccupied. These sites have much higher resource availability levels, granting a higher probability of survival to immigrant propagules, and hence, fostering a more diverse community with a high proportion of rarer transient species. With high dispersal rates,

immigrants that happen to succeed are much more likely to quickly establish stable population sizes. This also produces a diverse community, but one with a constant species composition.

## Discussion

Many empirical studies highlight important roles for functional diversity (Petchey and Gaston 2002, Duffy 2009), ecological invasion and speciation (Schluter 2000), and dispersal limitation (Shurin 2000, Foster and Tilman 2003) in shaping community structure and function. Our simulations address the interaction between these factors and niche and neutral processes, and the patterns of diversity and invasion dynamics that they produce. The main result of our analyses is that while the persistence of neutral coexistence is possible in a spatially heterogeneous habitat under very particular conditions, both ecological and evolutionary changes in community functional diversity tend to eliminate neutral species in favor of niche differentiation. In our simulations, neutral coexistence is favored in communities with low functional diversity, low dispersal success, and isolation from sources of new species. The instability of neutral coexistence under common ecological and evolutionary processes suggests that neutral theory describes only a very limited domain of situations.

Additionally, we investigated the impacts of variable dispersal success, and found that greater propagule establishment rates may increase or decrease community species diversity depending on local functional diversity, and that distinct patterns of community structure characterized communities with low or high success.

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*Ecological and Evolutionary Stability of Neutrality*

Our central finding is that while neutral coexistence is possible and even quite likely
under certain conditions, both ecological and evolutionary expansions of trait diversity
exclude neutral species in spatially heterogeneous habitats. This result is germane to
current discussions about the proper role for neutral theory (Hubbell 2005), further
theoretical integration of niche-based and stochastic processes in community ecology
(Adler et al. 2007, Allouche and Kadmon 2009), and for understanding how processes
acting on long timescales, such as biotic interchange and functional differentiation, can
ultimately drive local community structure (Webb et al. 2002).

Two key processes, ecological invasions and evolutionary adaptation and speciation,
introduce new species to a community, and potentially new functional traits. The
questions we ask are: what conditions must these new species and the processes that
spawn them satisfy in order to prevent the emergence of stabilizing forces? What is
required for ecological equivalence to persist in a community undergoing ecological
invasions or evolutionary diversification? Though implicit, these conditions are an
essential component of the neutral model. Some amount of empirical data exists to
suggest that whatever they are, these conditions are not typically met.

With respect to ecological invasions (Mitchell et al. 2006), neutrality demands that
invading species, either into local communities from the regional metacommunity, or into
the regional pool from other realms, introduce no functional differences relevant to

demographic processes. Furthermore, neutral theory predicts that an increase in immigration of new species should also lead, after a period of equilibration, to an equally higher extinction rate. However, with respect to biotic interchanges, evidence from the fossil record suggests that these major species exchanges rarely produce extinctions, instead resulting in a persistent increase in diversity in the target biome (Tilman 2011).

Evolutionarily, ecological equivalence can only persist if trait evolution and speciation fail to create sufficiently differentiated species for stabilizing processes to emerge. Either coexistence between ecologically equivalent species is robust to diversification of non-neutral, or ecologically distinct, species, or newly evolved species must be effectively equivalent to extant species in spite of functional distinctions. However, evidence of phylogenetic overdispersion of ecological traits in many taxa suggests that speciation events do tend to increase meaningful functional diversity (Cavender Bares et al. 2004).

If none of these conditions hold – that is, if invasions or evolution do regularly introduce demographically significant functional differences – neutrality hold only for a limited time before niche processes come to influence community dynamics. Neutrality, in this case, would describe the transient early phases of community assembly in the special case that the original species were functionally equivalent.

*Emergent Neutrality*

Several papers have argued for the possibility of neutral coexistence over evolutionary time (Hubbell 2006, Scheffer and van Nes 2006). Both papers considered "emergent

neutrality", in which niche-differentiated species evolve towards neutrality, rather than maintaining or deepening functional differences. If it were demonstrated as a plausible evolutionary process, emergent neutrality would provide strong support for neutral theory, as neutrality as a stable outcome of evolutionary processes is even stronger than identifying cases in which existing neutrality can persist. However, both papers' findings are subject to strong limitations.

The first of these papers, Hubbell (2006), considers a model in which species' abilities to gather resources from each of 20 discrete niches evolve over time. At the beginning of the simulation, species' traits are distributed in a bell-shape representing niche-specialization with distinct means for each species, but evolve as the model progresses. This evolution results in each species' resource utilization abilities spreading across different niches, which appears to suggest evolution of ecologically equivalent generalists. However, a closer examination of the results reveals that this model in fact yields a high degree of niche partitioning, as each niche ends up with just a single species with a high efficiency. Species appear to be generalists due to the fact that their specializations are no longer related in trait space, but specialization still exists. This occurs because the model includes no mechanism relating individuals' abilities to utilize resources from adjacent niches, as would be expected if the niches represented a true gradient, and consequently the initial ordering of trait values is essentially arbitrary.

The second paper to consider evolutionary paths to neutrality is Scheffer (2006). This paper describes off-equilibrium dynamics of a species-rich niche-structured community

governed by the Lotka-Volterra equations. In a model without stabilizing forces or evolution, Scheffer's model predicts long-lasting transient patterns of essentially convergent community assembly, in which clusters of species with very similar traits persist, while those with intermediate traits quickly go extinct. With the addition of negative density-dependence or trait evolution, this "neutral" coexistence becomes permanent, resulting in stable neutral clusters. This finding, however, depends strongly on the model underlying the calculation of the Lotka-Volterra interaction terms. The method used by Scheffer – integrating the intersection of normal curves centered at each species' trait optimum – has the effect of encouraging species clustering rather than species differentiation. This occurs because the relatively slow falling-off of the normal curve means that when competing with two extreme species, an intermediate species experiences a lower net competition by being similar to one of the extremes than by being midway between them (Fort et al. 2009). Kernels with steeper fall-offs favor the intermediate position, and produce stably niche-differentiated communities, rather than the transient neutrality pattern found by Scheffer. Thus, while Scheffer's model identifies one particular case in which neutrality represents the stable endpoint of demographic and evolutionary processes, it is highly contingent on the assumed shape of the interaction kernel and the particular modeling framework. Whether the normal kernel or another is appropriate, or whether the Lotka-Volterra model is appropriate, is an issue that deserves further consideration.

*Neutrality and species pool functional diversity*

So far, then, there is little support in the literature for evolutionary or even ecological stability of the equivalence property, though existing analyses are limited in scope and do not conclusively rule it out. In our model, we address the issue in two ways. First, we analyze the persistence of neutral species in spatially heterogeneous communities with varying degrees of functional diversity, and second, we observe the effects of invasions and speciation on these assembled communities.

We found that increasing functional diversity at low levels does not raise species diversity. Rather, a similar number of species is distributed among an increasing number of traits. Above a certain threshold, further increases in functional diversity do lead to increases in species diversity, accompanied by the elimination of functional redundancy (Northfield et al. 2010). For lower functional diversities, demographic equivalence within each group means that neutral processes determine species establishment and persistence. Thus, for functional diversity levels below the threshold, diversity within a group depends mostly on its total population size, which is determined by the range of supply ratios for which the functional group is the dominant competitor. As a functional group's share of habitat sites shrinks due to displacement by species from better-suited functional groups, the average population size of each species in the group declines (Quinn and Hastings 1987). Average time to extinction in a random walk process is monotonically related to population size, and so the loss of niche-space as functional groups are added shifts the balance of immigration and extinction towards a less speciose equilibrium within each functional group (Solé et al. 2004). Taken as a whole, however, the

functional groups fully partition the niche-space, and so the total population size remains constant and total species diversity is roughly the same.

These results show that limited niche-differentiation, resulting from trait differences and habitat heterogeneity, can allow persistence of neutrality, provided that the resulting niches are sufficiently large to allow the extinction/immigration balance to maintain an intra-niche diversity greater than one. Niche processes do act as a major limitation on neutral diversity, however, as seen by the fact that neutral coexistence is strongly constrained. Also, if existing species in a realm are mainly neutral, invasion of additional species from a different realm should lead to displacement, which is not seen….

Unchanging species pools are not consistent with a longer view of community, ecology, however, as biotic interchanges and speciation are constant, if slowly acting, processes (Williamson 1996, Coyne and Orr 2004, Davis 2009). Introducing these processes to our model eliminated neutral species almost completely, regardless of the trait diversity of the initial metacommunity. We found that novel functional traits could easily invade functionally impoverished communities, while species with duplicate traits had little success (Fargione and Tilman 2005). According to our results, a community's assembly history should tell the tale of functional diversification, either through immigration or evolution (Chase 2003, Fukami 2004). If that is the case, it seems very unlikely that any actual ecological community will resemble the communities of our low functional diversity simulations, and it is therefore unlikely to expect to find ecological equivalence.

*Dispersal Limitation*

Community-wide dispersal limitation induces several major community traits in our simulations: rapid local species composition turnover, permissiveness toward neutral coexistence, and a higher success rate for immigrating species. Both the first and third factor suggest that in areas with local dispersal limitation, locally diversity is maintained by regional dispersal.

Most authors have agreed that neutrality is more likely to persist given dispersal limitation, and our results support this hypothesis (Thompson and Townsend 2006, Etienne and Alonso 2006). Generally, higher dispersal success increases the extinction rate of neutral species by speeding up the demographic random walk relative to speciation and increasing the rate at which species with potential niche-differentiation interact, thus speeding competitive exclusion. In our model, several additional factors appear. Lower dispersal rates mean that communities are not spatially saturated. As immigration success increases with resource availability, more open communities are more easily invasible by both differentiated and neutral species (Funk and Vitousek 2007). In a high dispersal rate community, invasions by neutral species are very rare due to much lower nutrient availability in the appropriate resource ratio. In both cases, the highest average nutrient availability occurs between species, but this difference is proportionally much greater in a spatially saturated community.

Dispersal limitation also introduces a contradictory effect relative to niche-saturation and diversity. As mentioned, dispersal limitation yields higher immigrant success. On the

other hand, successful immigrants are less likely to establish large populations and have much shorter expected residence times than immigrants in high-dispersal communities.

Two contrary dynamics produce a U-shaped response of total diversity to local dispersal ability in our model. First, low dispersal tended to increase the number of neutral species that are able to coexist. Low dispersal also fostered higher diversity of similar species, as more open sites and less interaction mean that limiting similarity is less binding. As dispersal rates increased relative to neutral immigration, pseudo-random-walk demographics increasingly reduced diversity in a FG to a single species. Second, low dispersal tended to limit the accumulation of persistent species as newly established species with low abundances and low growth rates were likely to go extinct quickly. With higher dispersal rates, immigrants were much more likely to establish persistent population sizes upon successful invasion, yielding an increasing diversity response to dispersal level. In our simulation, these two factors produced the least diverse communities for intermediate local dispersal levels, with maxima for very low and very high dispersal.

Comparison of the 1 and 16 propagule cases, which produced the same diversity levels, reveals major differences in community structure between low and high dispersal communities. The low dispersal community had a much larger proportion of neutral species, nearly equivalent to what would be expected by randomly sampling the metacommunity. Most dramatically, over half of the species in the low dispersal case were lost following immigration cessation, in contrast to the loss of a single species in the

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high dispersal case. The low dispersal community was characterized by a number of "core" species with large enough population sizes to persist on the time scale of the simulation, and rarer "transient" species that are maintained in number by immigration from the metacommunity (Magurran and Henderson 2003). The low dispersal community also had a much larger proportion of neutral species, nearly equivalent to what would be expected by randomly sampling the metacommunity. The high dispersal site was characterized by relatively even abundances, very long persistence times, and nearly complete elimination of neutrality.

Note that high and low dispersal sites do not differ in the probability that propagules will succeed or fail at a given site. Rather, they differ in the number of viable propagules dispersed by individuals in that community. An adult individual's actual expected number of offspring depends both on seed output and on resource availability in the individual's neighborhood. We take this number as a given in the models, though it is likely that evolutionary pressure would act on propagule production. Further work on this point would be especially interesting, as we have already begun to include evolution of resource trade-offs.

### *Habitat Heterogeneity and trade-off curves*

The key assumptions made in our model to differentiate it from the neutral model were the existence of habitat heterogeneity and a corresponding functional trade-off allowing species to specialize in certain habitat values. However, while the model underlying this trade-off is based on resource-ratio theory, we expect that the results are not particular to

this example of functional trade-offs. For instance, any other habitat-

heterogeneity/functional trade-off pair, such as species specializing in a particular

temperature or water availability along a corresponding environmental gradient is likely

to produce similar results. The fact that our model is based on spatially explicit dispersal

is also likely not essential to our result about neutral instability, as niche-axes such as

food-size preference may not be spatially structured, but still offer the same advantages to

differentiation.

On the other hand, it is not clear whether predictions of models based on life-history

trade-offs, such as a competition-colonization trade-off, are more likely to differ from

ours. Competition-colonization models, like environmental specialization models, do

permit the coexistence of an arbitrary number of species (Kinzig et al. 1999), but

spatially-explicit versions of the model with large numbers of species have not been

tested yet (Higgins and Cain 2002). One difficulty with such models is that the

appropriate shape of the trade-off curve is harder to determine, and for high-dispersal

niches, the importance of stochastic events makes individual-based simulations unwieldy.

Integration of life-history trade-offs into this framework would mark a useful next step.

