Effects of predation and variation in species relative abundance on the parameters of neutral models

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Abstract: Hubbell (2001) proposes that random demographic processes (i.e., neutral dynamics) can explain observed levels of variation in the richness and abundance of species within and among communities. Hubbell's neutral models have drawn attention because they reproduce several characteristic features of natural communities. But neutral models are criticized for ignoring nonrandom processes known to cause species densities to fluctuate. We parameterized neutral models using the population counts of 64 species of aquatic invertebrates collected from 49 discrete rock pools over a 13 year period. We used Hubbell's numerical modeling approach to evaluate the effect of natural population fluctuations on the parameter settings. We also analyzed the effect of observed variation on the species proportional abundance predicted by neutral models. We find that observed levels of variation in abundance are much higher than predicted by neutral models, forcing estimates of the migration probability, m, and fundamental biodiversity parameter, θ, to fluctuate over time. Much of the observed variation is mediated by predator-prey interactions. Low predator densities are associated with fewer species and less even relative abundances of species, resulting in lower estimates of m and θ compared to periods of high predator densities. Our results show that by assuming an identical survival probability for all species, neutral models misrepresent substantial aspects of community dynamics.

Introduction

Despite many decades of theoretical development, experimentation, and debate, ecologists continue to disagree about whether communities represent a select group of ecologically compatible organisms, or are simply a random subset of the regional species pool (Chase 2005). Many studies have shown that competition and environmental conditions can select the species that coexist at a particular location, and influence species' local abundance (Menge 1976, Tilman 1982, Roughgarden and Diamond 1986, Wellborn et al. 1996, Bohannan and Lenski 2000, Brown et al. 2001). These studies support the niche-assembly view of community structure, which is that communities represent non-random subsets of compatible species. This view is challenged by neutral theory (Bell

2000, Hubbell 2001) which assumes that species have identical per capita probabilities of birth, death, and migration. As such, species have an equal probability of winning a competitive interaction and are therefore competitively "neutral". The niche-assembly and neutral paradigms represent opposing views on community dynamics. Because they differ in their explanation of community patterns, they have important implications for theoretical and applied problems in ecology.

Neutral theory has been criticized on the grounds that it ignores processes known to influence the abundance and distribution of species (McGill 2003, Chave 2004, Chase 2005). Several recent studies evaluate neutrality by comparing observed species patterns with the explicit or implicit predictions of neutral models. These studies gen-

erally either examine static patterns of species relative abundance in one or more natural communities (Hubbell and Foster 1986, Condit et al. 2000, 2002, Clark and McLachlan 2003, McGill 2003), or use models to investigate the relationship between species patterns and community dynamics (Bell 2000, Chave et al. 2002, Volkov et al. 2003). However, we know of no studies that combine dynamical analysis with data from natural communities to test the predictions of neutral theory. Such studies are needed to evaluate the underlying assumptions of neutral models, such as the assumption that metacommunities are at equilibrium (McGill 2003). Here, we compare the temporal variation in species abundance predicted by neutral models with that of aquatic invertebrates living in 49 rock pool communities. To generate model predictions, we use the community and metacommunity assembly algorithms described by Hubbell in his monograph on the neutral theory (Hubbell 2001). Our purpose is to determine whether the algorithms correctly describe patterns of species abundance in a natural metacommunity. To this end, we use Hubbell's algorithms to determine the value of two key parameters: the fundamental biodiversity of the metacommunity, θ, and community migration probability, m. Hubble defines the dimensionless parameter θ as the product of the number of individuals in the metacommunity, J_m, and the mutation rate, ν (Hubbell 2001). Specifically, $\theta = 2J_m\nu$. The value of θ determines the number of species found in the metacommunity and their relative proportions. The value of m determines the rate at which immigrants arrive at a particular community, and reflects the relative connectedness of the community with the metacommunity. When the value of m is high, the relative proportions of species in a community closely follow those of the metacommunity. Low values of m reduce the occurrence of rare species and increase the influence of local community dynamics on the number and relative abundance of species within the community.

We first estimate the value of θ using a maximum likelihood approach, the observed average size of the metacommunity, and the averages of species relative proportions at the metacommunity scale. We then estimate m for three of the pools using our estimate of θ and the observed annual community sizes and species abundances of each pool. Thus, we directly apply Hubbell's method to test the predictions of his model.

Hubbell (2001) showed that neutral models that couple random demographic change with zero-sum community dynamics generate multinomial species distributions that often well approximate the observed distributions of natural communities. Zero-sum dynamics refer to the compensatory population dynamics of species in communities in which all available resources are fully exploited. When all available resources are utilized by the members of a community, no additional individuals can be supported. Under these conditions, the population sizes of different species are interdependent; no species can increase in abundance without a concomitant decrease in the abundance of one or more other species. In the neutral theory, individuals are assumed to be equally competitive. Therefore, variation in species proportions among communities is due solely to the effects of finite community size and stochastic demographic processes. Under neutral dynamics, the long term average of the numerical proportion of each species in a community that receives immigrants is equal to its proportional abundance in the metacommunity.

At the community scale, neutral models reproduce several well-known species distributions, including Taylor power laws (Taylor 1961), species-area relations (Rosenzweig 1995), and the distribution of species abundance within communities (Bell 2001, Hubbell 2001). However, whether these particular patterns are indicative of community dynamics is by no means clear. Taylor's power laws can be generated from a variety of processes (Allen et al. 2002), and there are multiple hypotheses for the empirical relationship between the area of a sample and the number of species it contains (Rosenzweig 1995). Moreover, neutral and niche-based models generate identical patterns of species relative abundance (Chave et al. 2002, Chave 2004). Thus agreement between the above general species patterns and the predictions of neutral models does not represent a rigorous test of Hubbell's theory. Hubbell's theory pertains to species dynamics, and thus tests of his theory should focus on the dynamical aspect of community patterns (Chave 2004).

Methods

We used a combination of modeling, maximum likelihood, rarefaction, and statistical analysis to evaluate the ability of Hubbell's model to predict species richness and relative abundance. For clarity, we use the terms *observed* and *simulated* to distinguish respectively the communities and metacommunity represented by the natural (empirical) system of pools from the simulated (neutral) systems generated by models. Although several workers have contributed to the neutral theory (Caswell 1976, Hubbell and Foster 1986, Bell 2000), Hubbell provides the most complete development of the theory and related models (Hubbell 2001, Volkov et al. 2003). Hereafter, we mean specifically Hubbell's approach when we refer to neutral theory and neutral models. These models describe

the occurrence and abundance of species in a community in terms of the binomial distribution.

The study system: a natural metacommunity

For our analysis of observed species distributions, we used data on the invertebrate species that inhabit 49 small rock pools. The pools are located on a fossil reef, in the vicinity of the Discovery Bay Marine Laboratory, University of West Indies, Jamaica. The data were collected as part of an ongoing long-term monitoring project begun in December, 1989. We analyzed the contents of nine sets of samples that were collected in December 1989, and in January of 1990, 1991, 1992, 1993, 1994, 1997, 1998, and 2002. To evaluate neutral models at the community level, we focused on three of the 49 pools. To select three pools, we grouped the 49 pools into three volume classes (l = liters): < 10 l, 10 to 20 l, and > 20 l. We then chose a pool in each volume class at random. Pool #12 has a volume of 3.0 l. Pool #9 is characteristic of large pools, with a volume of 29.0 l. Pool #29 falls between the two other pools in volume at 20.0 l. Details on collection methods can be found in Kolasa et al. (1996). For a description of the physical features, water chemistry, and the environmental conditions of the pools, see Romanuk and Kolasa (2002). The study pools represent a random sample of 230 pools that occur within a radius of 25 meters. The pools in the study are less than one meter apart, on average. Pool volume ranges from 0.24 to 115.00 liters (mean: 14.96, standard deviation: 21.06). Most pools contain less than 30 l. During each collecting period a 0.5 l sample of well-mixed water and organisms is removed from each pool. Each pool sample reasonably represents the state of the pool community at the time of collection, including species richness, the number of individuals of each species, and proportions among them.

Natural community data treatment

In Hubbell's neutral theory, a community is constrained to include only the individuals of trophically similar species that potentially compete for resources. The rock pool communities meet the criteria implicit in this definition. Pools are small enough to allow potential interactions between any two individuals, yet have discrete boundaries that limit interactions to organisms that occur within a pool. To meet the requirement that species represent a single trophic level, we categorized the species into trophic groups and analyzed each group separately. Therefore, for our analysis we define an observed community to be the set of species in a particular trophic group, found in a single pool.

To determine which trophic groups are represented in the study system, and to assign each species to a specific group, we used standard texts (Pennak 1989, Thorp and Covich 2001) that describe the trophic characteristics of the families and genera present in the pools. We also used observations on the ecology and behavior of individual species (unpublished). Preliminary analysis showed that detritivores (33 species) have, on average, the highest population densities of the three trophic groups, followed by algal-filterers (9 species) and predators (22 species). To maximize statistical power, we limit our analysis of species distributions to detritivores. To determine the effects of predator density on species richness, we analyzed both the detritivore and algal-filterer trophic groups.