### *Conclusion*

Our results suggest that neutrality, understood as functional identity between species, is

unlikely to occur in nature when heterogeneity of environment or resources allows

functional differentiation. In our model, communities with high rates of functional

redundancy experienced almost complete extinction of neutral species when novel

species were introduced under invasion or evolutionary processes, while neutral coexistence was stable only when species pools were extremely functionally limited and fixed. The suggestion to treat neutral theory as a null-model for ecology should thus be interpreted not to mean that neutrality is the null expectation for ecological communities, but that it provides a set of predictions based on simple assumptions, and that divergence from these in a natural system can reveal something about the deterministic mechanisms at work.
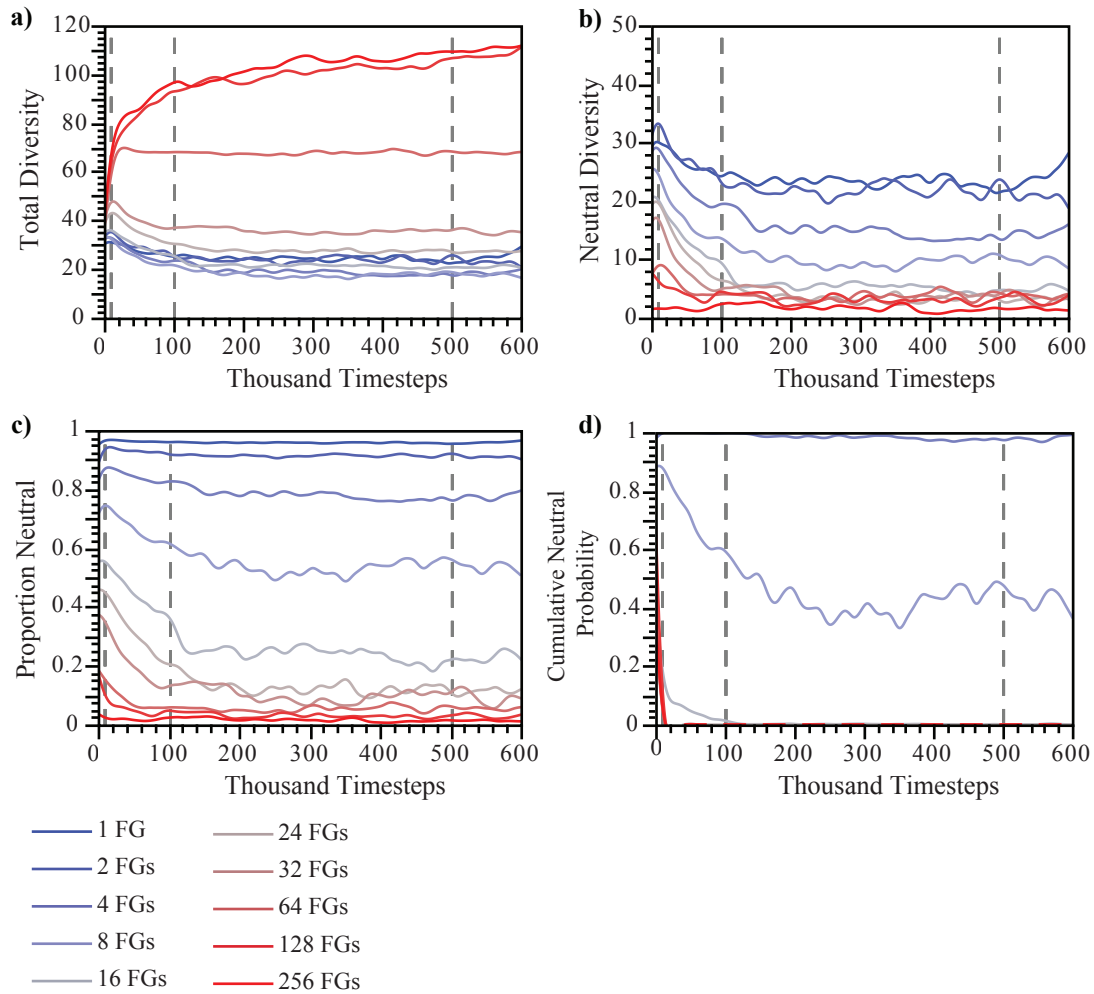
**Figure 2.1:** Results of long-term community assembly simulations. Lines correspond to mean results over 3 runs for each SPFD level, ranging from 1 (blue) to 256 (red). The dashed vertical lines indicate the times illustrated in Figure 2.2. Plot a) shows total diversity. All but the two most diverse species pools reach their equilibrium diversity by 200,000 timesteps, with the less functionally diverse communities losing species after an initial rapid increase. The time-slices reveal that initial differences in diversity across SPFD values (blue line) are magnified as the simulation continues (red line). Plot b)

shows neutral species diversity. Unlike total diversity, all SPFD values lose neutral species over time. In particular, the middle functional diversity runs exhibit severe loss of neutrals. Plot c) shows the proportion of species that are neutral. Again, we see large loss of neutrals in the 16, 32, and 64 FG runs. Finally, plot d) shows the probability of obtaining the observed number of neutral species or fewer given under pure neutrality. There is a very sharp distinction between runs with < 8, 8, or > 8 FGs. Those with fewer than 8 follow neutral predictions exactly, while those with more are all but impossible to obtain under neutral dynamics. The 8 FG case is exactly in the middle between the two.
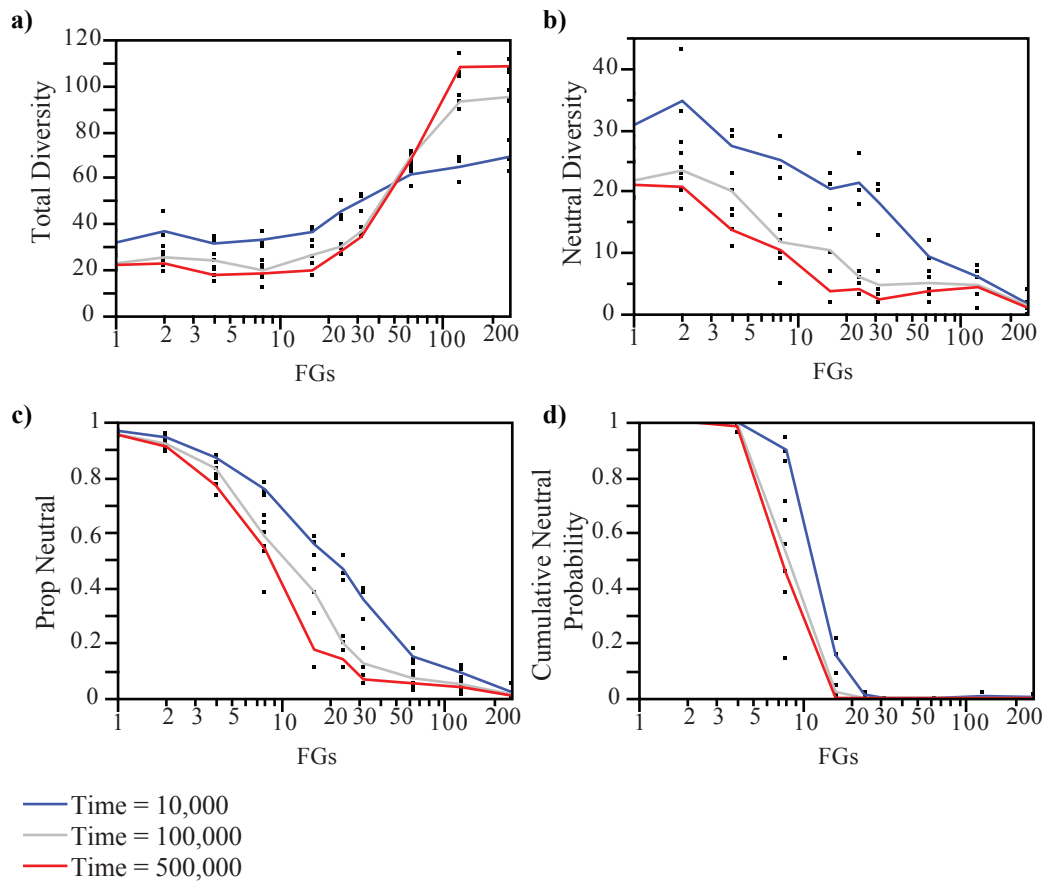
**Figure 2.2.** Time slices from the long-term assembly simulation runs in Figure 2.1. Each

line corresponds to a particular time in the run, and illustrates the dependence of a

particular community statistic on the runs' SPFD (number of functional groups in the

species pool).
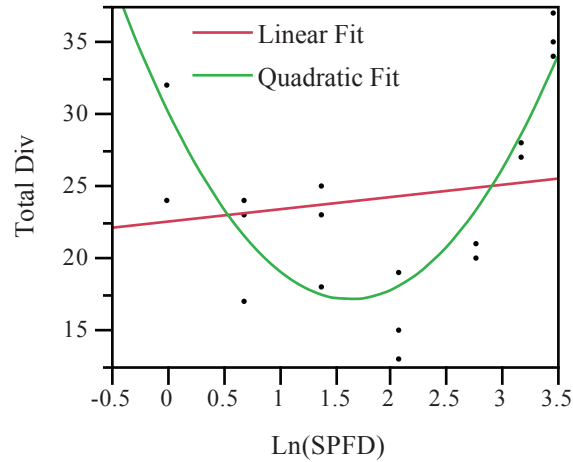
**Figure 2.3.** Linear and quadratic fits of total diversity against the log of species pool functional diversity at community equilibrium. There is a significant U-shape, indicating loss of species as we increase from 1 to 8 FGs, but increasing diversity after. The decline is caused by niche differentiation dividing a single neutral population into several smaller populations. This reduces the number of species in each niche to a greater degree than niche-stabilization is able to increase diversity. However, as the number of functional groups increases, niche-differentiation leads to more species.
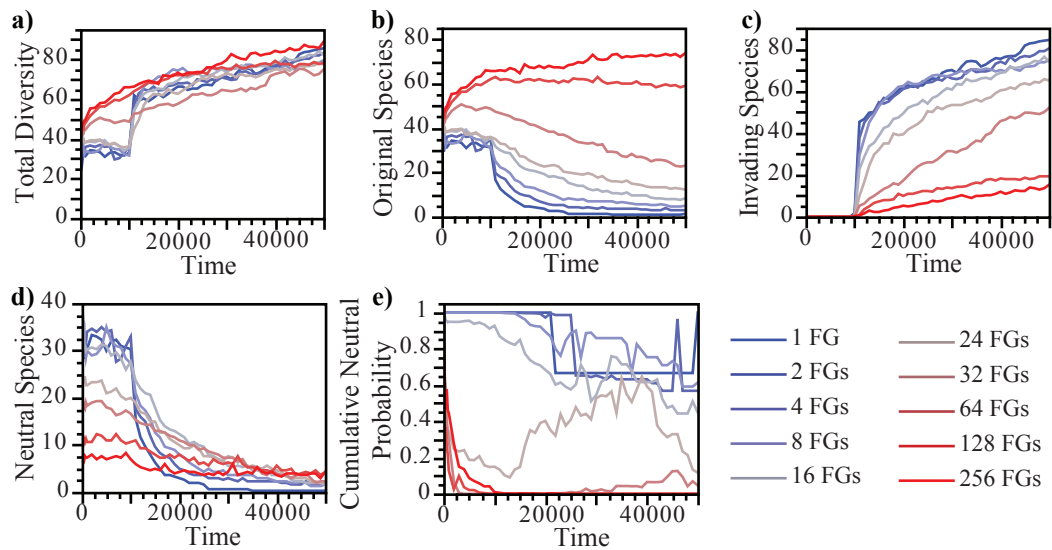
**Figure 2.4:** Community responses to invasion by uniformly distributed invaders. In these simulations, communities assembled from species pools with *n* functional groups are invaded by species with random traits at $t = 10000$. Plots show time series of a) total diversity, b) number of species from the original pool, c) number of species from the invading pool, d) number of neutral species (original species only), and e) the neutral probability. In spite of pre-invasion differences, all communities converge towards a high-diversity, low-neutrality equilibrium. Those communities with greater initial SPFD were more successful in resisting invasion, but only the 128 functional group run had no net loss of original species.
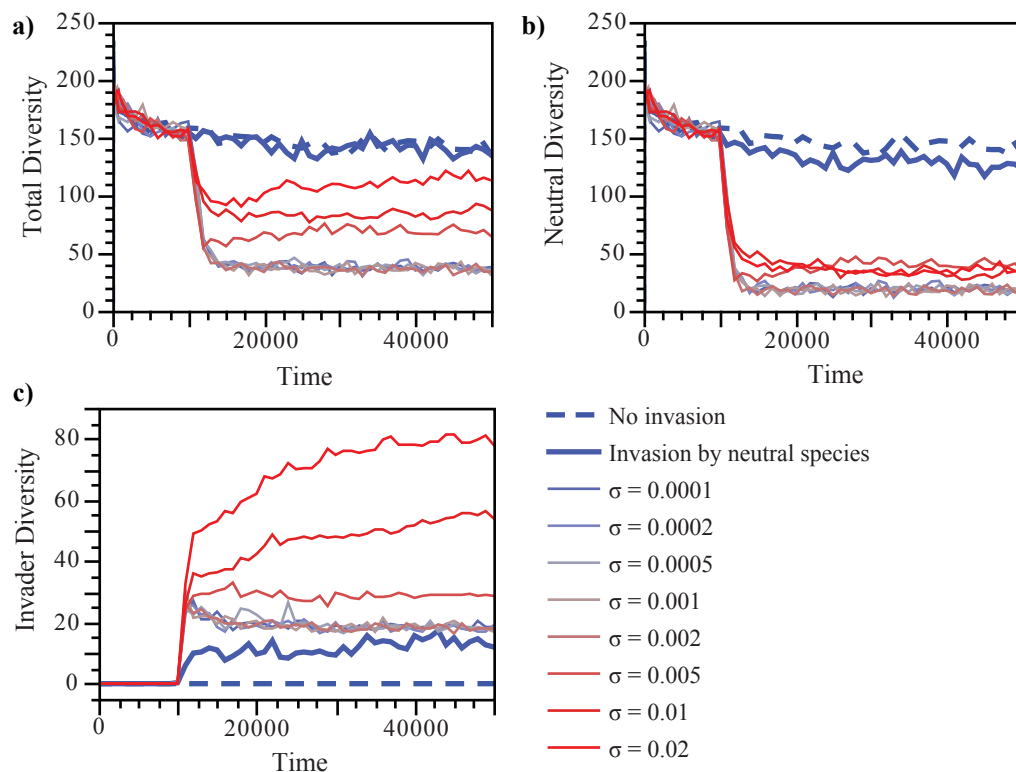
**Figure 2.5:** Community responses to invasion by evolutionarily constrained species. In these runs, communities assembled from species pools with 8 functional groups are invaded by species with traits drawn from normal distributions around each existing functional group. Simulations differed in the variance of the evolutionary distribution. Note that for extremely low widths, peculiarities of the model cause nearly neutral species to behave much differently than truly neutral species, in a way that is not realistic.
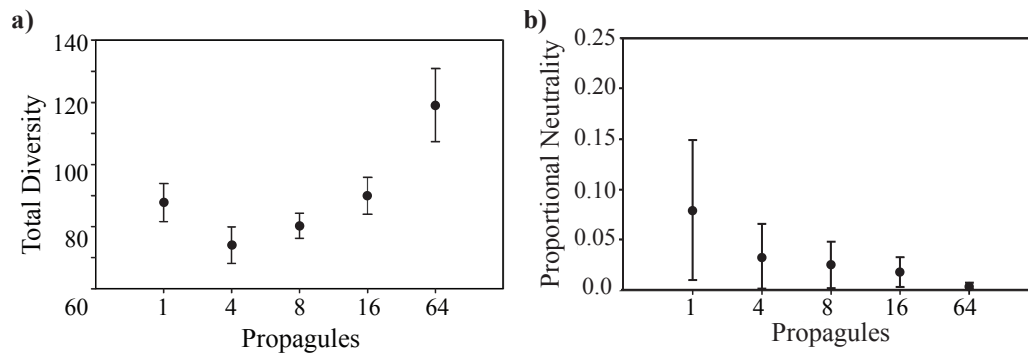
**Figure 2.6:** Diversity and neutrality responses to variation in per capita seed output. These runs differ from the base case simulations in that we changed the number of seeds dispersed annually by each adult plant. In all runs, the species pool consisted of 8 functional groups with 100 species each. Plots show: a) total diversity in assembled communities as a function of number of propagules dispersed per adult plant, and b) number of neutral species in the community as a function of # props. 6a shows a U-shaped relation between diversity and dispersal resulting from the contrary forces of neutral exclusion and increased establishment success caused by increased dispersal.

# Chapter 3: Statistical bias leads to overly conservative tests of transgressive overyielding and complementarity effects

Niche-complementarity predicts that communities consisting of functionally diverse species will more fully utilize available resources, and thereby achieve higher productivity, than any of their component species in monoculture. Empirical work to test against the competing hypothesis that polyculture productivity depends on the presence of certain particularly productive species has found inconsistent support for complementarity. Here we describe how the standard method of analysis has biased results against detecting this transgressive overyielding by using statistics that overestimate maximal monoculture productivity. We find four factors that increase the bias: low replication of species in monoculture, large numbers of species in monoculture, high within-species variance, and multiple co-dominant species. We also describe a parametric bootstrap procedure to estimate and correct the bias to obtain an unbiased estimate of maximal monoculture productivity. We apply the bias estimation to data from two biodiversity experiments and find biases ranging from 3-25%. Our analysis suggests that future tests of transgressive overyielding should not rely on *post hoc* identification of the most productive monoculture, and should change the experimental design to minimize the factors leading to the overestimation bias. Furthermore, the results of previous meta-analyses should be treated with caution, as the tests used were biased against detecting transgressive overyielding and complementarity.

**Introduction**

An open question in community ecology is how to determine whether the productivity of diverse assemblages is driven by functional diversity and niche complementarity on the one hand, or by the traits of particularly dominant component species on the other (Huston 1997, Hooper et al. 2005). For instance, in models of resource competition with interspecific niche partitioning, assemblages with greater variation in species' functional traits are predicted to have higher productivity as a polyculture than would any less diverse subset of these same component species and than any of the component species in monoculture (Tilman et al. 1997a). This phenomenon, known as transgressive overyielding (Trenbath 1974, Harper 1977, Vandermeer 1989), is an important metric for assessing the degree of niche complementarity among ecological communities. However, tests to detect transgressive overyielding in many biodiversity experiments may have been overly conservative because the experiments were not designed to allow clear statistical estimation of the maximal monoculture productivity. Contrary to the assumptions of some analyses, *post hoc* selection of the experimental maximum mean monoculture is a biased overestimate of the most productive species' true productivity, and introduces a conservative statistical bias against detecting cases of transgressive overyielding. Several papers have proposed metrics to measure transgressive overyielding and discussed their ecological interpretations (ex: (Loreau and Hector 2001, HilleRisLambers et al. 2004)). However, the statistical issues surrounding the application of these metrics, and in particular, the challenge of identifying the most productive species in monoculture, have received less attention (but see (Schmid et al. 2008)) but are important for accurately determining the frequency of transgressive overyielding.

The simplest measure of transgressive overyielding commonly applied to biodiversity experiments directly compares average polyculture biomass with the average experimental biomass of the highest yielding species in monoculture (Cardinale et al. 2006). The ecological interpretation of this metric is clear – when the average polyculture biomass is larger, transgressive overyielding has occurred, suggesting niche complementarity in the assemblage. Meta-analyses using this metric (Balvanera et al. 2006, Cardinale et al. 2007, 2011) have typically found a fairly low frequency of transgressive overyielding, tending to support the role of dominant species in promoting assemblage productivity over niche complementarity (known as the sampling or portfolio effect).

However, the application of this metric in most existing experiments is complicated by a combination of several factors, including low replication of species in monoculture and *post hoc* selection of the species with the highest monoculture biomass. In most field experiments, each species in monoculture is represented by one to at most five replicates (Cardinale et al. 2007). Due to large standard errors associated with this low replication and similar yields between several species, the identity of the most productive species is often not clear (Schmid et al. 2008). For example, in one of the biodiversity experiments at Cedar Creek Ecosystem Science Reserve, in central Minnesota, USA, that we discuss later in this chapter, 4 species had the highest average biomass in monoculture at least once over the course of 8 years (excluding one woody species because it is not readily compared to herbaceous species that lack aboveground perennial woody tissues). Furthermore, in any given year, the species with the highest monoculture biomass was

never significantly higher than all other species. Given this uncertainty about which species is the most productive, estimation of community's maximal monoculture productivity by way of individual species' productivities is likely to be biased (Schmid et al. 2008).

The typical estimation procedure used in the literature in fact overestimates the true maximum monoculture productivity, resulting in analyses skewed against detecting transgressive overyielding. We discuss the statistical issues leading to this bias, and one way to correct this bias in analysis. First, we discuss the cause of the overestimation bias. Then, we present an analytical treatment of the bias this problem can introduce to the detection of transgressive overyielding in biodiversity experiments. Next, we present a bootstrap method for estimating and correcting the overestimation bias for any given experimental data. Finally, we apply this method to data from two biodiversity experiments from the Cedar Creek Long Term Ecological Research (LTER) site and discuss the bias's magnitude relative to the experimental data.

**Why Former Estimates Are Biased**

Statistical bias in maximal monoculture productivity estimates occurs when using the maximum of a number of sample means as an estimate of the maximum of the unknown true population means. In short, this is because sample maxima and minima are non-robust statistics, meaning they are very sensitive to variability in the data and outliers. The maximum sample mean estimator ignores the fact that some species are likely to have an estimated monoculture productivity that is greater than their true means due to

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random variation. It becomes more and more likely with additional species that one of the randomly seemingly over productive species will also seem to outperform the highest true mean productivity.

As a simple example, consider the outcome of an experiment in which we randomly draw one card from each suit of a deck of cards. In this example, each suit is analogous to a species, and the card drawn is analogous to the species' observed monoculture productivity. Treating aces as low, the mean value of all the cards in each suit is 7 (cards range in value between 1 and 13). In this case, all the true population means are the same, so the maximum population mean is 7. However, it is likely that at least one or more of the 4 cards drawn will be greater than 7, so using the value of the highest single card drawn (estimated productivity for an individual species) as an estimate of the maximal mean across species is likely to be an overestimate.

This phenomenon also occurs when we have more than one replicate from each group and a more realistic data structure (Fig 3.1). Additional replicates reduce the severity of overestimation because sample means are less variable than individual data samples, but low replication means a relatively minor reduction in variability. Furthermore, as we will see later, as more and more species are included in the experiment, the likelihood of a highly biased overestimate increases.

A natural question is why the presence of stochasticity creates an overestimate rather than an underestimate. After all, in a given sample, each species is as likely to seemingly over

perform as underperform relative to its own mean. The reason is that by selecting the maximum, we focus only on the single highest value. In order for us to overestimate the maximum population mean, only a single species needs to seemingly over perform, while in order to underestimate it, every species must seemingly underperform.

Note that when we have *a priori* knowledge of which species has this highest monoculture productivity, we can use the sample mean for that species without bias, avoiding this problem. However, in the typical case for biodiversity experiments, we do not have prior knowledge of which species has the highest true monoculture yields, and must estimate the unknown maximum monoculture productivity based on our data.

**Formal analysis of two simple cases:**

Detecting transgressive overyielding depends on estimating two key quantities: true mean polyculture productivity, and the true mean productivity of the highest yielding component species in monoculture. Mean polyculture productivity is easily estimated without bias by taking the mean of all polyculture measurements, although there are the subtle problems of whether experimental polycultures are fully representative of natural communities, and if polycultures that have somewhat different composition should be lumped together, or analyzed separately in a way that mirrors the monoculture analysis we discuss below. Estimating maximal mean monoculture productivity without bias, however, is not so straightforward. Here we formally analyze the bias that arises from using the maximum sample mean as an estimate of the maximal true mean monoculture productivity under two particular simplified scenarios. In the general case, with many

species, each with different population means and variances, the maximal sample mean is difficult to describe mathematically, so we consider two special cases. These analyses demonstrate the general principle at work, and provide rough estimates of the potential magnitude of the bias arising in more typical cases of unknown true productivities.

Formally, we consider a collection of $n$ species, $s_i$ , each with a true mean monoculture productivity $\mu_i$, and let $\mu_{MAX}$ denote the maximal $\mu_i$ of all the species monocultures (see box 1 for an index of mathematical notations). In a given experiment with $k$ replicates of each species in monoculture, each of the species has a sample mean productivity, $\overline{\mu}_i$, and we have a corresponding maximal sample mean, $\overline{\mu}_{MAX}$. Note that $\mu_{MAX}$ and $\overline{\mu}_{MAX}$ are the maximal values of the true productivities and the sample mean productivities, respectively, and need not correspond to the same species. Similarly, we let $\mu_p$ be the true mean polyculture productivity and $\overline{\mu}_p$ the sample mean productivity of the set of the most diverse polycultures. By definition, transgressive overyielding occurs when $\mu_p > \mu_{MAX}$, that is, when the maximal true monoculture mean is less than the true polyculture mean. Since neither of these quantities is known we must rely on statistical estimators to approximate them. In principle, the sample mean of polyculture productivities, $\overline{\mu}_p$, provides an unbiased estimator for $\mu_p$, ignoring the issues mentioned above. On the other hand, we will see that the maximal sample mean monoculture $\overline{\mu}_{MAX}$ as defined above can be a highly biased over-estimator of $\mu_{MAX}$.

We model the value of $\bar{\mu}_{MAX}$ in two simple representative scenarios and demonstrate that it is a biased estimator for $\mu_{MAX}$ in both cases. In the first case, we consider an experiment in which several species are co-dominant, and share the same true productivity. In the second case, we consider a simple two-species scenario with differing productivities. These two cases were chosen because they are analytically tractable and illustrate clearly the factors that lead to increased bias.

*Case 1: Co-dominant species*

We assume that all *n* species share an identical monoculture productivity, that is, $\mu_i = \mu_j$ for any *i* and *j*. For simplicity (and suspending disbelief towards negative productivity values), we assume that the productivity in a given plot follows a standard Normal distribution – that is, $\mu_i = 0$ and $\sigma_i^2 = 1$. Further, we assume that each species is represented by *k* monoculture plots in the given data. By a well known result, the mean of a size-*k* sample drawn from a normal distribution $N(\mu, \sigma^2)$ is itself described by the normal distribution, $N(\mu, \sigma^2 / n)$. In our case, this means that each of the species-specific monoculture sample means, $\bar{\mu}_i$, is identically distributed as N(0,1/*k*).

Thus, in this scenario, the sample means of each species' monoculture plots are independent and identically distributed, and hence $\bar{\mu}_{MAX}$ can be considered as the highest-ranked value of *n* samples from the same distribution. In statistics, the *j*th highest member of a sample is known as the *j*th order statistic of the sample, and we can use the probability density function (pdf), $f(x)$, and corresponding cumulative density function

(cdf), $F(x)$, of the sample distribution, to describe the distributions of each of a sample's order statistics (Casella and Berger 2002). In this case, we are interested only in the $n$th, the maximum, which has the pdf $nF(x)^{n-1} f(x)$. Since the sample distribution is $N(\mu, 1/k)$, we have $f(x) = \sqrt{\dfrac{k}{2\pi}} \exp\left(-\dfrac{k(x-\mu)^2}{2}\right)$ and $F(x) = \Phi(0, 1/k)$ (there is no simpler algebraic expression for the normal cdf). Thus, the distribution of $Z = \overline{\mu}_{MAX}$ is given by

$$f(z) = n\Phi z^{n-1} \sqrt{\frac{1}{2\pi}} \exp\left[-\frac{1}{2}z^2\right],$$

where $\Phi(x)$ is the cumulative distribution for the standard normal.

Given the statistical distribution for the maximal monoculture sample mean, we can calculate the expected value of $\overline{\mu}_{MAX}$ to determine whether it is unbiased ($E[\overline{\mu}_{MAX}] = \mu_{MAX}$) or biased ($E[\overline{\mu}_{MAX}] \neq \mu_{MAX}$). Unfortunately, there is no closed form solution for $E(Z)$ as a function of $n$ and $k$, but we can see by inspection that it must be positive since $f(z)$ is positive for all $z$, and evaluate the expectation numerically for particular combinations of the number of species and number of replicates per species. Doing so, we observe that $E[\overline{\mu}_{MAX}]$ is positive for all $n$ and $k$ (Fig. 3.2), demonstrating that $E[\overline{\mu}_{MAX}] > \mu_{MAX} = 0$. Thus, we see that the maximal sample monoculture productivity is an overestimate of the true maximal monoculture productivity. Note that since we chose $\mu = 0$ and $\sigma^2 = 1$, the scale of the $y$-axis is in the units of the species' standard deviation of monoculture productivity. Therefore, in absolute terms, the expected bias is greater when species' monoculture productivities exhibit greater variability. This makes intuitive sense, as greater variability increases the likelihood of sample values greatly exceeding

the mean. Furthermore, the resulting bias is greater with more co-dominant species

(higher *n*), or with fewer replicates of each species in monoculture (lower *k*). Intuitively,

these represent the increased chance of exceptionally high averages when there are more

species, and increased variance of each species' sample means with fewer replicates.