Model parameterization: Hubbell's neutral metacommunity algorithm

We treat the 49-pool observed system as a metacommunity (Mouquet et al. 2001). In Hubbell's model, the species richness and proportions of a neutral metacommunity are a function of two parameters, the fundamental biodiversity number, θ, and the maximum metacommunity size (number of individuals), J_m. We estimate θ and J_m using a three-step process. In step 1, we calculate the average size of the observed metacommunity, and use this as a first approximation of J_m. We refer to this first approximation as J^*_m. To calculate J^*_m, we estimate the total number of individual organisms in each of the 49 pools during each collection period by multiplying the number of individuals in a 0.5 l sample by two and then multiplying the result by the pool volume in liters. Then, for each collection period, we calculate a metacommunity size as the sum of the number of individuals across all pools. We calculate J^*_m as the average size of the metacommunity over all collection periods.

In step 2, we use a log-maximum likelihood equation (MLE), developed for multinomially distributed data (Rice 1995), to find the best estimate of θ for a neutral metacommunity of size J^*_m. The MLE function compares the logarithms of the ranked values of two distributions. Here, we compare the ranked species proportions of the observed metacommunity with those of simulated neutral metacommunities of identical size. Following Hubbell (2001) we use only species above the median abundance in the observed metacommunity to estimate θ as their abundance estimates are less likely to suffer from sample size effects.

The log-likelihood of a given value of θ is:

$$l(\theta) = \log n! - \sum_{i=1}^{s} \log x_i! + \sum_{i=1}^{s} x_i \log p_i(\theta) \qquad (1)$$

where x_i is the abundance (number of individuals) represented by the species in rank i in the observed system, $p_i(\theta)$ is the proportion of rank i in a simulated metacommunity with a given θ, n is the size of the observed metacommunity, and S is the number of species. The result of the MLE calculation is a single value that represents how much the observed and simulated distributions deviate from one another. A perfect match yields a maximum MLE value of zero. To determine the best estimate of θ, we calculate a separate value of MLE for a series of simulated metacommunities, which differ in θ but not in size, until the maximum MLE value is attained.

In step 3, we compare the number of species, S, in the simulated metacommunity to the number in the observed metacommunity. If the values of S differ, we tune the value of θ until S is the same for both observed and simulated metacommunities. To do this, we calculate the maximum number of species, $S_{max}(J_m,\theta)$, generated for a simulated metacommunity of size $J_m = J^*_m$ and with θ set to the estimate calculated in step 2. The equation for $S_{max}(J_m,\theta)$, is (Hubbell 2001):

$$S_{max}(J_m,\theta) = \sum_{j=1}^{J_m} \frac{\theta}{\theta + j + 1}\,.$$

Using the value of θ estimated in step 2, and beginning with J_m set equal to the value of J^*_m estimated in step 1, we tune the value of J_m up or down until $S_{max}(J_m,\theta)$ is equal to the number of species observed in the natural system. We repeat the above three-step process for each trophic group.

Once we establish values for θ and J_m, we construct a neutral metacommunity using the algorithm described by Hubbell. We then calculate the distribution of species proportions expected for the simulated metacommunity and used it to construct the simulated communities. Hubbell's metacommunity algorithm begins with a single individual of a single species (metacommunity size $j = 1$, metacommunity richness $S = 1$). New individuals are added to the metacommunity until the maximum size, J_m, is attained. As each individual is added, it is assigned a species identity. With probability $\theta/(\theta + j -1)$, an individual is assigned to be a new (previously unrecorded) species, where j is the current number of individuals in the metacommunity. With probability $1- [\theta/(\theta + j -1)]$, the individual is randomly assigned to a pre-existing species. In the latter case, the probability of being assigned to a particular species, i, is equal to that species' current proportion of the metacommunity, P_i. This process is continued until all J_m individuals have been added and assigned to a species. To generate a statistical distribution for the neutral metacommunity species proportions for the estab-

lished value of θ, we constructed 1000 independent metacommunities using the above approach.

Hubbell's neutral community algorithm

We construct a separate simulated community for each pool sample of pools #9, #12, and #29. We first set the size of each simulated community equal to the number of individuals found in a respective sample, and then use Hubbell's neutral community algorithm to generate the relative proportion of each species. To generate the initial species proportions of each simulated community (colonization), we select individuals at random from the previously established neutral metacommunity, constructed as described above. The probability of an individual in a community being assigned to a particular species, i, of the metacommunity is equal to its metacommunity proportion, P_i. The colonization process is intended to mimic the random immigration of individuals from a metacommunity to a community, with no dispersal limitation.