*Case 2: Single dominant species*

While many communities contain several species with similarly high monoculture

productivities, in others there may be one truly most productive species. Nevertheless, in

these cases the estimator is still biased when the representative monoculture productivity

is selected *post hoc*. In our second case, we consider the simplest scenario that has a

single dominant species. In this scenario, there are only two species, *X* and *Y*, in the

experiment, and we assume that each species has only a single monoculture replicate. We

specify that species *X*'s monoculture productivity is normally distributed with mean $\mu$ ($\mu$

> 0) and variance 1 and species *Y*'s monoculture productivity is normally distributed with

mean 0 and variance 1. We refer to *X* as the dominant species because $\mu > 0$, though the

analysis here does not depend on that assumption. In this scenario, we cannot use the

order statistic analysis because the sample means of each species are described by

different distributions. Instead, the general form for the density of *z* is given by the

conditional probability expression: $Z \sim f_X[z]P[X$ is maximal$] + f_Y[z]P[Y$ is maximal$]$, or

$f_Z(z) = f_X(z)F_Y(z\,|\,\mu) + f_Y(z\,|\,\mu)F_X(z)$. In this case, we have

$$f(z\,|\,\mu) = \frac{1}{\sqrt{2\pi}}\exp\left[-\frac{1}{2}z^2\right]\Phi(z-\mu) + \frac{1}{\sqrt{2\pi}}\exp\left[-\frac{1}{2}(z-\mu)^2\right]\Phi(z).$$

Taking the expected value as before yields the expectation for the estimated maximal monoculture productivity in this scenario.

As with the first scenario, numerical analysis, Fig. 3.3 illustrates that $E[\overline{\mu}_{MAX}] > \mu_{MAX} = \mu$, so that $\overline{\mu}_{MAX}$ is a biased estimator. We see that in this scenario, the bias is largest for small $\mu$ – that is, when species $X$ and $Y$ are more similar in their true monoculture productivities. Nonetheless, even for fairly large differences between the species, the bias may be fairly large. While we do not analyze models with more than two species here, in general, the more species added, the greater the expected bias, as each additional species increases the chance of an exceptionally high sample.

These results provide an exact description of the estimation bias in two particular cases where we specified the underlying true productivities, but it is not possible to derive an exact expression for $E[\overline{\mu}_{MAX}]$ in the general case when the true monoculture productivities, $\mu_i$, are unknown. Furthermore, without knowing at least the distribution of the $\mu_i$, we cannot derive any other unbiased estimator for $\mu_{MAX}$. Nonetheless, based on these simple cases, we have identified four factors that lead to increase in estimation bias: low replication, large variability in species' productivities, larger pools of species, and multiple co-dominant species. For experiments with two or more of these factors, we should be particularly careful when estimating maximum monoculture productivity.

**Bootstrap Bias Correction:**

Given the ecological significance of detecting transgressive overyielding, it would be useful to have a method of analysis that can obtain an unbiased estimate of the maximal monoculture productivity. The approach we describe here is a parametric bootstrap bias correction (Efron and Tibshirani 1993),which provides an estimate of the overestimation bias caused by using $\overline{\mu}_{MAX}$ to estimate $\mu_{MAX}$ given a particular set of experimental data. An estimate of this bias can be used to discount the maximal sample mean productivity to obtain an unbiased estimate of $\mu_{MAX}$ before comparison with the average polyculture. We also discuss the issue of estimating the standard deviations of species' monoculture productivity.

The general application of bootstrap methods is to assess the quality of an estimator, usually in terms of its variance or bias, as it is applied to a given data-set. Because bootstrap methods do not rely on assumptions about the distributions underlying the data, they are applicable in situations like this one in which such knowledge is lacking. Non-parametric bootstrapping resamples the data itself a large number of times, but the bootstrapped estimates themselves are subject to high variance when the sample data replication is small, as is the case in many biodiversity experiments. In order to reduce that problem, we use a parametric bootstrapping method, in which the sample data are used to parameterize a set of normal distributions (one per monoculture species), which are then treated as a source of hypothetical data in the actual bootstrap procedure. Note that our procedure requires at least 2 replicates for each monoculture species since it relies on an estimate of each species' productivity variance.

*Determining Estimator Bias*

Our parametric bootstrap procedure works as follows. Given experimental monoculture data, in which species $s_i$ was sampled $k_i$ times in a year, we compute $\overline{\mu}_i$, the mean monoculture productivity, and $\overline{\sigma}_i$, the standard deviation of monoculture productivity, for each species. Using these empirically derived sample parameters, we perform bootstrap trials in which we randomly generate sample data and compare the simulated maximum sample mean to the largest productivity parameter to determine the proportional bias for that trial. Specifically, we first parameterize the sample distributions, setting $\mu'_i = \overline{\mu}_i$. Methods for estimating $\sigma'_i$ in long-term experiments are discussed below. Then, for each trial run, $t$, we generate simulated experimental data with the same number of replicates per species as the real experiment by taking $k_i$ random draws from $N(\mu'_i, \sigma'_i)$ for each species. We determine the simulated $\overline{\mu}'_{MAX,t}$ and compare this value to $\mu'_{MAX}$, the maximal value of the $\mu'_i$. Finally, we measure the bias, $b_t$, as the ratio $\overline{\mu}'_{MAX,t} / \mu'_{MAX}$. We repeat this simulation procedure 10000 times, taking the geometric mean of the $b_t$ to arrive at the overall bias estimate, $b$. We found that 10000 runs was sufficient to generate a desirable level of convergence in our estimate of $b$. Given $b$, we construct an unbiased estimator for $\mu_{MAX}$ by discounting $\overline{\mu}_{MAX}$ by $b$:

$$\tilde{\mu}_{MAX} = \overline{\mu}_{MAX} / b.$$

In short, this algorithm estimates the proportion by which the standard estimation statistic overestimates the maximum mean productivity, and adjusts the result accordingly.


*Testing Normality Assumption and Estimating \sigma bar*

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The major assumptions of this modeling technique are that annual monoculture productivities are normally distributed, and that we can obtain corresponding estimates of $\sigma_i$. So, before applying the parametric bootstrap in this way, we want to verify that the data do not violate this normality assumption and consider how to calculate $\sigma_i$. Because of variation in environmental factors, species' expected productivities are likely to differ from year to year. Consequently, simply calculating the standard deviation of all measurements for a species may overestimate $\sigma_i$. In this analysis, we compare the results of this pooled estimate with an approach that measures the standard deviation of year-adjusted residuals.

We consider two potential regression models of species' expected productivity values and analyze the residuals from each of them. The simpler model assumes that each species has an innate constant mean productivity, $\mu_i$. In this case, we simply calculate residuals as the difference between each data point and the species' overall mean productivity, where the overall mean is taken across all years for which we have data. The second model assumes that year-to-year environmental variability is likely to generate inter-annual variation in a species' mean productivities; in this case, variation within years may be normally distributed around a mean determined by annual climatic variables. Thus, rather than calculating $\sigma_i$ based on residuals from the overall mean, we considered residual productivity after subtracting out the species' average productivity for the appropriate year. The regression equations corresponding to these two models are:

$$x = \mu_i + \varepsilon \qquad \text{(pooled)}$$

$$x = \mu_i + dummy_{year} + \varepsilon \qquad \text{(year-adjusted)}$$

In order to assess normality across species, rather than on a species-by-species basis, we normalized the residuals from each case by dividing by the species' average productivity across all years. Finally, we perform a goodness of fit test to determine if the residuals differ significantly from a normal distribution.

These two estimates of $\sigma_i$ are upper and lower bounds on each species' actual variance of productivity. The pooled-years model assumes that all variation in measured productivity is due to the natural variation error term. Thus, any variation that can be explained through other factors such as climate is instead attributed to the species' productivity variability. On the other hand, the yearly-residual model captures all sources of error that vary between years in the dummy variable, so that no further reduction would be possible by adding extra explanatory variables such as yearly precipitation or climate. This minimizes the amount of variation attributed to the species. In general, model selection for estimating $\sigma_i$ will affect the results of the bootstrap procedure, so care should be taken in considering the assumptions of each approach, and a comparative approach might be best.

**Analysis of Cedar Creek Data**

We analyzed data from two biodiversity experiments at Cedar Creek – E120 (Big Bio) and BioCON. The two experiments differ in design, species composition, and in the number of years exhibiting transgressive overyielding. While transgressive overyielding occurred every year in E120, it occurred much less frequently in BioCON. For both experiments, we calculated the proportional bias introduced by the standard estimation

procedure, and for BioCON, we also analyzed how many cases of monoculture dominance are detected with and without our proposed bias correction.

*E120*

Cedar Creek's E120 experiment is a long-term biodiversity experiment consisting of 152 5m x 5m plots, each containing communities of between 1 and 16 species. In this analysis, we consider just the monocultures and the 16-species plots. Most species in the 16-species pool are represented by 2 monoculture plots (with the exception of *Panicum virgatum*, which had a single replicate, and two species represented by 3). While transgressive overyielding occurred every year in this experiment even without the bias correction (Table 3.1), we analyzed the monoculture data to provide an example of the bias' potential magnitude. We performed the bootstrap procedure using monoculture productivity data from 2001-2008, comparing estimated monoculture productivity to polyculture productivity for each year separately. We calculated species' monoculture means on a yearly basis, taking $\mu'_i$ equal to that year's mean monoculture productivity. We estimated the bias of $\overline{\mu}_{MAX}$ as the mean of the biases of 10000 runs of the bootstrap procedure.

As mentioned in the discussion of estimating $\sigma_i$, we tested two alternative models for species' productivity to determine whether either violated the normality assumption. We found that residuals based on species' mean productivities across all years were significantly non-normal (Shapiro-Wilk W test, $P < 0.0001$), while residuals based on single-year means were sufficiently normal (Fig. 3.4. Shapiro-Wilk W test, $P = 0.4209$).

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In both cases, residuals were normalized to test across species by dividing the residual by the corresponding mean. Because it provides a better fit for our parametric method, we used the second regression model to estimate species' variability, setting $\sigma_i$ equal to the standard deviation of species $i$'s year-adjusted residuals.

With the E120 data, the biases estimated by the bootstrap process are on average actually fairly small (Table 3.1). The mean bias for the year-to-year measurements is 9.11 $g/m^2$, accounting for an average of 5% of the maximal monoculture mean estimate across years. As suggested by the analytical results, small biases result when there is a large difference between the most and second-most productive species in the dataset. In these cases, it is less likely that a non-maximal species will over-produce the true maximal species. This productivity gap between the top two species is the main driver of the amount of bias in the E120 data (Fig. 3.5). In years with similar yields between the top two species, the bias was as much as 10-25% of the estimated maximum.

Notably, in these data, there are 4 species that are dominant for at least one year: *Liatris aspera*, *Panicum virgatum*, *Lupinus perrenis*, and *Lespideza capitata*. In no year was the most productive species significantly greater than the second most. When measured across all 8 years, only *Panicum* was significantly lower than the other three. In contrast, the polyculture was significantly greater than the greatest monoculture in every year considered. If we apply the bootstrap algorithm to just these species, using means and standard deviations measure across all 8 years, the expected bias is 16.0 $g/m^2$, or about 10% of the maximal mean (*Liatris*, 152.8 $g/m^2$).

*BioCON*

BioCON (Reich and al 2001) differs greatly from Big Bio in that additional experimental treatments are overlaid with variation in species richness. Monocultures and 16-species polycultures are subject to two experimental conditions – elevated $CO_2$ and elevated N – in a factorial design (4 and 9 species plots are also subject to a water availability treatment, but we do not consider these plots), and were sampled twice each year. For the purposes of this analysis, we compare monoculture and polyculture productivity for each experimental treatment and sample separately, producing 8 different cases per year, for a total of 96 separate cases.

The results from BioCON are quite different from Big Bio's in terms of the amount of transgressive overyielding. Of our 96 cases, the maximal monoculture was greater than the average polyculture in 71, in contrast to 100% polyculture dominance in Big Bio. There are several differences in experimental design that may explain this difference, but here we are just interested in the effects of estimation bias. On the other hand, BioCON also had several species alternating as the most productive monoculture. The June samples were dominated by *Lupinus perennis* (dominant in 32 of 48), but *Solidago rigida*, *Agropyron repens*, *Amorpha canescens*, *Lespedeza capitata*, and *Bromus inermis* were each dominant at least once. For the August sampling, 8 species were dominant at least once, with *Amorpha canescens*, *Solidago rigida*, and *Petalostemum villosum* dominant in 10, 10, and 9 cases, respectively.

We determined the bootstrap distributions' means in the same way as in the Big Bio analysis. In this case, however, we compared the results of estimating $\sigma_i$ using year-adjusted residuals as above with those of using pooled across-year values. These two cases provide, respectively, low and high bounds for the true productivity deviation. The magnitude of this variance term had a large impact on the estimated bias, and consequently on the number of cases of measured monoculture dominance. As above, we measured the average bias across all cases. Using the pooled across-year measure of variance led to a proportional bias estimate of 0.13, while the year-adjusted residual variance led to a bias estimate of 0.05.

We found that simply adjusting for estimator bias reduced the number of cases with monoculture dominance from 71 to 66 if we used the smaller, yearly residuals SD estimate, or 56 if we used the larger, aggregate SD estimate. If we restrict our analysis to the August samples, we find that 37 out of the 48 year/treatment cases exhibit monoculture dominance without the bias correction. With the yearly-residual adjustment, this drops to 35, and with the pooled-year adjustment, to 28. Given the larger variance, this is an 81% increase in the number of cases estimated to have greater polyculture productivity (11 without adjustment, 20 with adjustment).

**Discussion**

These results demonstrate a potentially large complication in accurately interpreting comparisons between monoculture and polyculture productivities. Analytically, we found four key factors that increase the likelihood of overestimating monoculture productivity:

number of species in monoculture, low replication, co-dominance, and high variability in species' productivity. Empirically, we found that this bias was typically in the 5-10% range in two experiments a CDR, which is not huge, but contributed to potentially false detection of monoculture dominance in some cases.

Our results are complementary to (Schmid et al. 2008), who also pointed out this bias effect. Schmid *et al* focused on the fact that in many cases there is no single species that is significantly more productive than any other in monoculture. High within-species variance relative to between-species variance can easily lead to some species apparently performing better than others when in fact this apparent overyielding is due to sampling. Furthermore, this effect is increased the more species are planted in monoculture. When this is the case, analogous to our first analytic scenario, it is not justified to assume the maximal sample mean is representative of the maximal true mean. Our results extend these by providing generalized analytic descriptions of the bias in this case, and in the case of separate means.

Taken together, our results have implications for two situations. First, in analyzing existing biodiversity experiments, there are inherent design limitations that may hinder the ability to detect transgressive overyielding. Results detecting transgressive overyielding in meta-analyses using the standard tests (Balvanera et al. 2006, Cardinale et al. 2006) should be more convincing because they occurred in spite of the conservative bias of the tests. On the other hand, negative results should be less convincing. The

estimation bias is not extremely large, but may be significant in many borderline cases, particularly when experiments have low replication and several co-dominant species.

Meta-analyses of biodiversity experiments have found that transgressive overyielding occurs infrequently. The results of this paper suggest that adding a bias-correction procedure to the meta-analysis would contribute to the usefulness of its findings. Many of the experiments analyzed have the characteristics that our formal results indicate as leading to high bias: low replication, sometimes just one plot per species in monoculture, lack of significant difference between several most productive species, and large numbers of species in monoculture. In these cases, there may be a significant amount of bias introduced by the standard analysis, masking a higher frequency of transgressive overyielding that would be apparent with the bias correction.

Second, in designing new biodiversity experiments, it is possible to create designs that will allow more robust tests for transgressive overyielding. Specifically, the number of replicates of each species in monoculture can be increased. If species that are likely to have the highest monoculture biomass can be predicted, additional monocultures of those species can be established (with the hope that such predictions are accurate). Alternatively, the experiment could be established in two steps, with initial field trials to determine which species have the highest monoculture biomass, followed by a diversity experiment with sufficient replicates of that species. Finally, one may want to test whether overyielding occurs when diversity is increased from a specific species (for example a common dominant, or an agronomic species commonly planted in

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monocultures). In this case, the species whose monocultures will be used for comparison with more diverse communities can be determined a priori without field tests. We note that in all the cases where the identity of the species whose monoculture will be used for comparison purposes can be determine a priori, low number of replicates will not result in a biased estimate of its biomass. However, although low replicates will provide an unbiased estimate of the mean for that species, confidence in this estimate will clearly still be too low to provide a reasonable test.

We note that one limitation of our method is its high sensitivity to estimates of $\sigma_i$. Because of this, we recommend comparing the results of corrections using upper and lower bound variance estimates. This is less ideal than having a single, clear estimate, but the reality in low-replication experiments is such that this estimate is almost impossible to obtain.

### *Conclusion*

Tests of complementarity and selection in general, and transgressive overyielding in particular often rely on estimates of maximal monoculture productivity. Our results show, however, that these estimates have been biased overestimates, leading to tests that were more likely to reject transgressive overyielding. As a consequence these meta-analyses may have underestimated the frequency of transgressive overyielding and the strength of the complementarity effect in many systems. Correcting for this bias requires either statistical correction in analysis of existing data, or changes to experimental design for the future.

| Year | Avg. Polyculture | Max Avg. Monoculture | Bootstrap Bias Estimate | Proportional bias |
|---|---|---|---|---|
| 2001 | 272.113943 | 162.332333 | 17.6290929493 | 0.1085988 |
| 2002 | 374.3272 | 177.6415 | 2.17132276051 | 0.0122231 |
| 2003 | 379.143257 | 177.933333 | 7.52716223 | 0.0423033 |
| 2004 | 323.361929 | 182.105 | 6.40593190906 | 0.0351771 |
| 2005 | 346.612543 | 177.494667 | 1.76267052473 | 0.0099308 |
| 2006 | 259.463057 | 110.794667 | 26.2370478275 | 0.2368079 |
| 2007 | 323.698857 | 200.623333 | 2.43006007037 | 0.0121125 |
| 2008 | 319.115143 | 160.32 | 8.68840895736 | 0.0541942 |

**Table 3.1: Biases in the estimate of $\hat{\mu}_m$ based on annual data for species' mean monoculture productivities in CDR Big Bio experiment.** In none of these years was the maximal monoculture higher than polyculture. Furthermore, the bias in the maximum monoculture estimator was typically small. Two years, 2001 and 2006 stand out as having large biases. In these years, the top two species had similar productivities, which contributes to larger potential bias. In 2001 the top species were *Liatris aspera* (mean productivity: 162 gm/m^2) and *Panicum virgatum* (mean productivity: 151 gm/m^2); in 2006, the top two were *Amorpha* (mean productivity: 133) and *Lespideza capitata* (mean productivity: 110). In addition to these 4 species, *Lupinus perennis* was also dominant in one year, and close in several others. As suggested by the analytic results, this co-

dominance between multiple species increases the bias of the standard estimation
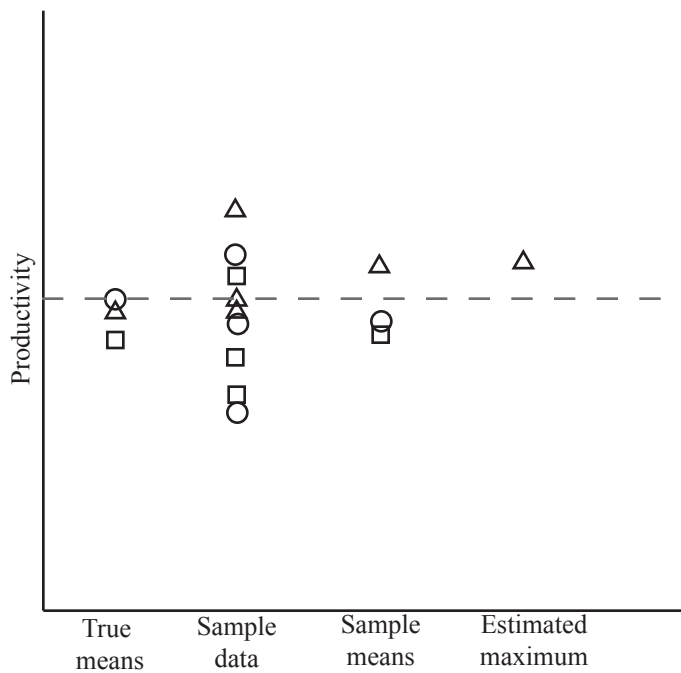
procedure.

**Figure 3.1: Illustrating the cause of the bias in estimating maximal monoculture productivity.** In the left-most column, each symbol represents the true mean of a species in an experiment. Samples for each species' monoculture plots are found (column two), and the means are calculated (column 3). Although circle has the highest true productivity, random variation in this sample causes triangle's sample mean to exceed circle's productivity. The more species that are included in an experiment, the more likely it is that at least one species will over perform in this manner, causing us to overestimate maximal monoculture productivity. Note that the point isn't that triangle's mean was estimated as the max rather than circle, but that the estimated max was higher than the true max.
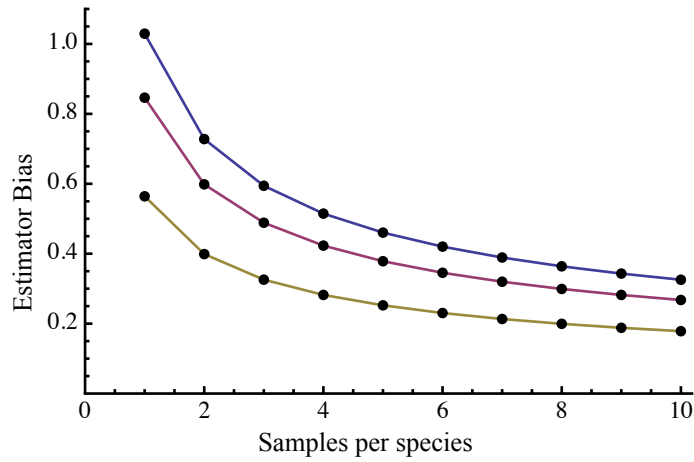
**Figure 3.2: Bias in estimating highest monoculture mean as a function of samples per species and the number of co-dominant species.** Lines represent (from bottom) cases with 2, 3, or 4 species tied as the most productive monoculture species in the experiment. Note that a value of 0 indicates an unbiased estimator and that the *y*-axis is measured in standard deviations. Both co-dominance of species and low replication contribute to larger overestimation biases.
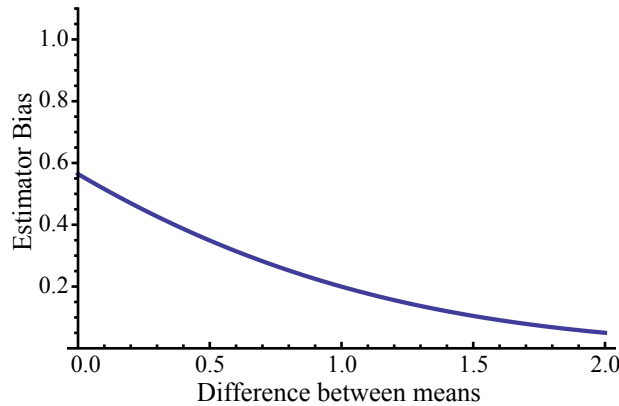
**Figure 3.3**: **Bias in estimating highest monoculture mean as a function of the difference in mean monoculture productivity between the highest and the second highest producing species [i.e. μ, where X~N(μ,1), Y~N(0,1)].** The closer the two species are in mean productivity, the greater the resulting bias. Even in cases where the difference is a full standard deviation, the expected bias is 20% of the standard deviation. This analysis assumes that the third highest productive species is never estimated to have the highest biomass.
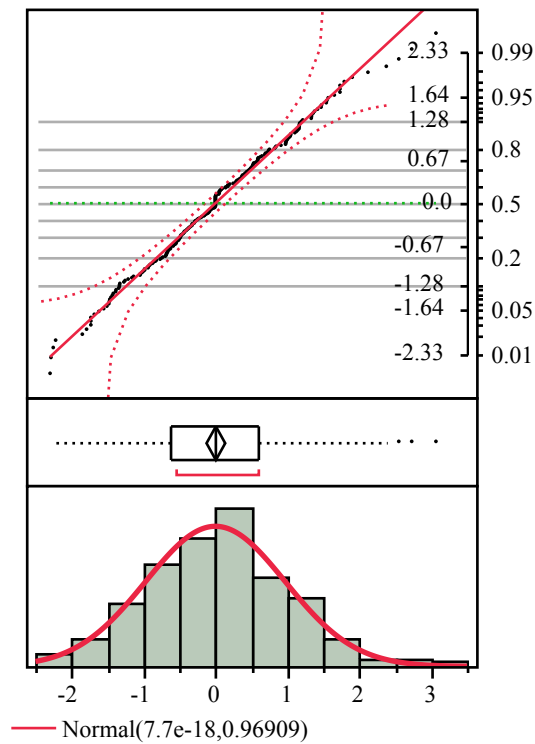
**Figure 3.4. Distribution of normalized year-adjusted residuals of monoculture biomass measurements from Cedar Creek's Big Bio experiment.** Top graph shows a normal QQ plot, bottom shows histogram of data with a fitted normal curve (*Shapiro-Wilk W* 0.9935, Prob < *W* 0.4209). Residuals do not reject fitting productivity with a normal distribution.
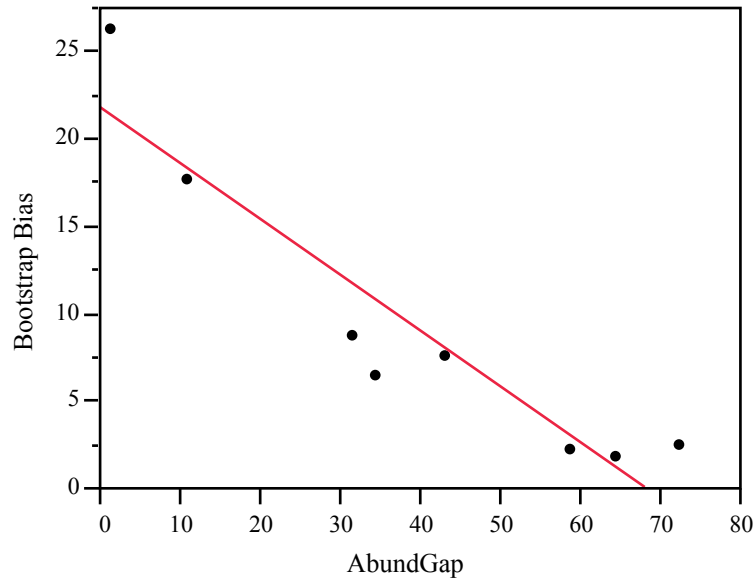
**Figure 3.5: Response of estimated bias to the gap between most and second-most productive monoculture means.** Analyses of CDR's biodiversity experiment found relatively small biases in the maximum monoculture productivity estimate for 6 of the 8 years tested. Comparing the estimated bias ($y$-axis) with the difference in abundance between the most and second-most productive species ($x$-axis), indicates that the bias is higher when these two species are more similar ($p<0.001$, $R^2 = 0.8700$), as suggested by the analytic treatment.

**Box 3.1: Mathematical Notation**

$\mu_i$ — productivity of species $i$ in monoculture

$\mu_{MAX}$ — maximum monoculture productivity: $\max\{\mu_i\}$

$\bar{\mu}_i$ — sample mean of species $i$ in monoculture

$\bar{\mu}_{MAX}$ — maximum monoculture sample mean: $\max\{\bar{\mu}_i\}$

$\mu_p$ — polyculture productivity

$\bar{\mu}_p$ — polyculture sample mean productivity

$Z$ — distribution of $\bar{\mu}_{MAX}$

$\mu_i'$ — mean productivity for species $i$ used in bootstrap procedure

$\mu_{MAX}'$ — maximum value of bootstrap productivities: $\max\{\mu_i'\}$

$\bar{\mu}_{i,t}'$ — sample mean for species $i$ in bootstrap run $t$

$\bar{\mu}_{MAX,t}'$ — maximum sample mean measured in bootstrap run $t$: $\max\{\bar{\mu}_{i,t}'\}$

$b_t$ — proportional bias measured in bootstrap run $t$

$b$ — overall bias estimate: geometric mean($b_t$)

$\tilde{\mu}_{MAX}$ — bias-discounted maximum monoculture estimate

# Chapter 4: Metacommunity processes are as important to local species diversity as nitrogen supply

Synthesis of niche and neutral paradigms requires refining our understanding of the appropriate domains of deterministic and stochastic forces in ecological communities. In particular, studies of stochastic dispersal and metacommunity processes on the one hand, and local competition and environmental filtering on the other, clarify the spatial and temporal scales appropriate to each process. In this study, we analyze effects of neighborhood density at several scales, nitrogen enrichment, and patch-level species richness on colonization and extinction rates in a prairie grassland. We found that short-range (<20 m) conspecific density was significantly more influential than longer-range dispersal. Furthermore, all three drivers we investigated had a significant effect on species' patch-level colonization and extinction rates. Because of the non-equilibrium state induced by the experimental nitrogen enrichment treatment, we were able to observe the mediating effect of dispersal limitation on the community's response to habitat modification. The large loss of species from control plots is consist with the hypothesis that dispersal is important to the maintenance of biodiversity even on small scales, but not with the hypothesis that composition is driven purely by local environmental characteristics. This research shows that spatial metacommunity processes and demographic stochasticity can be as important as resource supply and other manipulative treatments as drivers of local species richness, even in well-controlled and well-replicated experiments.

Metacommunity theory synthesizes the effects of dispersal-driven spatial processes with those of local processes driven by species' interactions with each other and the environment (Leibold et al. 2004, Holyoak et al. 2005). This effort has produced four

theoretical paradigms that make distinct assumptions about dispersal rates, environmental heterogeneity, and the role of species' traits: neutral, patch-dynamics, mass-effect, and species-sorting models. Two of these paradigms, species-sorting and mass-effect, assume a heterogeneous habitat and meaningful functional differences between species, but differ in assumed dispersal rate (Mouquet and Loreau 2002, Chase and Leibold 2003). The patch-dynamics approach is based on the competition-colonization trade-off, and assumes significant species differences but homogeneous habitat (Tilman 1994). Finally, the neutral model assumes identical species, dispersal limitation, and homogeneous habitat (Hubbell 2001). This partitioning of possibilities along the axes of dispersal, species equivalence, and heterogeneity is useful, but is not an exhaustive coverage of possible metacommunity types (Logue et al. 2011), and empirical work can help determine the mixture of these characteristics found in natural systems.

Similarly, increasing theoretical attention to the conflict between niche and neutral theory has led to integrative models including stochastic and deterministic processes (Tilman 2004, Gravel et al. 2006, Adler et al. 2007). Many empirical analyses have rejected pure neutral theory's prediction of trait-environment independence (McGill et al. 2006), but others have found that niche forces alone do not explain observed assembly dynamics in some communities and that stochastic dispersal play a significant role (Chase 2007, Myers and Harms 2011). While stochastic and spatially-explicit versions of classical metapopulation theory have recently been analyzed (Keeling 2002, Roy et al. 2008), there is a need for a parallel development in metacommunity models and in particular, for

models that will help generate predictions for metacommunities with novel combinations of dependence dispersal limitation, habitat heterogeneity, and species traits.

Propagule dispersal is known to be an important driver of population dynamics in ecological communities (Tilman 1997, Levine and Murrell 2003). Many large scale processes such as succession (Connell and Slatyer 1977) and metapopulation dynamics (Levins 1969, Pulliam 1988, Hanski 1999) clearly depend on the ability of species to colonize new sites across long distances. Spatial dynamics are also relevant at smaller spatial and shorter temporal scales, driving negative density-dependence through the effects of natural enemies (Janzen 1970, Connell 1971), or positive density-dependence due to limited dispersal distances or Allee effects (Keitt et al. 2001). At a community-level, dispersal can have varying effects on species richness, depending on scale and dispersal rate (Cadotte 2006). Theory predicts that local species richness increases in response to regional dispersal (Loreau and Mouquet 1999), but that as a whole, metacommunities attain maximal diversity under intermediate dispersal regimes (Kneitel and Miller 2003, Mouquet and Loreau 2003).

The predicted importance of propagule dispersal at local scales is demonstrated in seed enrichment experiments, in which seeds of novel species are added to established plots. These experiments typically produce increases in local diversity across a wide range of community types (Turnbull et al. 2000, Clark et al. 2007). In many cases, however, competitive limitation of establishment is also seen, and the number of added species able to colonize is negatively correlated with initial species richness (Fargione et al. 2003,

Foster and Dickson 2004). Taken together, these results suggest that niche spaces in many local communities are not fully saturated and could support more species, but that diversity is co-limited by low seed arrival and competitive effects inhibiting successful colonization. Other limitations to coexistence operate during the life-stages between seed and reproductive adult. In particular, seedling survival is often a major bottleneck to colonization, and is largely determined by competitive interactions and predation (Moles and Westoby 2004, 2004). The multiplicity of factors controlling colonization and coexistence underscores the importance of the metacommunity approach, integrating both stochastic mechanisms (dispersal) and deterministic niche mechanisms (competition and environmental heterogeneity) as important factors in models of community dynamics. The relative importance of each mechanism determines the degree to which population demographics are controlled by propagule arrival relative to competitive or environmental filters.

The implications of seed addition experiments for metacommunities are limited to the extent that they simulate the effect of an increase in immigration from an experimental regional species pool on a single local patch, rather than accounting for the role of dispersal between patches in maintaining diversity at both the local and regional scales. However, the consistent finding of recruitment limitation does help explain variation in composition between sites with identical environmental characteristics (Stevens et al. 2004). Without dispersal limitation, differences in composition between plots depend exclusively on environmental characteristics. In contrast, with limited dispersal and stochastic establishment, historical contingency can produce distinct compositions in

otherwise identical habitats. Furthermore, historically dependent priority effects are magnified in communities where asymmetric competition between adults and seedlings further limits colonization (Ejrnæs et al. 2006).

Current interest in the varieties of metacommunities and integration of niche and neutral processes thus focuses on ways in which multiple mechanisms operate to mutually drive community dynamics. Key questions in this research concern which mechanisms are present in real world communities and what are the appropriate scales for modeling dispersal and spatial structure. Among metapopulation models, the scale question is relatively well explored in different models. Spatially implicit models such as the Levins model (Levins 1969) and models of the competition-colonization trade-off (Tilman 1994) assume global dispersal, so that dispersed seeds fall evenly across the entire habitat. Spatially explicit models (e.g. (Hanski and Ovaskainen 2000)) characterize the contributions of each patch to the others in terms of inter-patch distance and the dispersal characteristics of the species in question. Since limitation of dispersal to local neighborhoods has significant effects on model predictions (Lande 1987), it is an important question in metacommunities to what extent these density-dependent limitations act in concert with niche-based processes.

The four main metacommunity paradigms differ in their assumptions about spatial heterogeneity, relative rates of dispersal and within patch dynamics, and degree of equivalence between species but cover only a small range of the possible combinations of these factors (Logue et al. 2011). Only one paradigm, the neutral model, assumes any

degree of equivalence. The other three assume significant differentiation among species, and differ in that patch-dynamic models assume spatial homogeneity and a competition-colonization tradeoff, while mass-effects and species-sorting assume heterogeneity and corresponding differences in species' abilities to compete in different sites. The latter two differ in their assumptions about dispersal rates. Species-sorting assumes that local dynamics happen fast relative to dispersal, while mass-effects models assume that dispersal is fast enough that it can change the outcome of local processes. None of the four paradigms combine equivalence or stochasticity with niche differences, or equivalence with very high dispersal rates. In applications of metacommunity theory to smaller scales, however, dispersal limitation is very likely to lead to stochasticity, decreasing the role of species differences in short-term dynamics.

In this paper, we examine the influence of local dispersal, habitat heterogeneity, and competition on the metacommunity dynamics of a prairie plant community in a nitrogen addition experiment. First, we isolate dispersal, and analyze the scale of species' metapopulation dynamics relative to the experimental scale. We contrast predictions of internal and external dispersal Levins models to assess the relative scales of demographic density-dependence. Next we add niche-processes, and analyze the effect of field-level density, nitrogen addition, and competitive interactions on species' colonization and extinction rates. Finally, we consider the role of explicit space and analyze the contributions of density at increasing distances to demographic rates. One distinguishing feature of our analysis is that rather than analyzing spatial correlation in time slices, we focus on the effects of each mechanism on metacommunity demographic rates across

time. Our analyses demonstrate that metacommunity dynamics are a measurable and influential factor in this community's dynamics, even at the localized scale within a single field.

**Field methods:**

We performed our analyses of spatial and competitive processes on data from two long-term experiments based at the Cedar Creek Ecosystem Science Reserve LTER site (CDR). The first of these, E001, is a long-term study established in 1982 of the effects of nitrogen addition on the established prairie communities in 4 separate fields. The second, E120 (Big Bio), is a large-scale biodiversity experiment at CDR, consisting of 342 plots that were seeded with particular sets of species in 1994. We focused our analysis on 150 plots which were established at the same time as the main experiment, but have not been weeded to maintain a particular species composition like the biodiversity experiment plots.

*E001:*

Detailed methods can be found in Tilman (1987). This experiment was established on 4 fields on the Anoka sand plain in Minnesota. The three fields we analyze here, known as A, B, and C, had been abandoned for 14, 25, and 48 years before the experiment was established. All fields contain prairie communities typical of the level, sandy, high-drainage soil of the area. Two of the fields, A and B, are burned regularly as part of CDR's burning program. Field C is within the non-burning zone, and has not been burned since the experiment was established.

In each field, 54 4m X 4m plots were established in an 9 X 6 grid with 1m between plots, with no changes made to the existing community. Each plot was assigned an experimental nitrogen addition treatment, ranging from control plots with no added nitrogen to 27.2 g N m$^{-2}$ y$^{-1}$, plus an additional 0 N treatment that received additional P, K, Ca, Mg, S, and trace metals. Each treatment was represented by 6 plots in each field. Plots receiving nutrients other than nitrogen were not significantly different in species composition from the pure control plots, so we treat them as additional 0 N plots in our analyses. Each plot was sampled annually by clipping a 0.1 m X 3 m strip, which was sorted to species and weighed. Clip strips were taken from different parts of the plot each year.

In our analysis of individual species in this experiment, we exclude species that were observed fewer than 50 times in a field between 1982 and 2003. These rare species do not have enough data to accurately estimate demographic rates or colonization probabilities. This leaves 27, 29, and 36 species with at least 50 observations in fields A, B, and C, respectively. Because we ignore rare species, it is possible that our results apply only to more common species for which significant and measurable variation in local density exists.

*E120 (Big Bio):*

Detailed methods can be found in (Tilman et al. 2001). In 1994, a set of 342 5m X 5m plots was established in a 18 X 19 grid, treated to remove existing vegetation, and seeded

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with experimental assemblies of different numbers of species. Each plot received seeds of 1, 2, 4, 8, 16, or 32 species drawn from a pool of 32 typical prairie species. Of these 342 plots, 266 were maintained as part of the biodiversity experiment by removing individuals of any non-treatment species. The rest were left unmaintained so that new species could establish.

In 2007, the unmaintained plots were surveyed. Species were identified and assigned to cover classes in 4 1m x 1m subplots in each of the 76 unmaintained plots. Of the species identified, those that were part of the initial experimental treatment are called "planted species", while those that were not are called "invading species".

*Neighborhood classification:*

In our analysis of both experiments, when estimating the effects of local density on establishment and extinction in a particular plot, we count the number of nearby plots containing a particular species in various distance classes. We refer to distance classes are known as ring 1, ring 2, and ring 3. Rings are determined by the distance between the center points of the focal plot and the neighboring point. If the distance ($d$) is 1 (measured by plot coordinates) or less, the neighbor is assigned to ring 1; if $1 < d <= 2$, the neighbor is assigned to ring 2, and if $2 < d <= 3$, the neighbor is assigned to ring 3. Note that the distance is measured according to a coordinate system scaled to the experiment, so the actual radius is different between E001 and E246. There are 4 plots in ring 1 (the focal plot's nearest neighbors), 8 in ring 2, and 20 in ring 3.

**Detecting the scale of density-dependence: plot vs. field level**

The first question we address is whether annual demographics in the E001 experimental community are in fact sensitive to density within the experiment, or instead to whole-field density. If dispersal ranges are great enough that the seed rain from the rest of the field overwhelms internal dispersal, we do not expect to find metacommunity dynamics operating within the experiment. On the other hand, if dispersal ranges are sufficiently limited, then species' dynamics within the experiment will exhibit local density-dependence. To this end, we compare the results of fitting two alternative metapopulation models to time-series of plot occupancy from the nitrogen addition experiment.

The basic model we use, the classic Levins model (Levins 1969), describes a habitat divided into discrete patches, a proportion $p$ of which are occupied by a particular species at a given time. In our case, this describes the number of plots in which a species is present in a given year. The species' metapopulation density changes through time as the species colonizes new patches and is lost from others. Formally, the model assumes that loss rate in a given patch is independent of overall abundance of the species and that per-patch colonization rate is directly proportional to the number of occupied patches. This yields the dynamical equation:

$$\frac{dp}{dt} = cp(1-p) - mp ,$$

where $c$ and $m$ are constants describing the gain and loss rates. This model has stable equilibria at $p* = 0$ and the non-trivial $p^* = \frac{c-m}{c}$ (Gotelli 2008). So long as $c > m$, the model predicts stable metapopulation persistence.

However, this model assumes that all propagules arriving at local patches originated from another local patch. While the experimental plots can be treated as metapopulation patches for the purposes of measuring species' proportional distributions, they are in reality a subsection of an otherwise continuous habitat, and hence represent only a sample of the field's population. Furthermore, because of the surrounding field, propagules are expected to also come from sources outside the experimental plots, so that colonization rates may not depend solely on plot occupation. Since the experimental plots represent a relatively small fraction of the whole field, we need an alternative model to account for the seed rain from the rest of the field.

*Generalized Levins Model*

We divide propagule flow into two categories: internal, which consists of propagules originating from one of the modeled habitat patches, and external, which consists of those originating from surrounding habitat sources. The contribution of internal propagules to colonization rates is exactly as in the original model. External propagule rain contributes a fixed input of propagules uniformly to all patches in the habitat, independent of the number of occupied patches (Gotelli 1991). The formal equation for a model with both local and regional seed distribution is

$$\frac{dp}{dt} = c_I p(1-p) + c_E(1-p) - mp$$

where $m$ is the loss rate for occupied patches, and $c_I$ and $c_E$ are constants determining colonization rates from local and regional propagules, respectively (Hanski 1999).

By utilizing alternate versions of the Levins model that make different assumptions about the scale of propagule flow, we can compare the two based on experimental parameterization and determine which version leads to better predictions for our study system. As an alternative to the original Levins model, the strongest assumption is that the vast majority of propagules are generated outside the observed patches and distributed evenly over the observation area. Under this pure propagule rain assumption ($c_I = 0$), the generalized model simplifies to the classic mainland-island model:

$$\frac{dp}{dt} = c_E(1 - p) - mp.$$

This purely external model predicts a nontrivial equilibrium occupancy of $p_E^* = \dfrac{c_E}{c_E - m}$, again requiring $c > m$ for a stable metapopulation. Ideally, we could also test predictions generated from the mixed model, but estimation of model parameters is complicated by the relation between predictors $p$ and $p(1-p)$. Hence we restrict our analysis to the two pure models.

*Testing between internal and external dispersal models*

Our analysis consisted of using the first 17 years of data to generate parameter estimates for each species, determining each model's predicted equilibrium, and comparing this to the mean occupancy for the last 5 years of data. To estimate model parameters, we used

the number of colonizations and extinctions in a year to calculate the parameter value that would produce the appropriate number of changes in a given year using a linear approximation to the differential equation. For example, we solved $e_t = cp_t(1 - p_t)$ for $c$, given observed initial density and number of establishments ($e_t$). The formulas used to calculate annual model parameter estimates from the data were:

$$g_I = \frac{C_t}{P_t(1 - \frac{P_t}{N})} \quad \text{and} \quad l = \frac{E_t}{P_t}$$

for the local model, and

$$g_E = \frac{C_t}{N - P_t} \quad \text{and} \quad l = \frac{E_t}{P_t}$$

for the regional model, where $C_t$ is the number of new plots colonized between years $t$ and $t+1$, $E_t$ is the number of plots lost between $t$ and $t+1$, $P_t$ is the number of plots occupied in year $t$, and $N$ is the total number of plots in the field (54 in all cases). In all cases, parameters for each species were estimated for each field separately, so that a given species may have as many as three sets of parameters. Note that $P/N$ in these computations is equivalent to $p$ in the Levins model. Overall estimated parameters for each species, $\hat{c}_I$, $\hat{c}_E$, and $\hat{m}$ were calculated as means of the species' annual estimates.

Given overall $\hat{c}_I$, $\hat{c}_E$, and $\hat{m}$ values, we calculated predicted equilibria for each species under our alternative models. $P^*$ values were calculated from the mean $l$ and $g$ estimates for each model, with corresponding equilibria

$$\hat{P}_I^* = \frac{\hat{c}_I - \hat{m}}{\hat{c}_I} \quad \text{and} \quad \hat{P}_E^* = \frac{\hat{c}_E}{\hat{c}_E - \hat{m}}.$$

In cases where $\hat{P}_I^*$ was negative, we treated it as an estimate of zero. We then calculated $\tilde{P}^*$, the observed equilibrium metapopulation density, for each species as the mean of its proportional occupancy in a particular field over the final 5 years. Finally, we regressed $\tilde{P}^*$ against $\hat{P}_I^*$ and $\hat{P}_E^*$ for each field individually and for all fields together, to determine which model was a better predictor of equilibrium metapopulation density.

*Results:*

The first step was to verify that 1999-2003 occupancies were, in fact, metapopulation equilibria. To that end, we regressed annual *P* values from these years against time for each species. We found that almost all species had reached metapopulation equilibrium by 1999. Of the 92 species/field pairs considered, only 4 had significant changes in proportional occupancy between 1999 and 2003, all of which were in field C. In contrast, most (32 out of 36) species in field C exhibited significant changes between 1982 and 1998. Because of this, we conclude that mean proportional occupancies between 1999 and 2003 represent good estimates of each species' true metapopulation equilibrium, and are therefore appropriate for use as validation data.

In our regressions of $\tilde{P}^*$, we found strong support for the internal model and none for the field-level model. In each individual field, proportional occupancy estimates from the internal Levins model were significant predictors of actual occupancy. Regressions were significant ($P<0.0001$) in all fields, with $R^2$ values of 0.57, 0.85, and 0.51 in fields A, B, and C (Fig 4.1A). When data from all fields were combined, the result was also significant ($P<0.0001$), with $R^2$ of 0.60. Interestingly, the predicted equilibria were

significant overestimations of the observed mean occupancies (regression intercept $< 0$,

slope $< 1$). In contrast, the regional version of the Levins model was not a significant

predictor of final occupancy in any fields (Fig 4.1B). The regression for field C was

significant, but produced a negative relation between predicted and observed occupancy.

One distinguishing characteristic was that the local model predicted a wide range of

equilibrium values $(0.0 - 0.9989)$, while the regional model's predictions were in a much

narrower range $(0.20 - 0.69)$.

The contrast between these results suggests that, at this scale, internal dispersal between

plots far outweighs the impact of propagules arriving from the surrounding field.

Interestingly, despite the extreme simplicity of the Levins model and its exclusion of

many biologically important processes, it provided generally accurate predictions of

metapopulation equilibria for most species. Given the role of local density-dependence,

we conclude that we can understand species' dynamics within this experiment as driven

by metacommunity processes. The question then arises to what extent this community fits

in the four main metacommunity categories, or whether it lays in a novel region of the

model-space.

**Interactions between dispersal, environment, and competition**

Our second question is to what extent dispersal dynamics interact with local competition,

and whether both are active mechanisms in these fields. Previous work has demonstrated

significant importance of nitrogen addition in changing competitive outcomes in E001

and driving an overall reduction in species diversity (Clark and Tilman 2008), but the

Levins model ignores the role of site-specific environmental differences in metapopulation processes. In particular, nitrogen addition was a major driver of species loss (and reduction of colonization) in mid and high-N addition plots. Our question is whether this is sufficient to explain shifts in community composition and individual species' dynamics, or whether dispersal and competitive processes were both significantly active in the metacommunity.

To that end, we investigated the effects of local density, nitrogen addition, and species identity on colonization and extinction rates in E001. In particular, we regressed species' plot-level gain and loss rates within each nitrogen addition class (measured as changes in presence or absence between years $t$ and $t+1$) on the total number of plots occupied in year $t$ and the amount of nitrogen added to the focal plot. We measured separate gain and loss rates within each N-addition category to separate out the known effect of nitrogen addition on species composition in this community. Thus, for each time interval, we modeled colonization rates for each species in each field as the set of rates:

$$c_{N,i,t} = \frac{new_{N,i,t+1}}{unocc_{N,i,t}},$$

where $unocc_{N,i,t}$ is the number of plots in nitrogen addition class $N$ not containing species $i$ in year $t$, and $new_{N,i,t+1}$ is the number of those plots that are occupied by species $i$ in year $t+1$. Our regression data for each field consists of all $N$ and $i$ pairs for each year. Loss rates were defined similarly:

$$l_{N,i,t} = \frac{lost_{N,i,t+1}}{occ_{N,i,t}},$$

where $occ_{N,i,t}$ is the number of plots in nitrogen addition class $N$ containing species $i$ in year $t$, and $lost_{N,i,t+1}$ is the number of these plots that do not contain $i$ the next year. Note that if either denominator was zero, we excluded that year from the analysis.

Species that are generally more successful in this community are likely to have both higher colonization rates and higher average plot occupancy than less successful species, creating an overall positive relation between the two. In order to control for this species effect, we included species identity as a dummy variable in the complete regression. Again, for each field, we regressed the described gain and loss rates for each species in each N-addition class on the corresponding N-addition rate, species identity, the number of plots containing that species in the whole field, and all two-way interaction terms. We also performed individual regressions for all species that were counted as present at least 50 times in a field.

*Results:*

In agreement with the relative success of the local colonization Levins model, significant density-dependence in gain and loss rates was observed for all three fields (Table 4.1). Species' gain rates were significantly related to field-level density in two of the three fields (Field A: $F$ Ratio = 183.4, $P < 0.0001$; Field B: $F$ Ratio = 24.6, $P < 0.0001$; Field C: $F$ Ratio = 2.9, $P = 0.088$). Loss rates were significantly related to field-level density in field C ($F$ Ratio = 7.57, $P = 0.0060$). In all cases, the effects went in the expected directions – increased density led to increased establishment rates and decreased loss rates. In regressions excluding the species X density interaction term, gain and loss were

significantly related to density in all fields. In almost all individual species regressions with significant density effects, per-plot colonization rates increased with field density.

Both other first order terms had significant effects for gain and loss rates. Nitrogen significantly decreased gain and promoted loss in all fields ($P < 0.0001$ for all cases). It was known from previous studies that plot-level species richness is negatively related to the amount of nitrogen added. We see that this occurs from increased extinction, but also from decreased colonization success. Species identity was also significant for gain and loss rates in all fields ($P < 0.0001$ for all cases), though the effect size was small. Interaction terms were also significant in most cases, particularly species X nitrogen and species X density.

Individual species also tended to show positive colonization rate responses to field density. We ran separate regressions of colonization rate within each N-class vs. N-addition in that class and total field presence for each species that was counted as present 50 times or more in a field during the experiment. The number of species with significant regressions for each field was 23 out of 27 in field A, 28 of 30 in field B, and 31 of 37 in field C. Of these, field presence was a significant term for 22, 19, and 21 species, and had a positive effect on colonization rates for all but one species in field B.

**Plot-neighborhood analysis in E001 and E120:**

The final set of analyses focused on whether dispersal is wide-ranged enough that the

mean-field assumption suffices, or whether we can detect spatially explicit density dependence. In the context of E001 and E120, we expect that increased abundance of a given species immediately surrounding a plot leads to relatively higher establishment and lower extinction rates for that plot.

In this analysis, we used annual data from E001, and differences between 1994 and 2007 states for E246 to assess how a species' density at different distances from a focal plot and local niche mechanisms affected colonization and extinction probabilities. In both experiments, the response variables were binary (either establishment vs. no establishment, or loss vs. persistence), so we used binomial logit regressions to estimate the probability a plot would change state between time-periods. For E001, we estimated colonization probabilities by considering all cases in which a plot was unoccupied by a species in a given year, and regressing its state the following year (occupied or unoccupied by the focal species) on species identity, the summed biomass of that species in rings 1 or 2, the number of other species in the plot, and the N-treatment of the given plot. We also included all 2-term interaction effects. As before, we performed the analogous regression for extinction probabilities by looking at occupied plots and checking whether they were still occupied next year.

In E246, limited data on the unmaintained plots meant that we could not analyze density dependence on an annual basis. Rather, species presence and abundance were only measured in the unmaintained plots in 2007, so we therefore analyzed how spatial pattern in the initial seeding in 1994 affected the presence of species in unmaintained plots in

2007. In this case, we considered each case in which one of the 32 experimental species was not planted in a given plot, and regressed a binary 2007 presence/absence variable on the number of plots in each distance ring which were seeded with that species. We also included the number of species seeded into the focal plots as a predictor variable because of the potentially strong inhibitory effect of more diverse communities. We did not analyze extinction in this experiment.

*Results*

*Neighborhood density effects in E001:*

We found significant increases in plot-level establishment probability and decreases in plot-level loss probability as a function of same-species neighborhood density in all three fields (Table 4.2). Logit regression showed increased probability of inter-annual establishment when the local neighborhood contained more plots with the given species present. Both the colonization effect and rescue effect were stronger for plots in neighbor ring 1 than 2, suggesting a decline in propagule contribution from more distant plots.

*Neighborhood density effects in Big Bio:*

Colonization rates in the unmaintained plots in the E120 biodiversity experiment showed a strong positive relation to local-neighborhood density dependence (Table 4.3). There were 7,779 possible colonizations; that is, pairs of a given experimental species and a plot it was not planted in during the initial seeding. Of these, 1,283 resulted in successful colonization. We estimated the effects of the number of plots in rings 1, 2, and 3 containing a given species on the probability that it would establish in a particular

unmaintained plot. We also included the effects of the number of planted species in the plot from the given species' functional group and the number of planted species from other functional groups. Analyses ignoring the spatial component show a significant inhibitory effect of same-FG diversity.

Density in all three rings contributed positively to establishment probabilities, with the highest effect size coming from ring 2, and the lowest contribution from ring 3, while increased diversity in the focal plot led to decreased colonization rates (Table 4.3). The decreased effect of occupied plots in ring 3 relative to rings 1 and 2 is consistent with the decreased number of seeds from those plots expected to reach the focal plot.

## Discussion

Our results demonstrate the presence of metacommunity processes at small scales in a Minnesota grassland. In addition to confirming the previously recognized importance of nitrogen availability and species differences, we found that small-scale positive density-dependence is an important mechanism controlling population dynamics, and consequently community structure and composition. Specifically, we first found evidence for locally driven demographics by comparing predictions of alternative metapopulation models to observed equilibria. Second we found that species' metapopulation demographics were co-determined by N-addition rates, density, and species identity. Finally, we found that the neighborhood most relevant for annual colonization and extinction was approximately 15m or less, and that the signature of initial spatial pattern

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persisted for 14 years. These results suggest further development of spatially-explicit theory integrating localized dispersal with competition and heterogeneity. Moreover, they suggest that interpretation of the results of manipulative experiments like the two discussed could benefit from taking into account the effects of metacommunity dynamics on species' persistence and abundance.

A spatial perspective further helps explain the loss of species from control and low-N plots. Although these plots experienced minimal or no manipulation, average species richness showed large declines (Clark and Tilman 2008). For example, at the beginning of the experiment in 1982, plots that received no added nitrogen (control and non-N fertilization plots) had mean species richnesses of 12, 10, and 12.6 in fields A, B, and C. In 2004, the corresponding values were 7.6, 8.2, and 11.6. In contrast, other fields at Cedar Creek that were surveyed every 4 years but not subject to any experimental treatments showed no significant change in diversity over the same period. These declines are not explainable in terms of the experimental treatment, but given the competitive exclusion of many species from N-addition plots, would be predicted by metapopulation models of habitat destruction (Tilman et al. 1994). In particular, experimentally induced population decreases are expected to lower affected species' colonization rates, effectively acting as habitat destruction. Without a similar reduction in plot-level mortality, this reduces species' metapopulation abundances, and in many cases can result in local extinction. However, this is only expected to happen if dispersal is sufficiently limited that the much larger population outside the experiment contributes

minimally to internal colonization rates. Thus, this explanation is dependent on determining the relevant scale for the emergence of metacommunity dynamics.

*Internal vs. external dispersal*

We found that a metapopulation model that assumed colonization rates were proportional to internal density significantly outperformed the alternative model in which colonization was dependent on external seed-rain. This result indicates that the dispersal scale relevant to annual demographics is on the same order as the size of the experiment and smaller than the entire field. Because of this, we expect that spatial effects do influence local demographics on an annual basis. It is true that, at a larger scale, colonization and extinction at the field level might also exhibit metapopulation dynamics in a fragmented landscape, but these dynamics occur over longer time scales.

There were several points of tension between the Levins predictions and experimental results. One indicator of this conflict is that the internal model's predictions were consistent overestimates of the final observed equilibria. Regressions of observed equilibrium metapopulation densities against predicted values using a fixed intercept were significant and had slopes less than one. This overestimation could have resulted because of violations of two of the Levins model's assumptions. First, the model assumes global dispersal between all patches, which may have been approximately correct early in the experiment when most species were widespread, but became less so as many species were competitively excluded from high N-addition plots and the spatial pattern became more fragmented. Limits on dispersal distance in metapopulation models predict lower

equilibrium abundances and in some cases, extinction (Lande 1987), relative to equivalent models with global dispersal. Next, the nitrogen addition treatment changed competitive rankings, resulting in competitive exclusion and "virtual" habitat destruction for many species. The unmodified Levins model, on the other hand, assumes homogeneous habitat, but a more realistic model which discounts the proportion of sites available for colonization based on a species' success in N-addition plots could be more accurate. In particular, ignoring the effect of habitat modification leads the model to overestimate the number of sites available for colonization, and thus the potential metapopulation abundance. However, in spite of these oversimplifications in the models' assumptions, the internal model was a generally good predictor, indicating that most year-to-year changes in plot occupancy were driven by colonization by nearby adults.

*Dispersal and N-addition both drive demographic rates*

Our second objective was to determine whether dispersal and nitrogen-mediated competition interact in determining species demographics. We found that both were significant factors, and in addition, we found significant interactions between each of these and species identity. Two of the three fields showed a significant positive response in colonization rates to field-level density across species, while the other showed a significant reduction in extinction. In fields A and C, the nitrogen addition by density interaction was a large contributor to the regression (F-ratios 140 and 55, respectively). In both cases the estimated parameter was negative, indicating that the densities of abundant species were reduced by N-addition more than the abundances of less common species. Across all fields, N-addition was the biggest contributor to extinction rates.

Given the importance of habitat heterogeneity, these data could support either the mass-effect or species sorting perspective, depending on whether they satisfy the model's other assumptions. The key difference between the two is the relative rate of within patch dynamics to dispersal. Under species sorting conditions, local dynamics are assumed to be fast enough that propagules of inferior competitors are rapidly excluded. Species-sorting also assumes that regional dispersal is fast enough that species are able to reach all habitable sites. Our results do not support these assumptions. First, it is true that many species were lost from modified patches, but the loss took place over several years. Second, instances of patch-level extinction followed by recolonization indicate that species did not reach stable equilibrium in all habitable patches, and were not able to colonize all suitable sites. The main characteristic of the mass-effects model is that between-patch dispersal can be sufficient to maintain species' populations in sink patches. We observed, rather, nearly complete extinction of most species from nitrogen addition plots, and very few instances of low-nitrogen specialists surviving or re-establishing. Neither metacommunity perspective is completely correct, though there are elements of each present.

*Neighborhood density*

Finally, we tested whether the Levins model's assumption of global dispersal was accurate, or whether we could detect an influence of conspecific density in a plot's immediate neighborhood. In both experiments, we did find significant positive effects of neighbor density on plot-specific colonization rates, and in both cases, the contribution

declined with distance. This finding supports our hypothesis that the Levins model overestimates equilibrium density because it assumes global dispersal, when in fact dispersal is even more limited. In E001, we also found a significant negative relation between extinction rates and neighborhood density, indicating the presence of a rescue effect.

Limited dispersal distances and small population sizes lead to very different dynamics than global dispersal and large populations. In the former case, patch-level populations are much more likely to face stochastic extinction, and are more sensitive to changes in nearby patches. The effects of this sensitivity are clear given the loss of species even from control plots in the nitrogen addition experiment. Dispersal limitation also slows down community equilibration, preventing species from reaching sites in which they could potentially coexist. In the case of Big Bio, the signature of the initial seeding pattern is visible 14 years later in the composition of unmaintained plots.

*Density dependence and interpretation of experimental treatments*
The results of this analysis have important implications for the interpretation of manipulative experiments when the treatment results in indirect, spatially driven changes in control plot abundances and composition. For example, in the E001 nitrogen addition experiment analyzed in this chapter, the experimental treatment was indirectly responsible for loss of species from low N and control plots due to the metapopulation habitat destruction effect. Analyses of this experiment and other nutrient manipulation studies (Suding et al. 2005, 2005) typically estimate the impact of the treatments by

comparing species richness or abundance between treatment and control plots from the same year. However, when dispersal limitation leads to loss of species in control plots, this comparison underestimates the total effect of the experimental treatment because of the unintended indirect changes of control richness. For example, (Suding et al. 2005) use the log ratio of a functional group's relative abundance in fertilized and control plots ($lnRR=ln(RA_{fert}/RA_{control})$), and a similar metric can be used for species richness. In experiments where fertilization reduces species richness, which yields a lower response ratio, the metapopulation effect may also reduce species richness in controls, which increases the response ratio. As a result, the response ratio does not reflect just the experimental treatment, but also the spatial effect, which acts in the opposite direction. The result is similar if the treatment effect increases richness or relative abundance, producing in a similar increase in nearby control plots.

This underestimation will not occur in all systems and experiments, as it depends on density dependence on the experimental scale. In some cases, dispersal may be sufficiently wide-ranged that all plots experience a regional mean-field seed rain, while in others, dispersal may be even more restricted so that each plot is essentially independent. Because of the non-uniformity of this effect across systems, it may be difficult to easily account for it in meta-analyses of manipulation experiments. At least for those with sufficient long-term spatially explicit data, analyses like I presented in this chapter could show whether there are strong metapopulation dynamics in the given system. A possible suggestion for future experiments is to establish controls at a sufficient distance from the main experiment that they can reasonably be considered independent. If these controls

and the within-experiment controls follow different trajectories, this would suggest that the latter are subject to metapopulation effects, and that interpretation of experimental results should reflect this possibility.

### *Conclusion*

This analysis demonstrates the influence of multiple mechanisms controlling colonization and extinction, and that dispersal-driven local metacommunity processes are as important as competition to local species richness. While studies of this community have found clear evidence for the influence of nitrogen competition on community assembly, we previously had only indirect evidence of the role of dispersal. Strong positive density-dependence at local scales, together with evidence from seed addition experiments, suggests that a major factor controlling plot-level species richness is dispersal limitation. Along with priority effects, stochasticity introduced by propagule limitation can increase the degree of neutrality in a community, increase local susceptibility to habitat modification, and decrease overall field diversity due to increased stochastic extinction. Finally, density dependence between experimental plots can change outcomes by indirectly inducing loss or gain of species in control plots. Because of this, comparison between treatment and control plots can actually underestimate the effect of the manipulation in many cases. The simultaneous operation of stochastic and niche driven processes observed in this analysis encourages further efforts to integrate the effects of stochasticity into niche-based models.
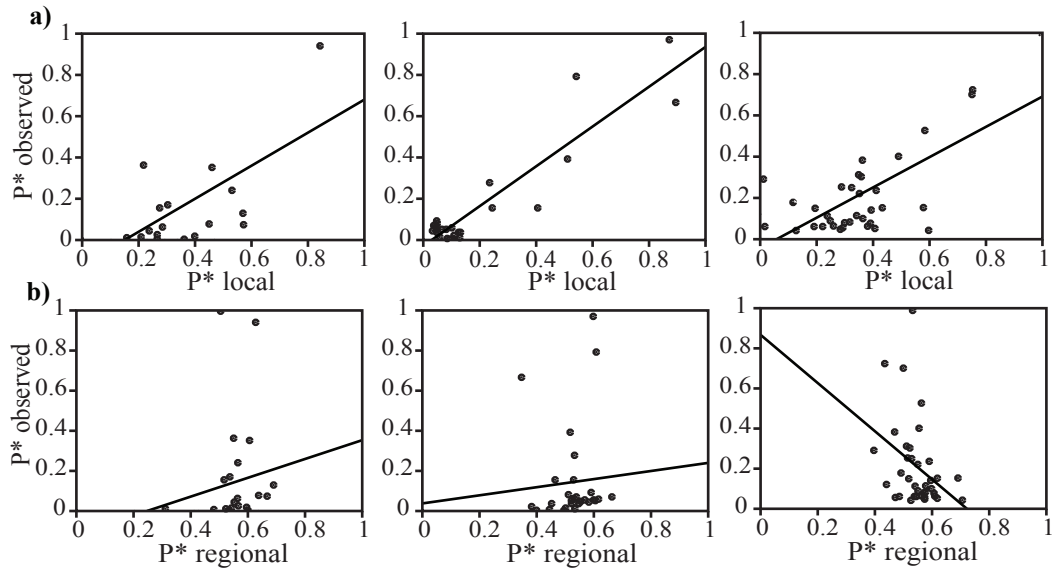
# Figures



**Fig 4.1:** Relation between predicted equilibrium proportional occupancy and mean occupancy between 1999 and 2003. Each data point represents the estimate and observation for a single species. Individual plots are for fields A, B, and C, going across, and for the local Levins model in a), and the regional Levins model in b). All fits for the local model are significant with $P<0.0001$, while only the field C fit is significant for the regional model. This analysis shows support for the within-field metapopulation model, and rejects the regional seed rain model.

# Tables

| | Field | Colonization | | Extinction | |
|---|---|---|---|---|---|
| | | F Ratio | Prob > F | F Ratio | Prob > F |
| Nadd | A | 96.3031 | **<.0001** | 28.5949 | **<.0001** |
| Species | A | 5.3625 | **<.0001** | 4.4988 | **<.0001** |
| Pres | A | 183.363 | **<.0001** | 2.4221 | 0.1198 |
| NAdd*Species | A | 4.0591 | **<.0001** | 3.1788 | **<.0001** |
| Nadd*Pres | A | 140.7567 | **<.0001** | 9.1308 | **0.0025** |
| Species*Pres | A | 5.2398 | **<.0001** | 2.5574 | **<.0001** |
| Nadd | B | 140.1738 | **<.0001** | 22.5385 | **<.0001** |
| Species | B | 5.7296 | **<.0001** | 4.7474 | **<.0001** |
| Pres | B | 24.5662 | **<.0001** | 1.3258 | 0.2497 |
| NAdd*Species | B | 7.6526 | **<.0001** | 6.2067 | **<.0001** |
| Nadd*Pres | B | 0.0401 | **<.0001** | 2.2168 | 0.1367 |
| Species*Pres | B | 2.9578 | **<.0001** | 1.823 | **0.0047** |
| Nadd | C | 217.0185 | **<.0001** | 76.6745 | **<.0001** |
| Species | C | 3.5846 | **<.0001** | 8.3134 | **<.0001** |
| Pres | C | 2.9147 | 0.09 | 7.5722 | **0.006** |
| NAdd*Species | C | 9.1991 | **<.0001** | 8.4859 | **<.0001** |
| Nadd*Pres | C | 55.4199 | **<.0001** | 1.4243 | 0.2328 |
| Species*Pres | C | 4.0803 | **<.0001** | 2.1854 | **<.0001** |

**Table 3.1:** Results from regressions of annual colonization and extinction rates on nitrogen addition (Nadd), species identity (Species), and the number of plots occupied by the species in the whole field (Pres). Two of the three fields (A and B) show significant increases of colonization rates in response to species presence, and the third (C) shows significant reduction of extinction rates.

|  | Colonization | | | | Extinction | | | |
|---|---|---|---|---|---|---|---|---|
| **Source** | **DF** | ChiSq | P | Estimate | DF | ChiSq | P | Estimate |
| Ring 1 | 1 | 17.183 | **<.0001** | 0.005459 | 1 | 15.287 | **<.0001** | -0.00478 |
| Ring 2 | 1 | 19.581 | **<.0001** | 0.002534 | 1 | 47.184 | **<.0001** | -0.003197 |
| Sqrt(Nadd) | 1 | 0.984 | 0.3237 | -0.0204 | 1 | 2.810 | 0.0937 | |
| Species | 14 | 562.056 | **<.0001** | | 14 | 262.178 | **<.0001** | |
| Sqrt(Nadd) X Species | 14 | 21.001 | 0.1016 | | 14 | 35.386 | **0.0022** | |

**Table 3.2: Neighborhood density effects on colonization and extinction probabilities in experiment 001**. Results of binomial logit regression of colonization or extinction variable against summed biomass in neighbor rings 1 and 2, Sqrt(Nadd) (the square root of the amount of nitrogen added) in the focal plot, species identity, and the nitrogen X species interaction. As expected, colonization and extinction rates both respond significantly to biomass in nearby sites, with colonization increasing, and extinction decreasing. Interestingly, nitrogen addition itself was not significant, while the nitrogen x species interaction term was significant for extinction.

| Source | DF | Chisq | P | Estimate |
|---|---|---|---|---|
| Ring 1 | 1 | 7.3049 | **0.0069** | 0.1581 |
| Ring 2 | 1 | 20.4285 | **<.0001** | 0.1752 |
| Ring 3 | 1 | 6.0104 | **0.0142** | 0.0583 |
| Planted Diversity | 1 | 16.0195 | **<.0001** | -0.0258 |

**Table 3.3: Effect of neighborhood density on colonization in experiment 120.** Results of regression of colonization in unmaintained plots on the number of plots planted with a given species in neighbor rings 1, 2, and 3, and on the number of species initially seeded in the focal plot. Colonization rate is significantly increased by local seed density, with the effect dropping off sharply at a distance of 3 rings. An inhibitory effect of local diversity is seen as colonization probability is negatively related to initial seeding diversity.

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