Once we establish each neutral community, we simulate random birth, death, and migration, using the community dynamics algorithm described by Hubbell (2001). This algorithm has four parameters: 1) community size, J, 2) the per capita probability of migration, m, 3) the disturbance level, D, which is the fraction (percent) of the community that is replaced each generation, and 4) the number of generations. For each simulated community, we set J equal to the size of its corresponding pool sample. Lacking data on the per generation rate of disturbance, we conservatively estimate the value of D at 10% per generation. In our simulations, J and D do not change over time. As a result of constant J, the dynamics are zero-sum: before an individual can migrate into a community, or be born there, a current member of the community must first leave or die.

To simulate the processes of birth, death, and immigration, we randomly change the species identity of community members to species chosen from either the community or metacommunity. Following Hubbell, in each generation $D \times J$ individuals are randomly chosen from the community for replacement. With probability m, an individual is replaced by an individual of a species drawn at random from the metacommunity. With probability $1 - m$, it is replaced by an individual from a species drawn at random from within the community. If the replacement comes from the metacommunity, the probability that a particular species, i, is selected is equal to its metacommunity proportion,. If the replacement comes from the community, the probability that a particular species is selected is equal to its proportion of the community. A gen-

eration ends when the identity of all of the $D \times J$ individuals has been reassigned.

Estimating migration probability

In Hubbell's model, the number of species in a community, and the proportion of the community represented by each species, depend on four parameters: 1) the community size (J, number of individuals), 2) the number of species in the metacommunity, S, 3) the proportions of each species in the metacommunity, P_i, and 4) the probability of migration, m, between community and metacommunity. We set the value of J to the size of each sample, and established values for S and P_i as described above for metacommunity construction. This approach leaves only one parameter, m, left to estimate.

The value of m determines the species richness and distribution of species relative proportions in a simulated community. Hubbell (2001) suggests using a MLE approach and species community abundances to determine the value of m that best characterizes a particular community. However, we found that with the small number of species found in the communities, the MLE does not converge on a single value of m corresponding to a particular species distribution. We therefore adopted a different approach. To find the value of m that best fits the observed species patterns of each pool we do not rely on a single measure of community structure but instead compare the observed and simulated communities for both richness and species proportions. We calculate the predicted species richness and relative proportions of simulated communities using Hubbell's community dynamics algorithm. Each pool sample contains a specific number of individuals, J and species, S. Because we have multiple samples for each pool, we can plot a J-S distribution for each pool (one value of richness for each sample). We compare the distribution of species richness in the samples to those of their corresponding simulated communities using a Wilcoxson matched pairs test. Each pool sample and simulated community also generates a distribution of ranked species proportions. For each pool, we compare the average proportion represented by each rank in the samples to that of the simulated communities, using a Chi-square test. To aid our ability to distinguish the species patterns generated by each simulated community we chose migration probabilities that span four orders of magnitude: 1.0, 0.10, 0.01, and 0.001.

We combined the results of the Wilcoxson and Chi-square tests to determine the value of the migration parameter, m, that best characterizes three pools: #9, #12, and #29. The best estimate of m is the value that yields no significant difference ($P > 0.05$) between observed and simulated communities for both species richness *and* species relative proportions. Thus, when both test statistics are not significant for a given value of m, we consider the tests to have been successful in estimating the value of m for that community. We consider the assignment of m to have failed for a particular community if the P-value of both tests is not > 0.05 for any of the four values of m tested, or if more than one value of m yields a non-significant result for both tests.

Community dynamics: coefficient of variation in rank proportions

As a measure of how well neutral models reproduce the variability of the observed communities we examine the variation in species proportions within each pool. To measure this variation, we use the coefficient of variation, CV, in the fraction of the community represented by each rank, expressed as a percent: (SD/mean $\times$ 100, where SD is the standard deviation. We use the simulated community distributions that represent the previously established estimates of m for each sample to compare the CV in species proportions between observed and simulated communities. If an estimate of m is not possible, we compare the observed CV to that of the simulated communities for each value of m. The variability of the proportion of the community represented by each rank is a measure of the stability of the relative abundance distribution.

Effect of predators on prey species distributions

As a test of the importance of niche-differences for species distributions, we analyzed the effect of predators on prey communities for all 49 pools. High densities of predators may alter the richness of prey communities, such as by affecting the intensity or outcome of competition (Hairston et al. 1960, Paine 1974, Morin 1983). With respect to neutral models, the presence of predators could influence the estimate of two parameters: community migration probability, m, and metacommunity species diversity, θ. Therefore, we examined the effect of predator density on each of these parameters.

Predators vary in density among the pools from year to year. In total, they are present in 52% of the samples. When present in a sample, predators average about 10% of the total number of individuals. To assess the impact of predators on prey species, we first need to calculate the probability of not detecting predators in a pool when they are present. The probability of observing c or fewer individuals of a species in a sample of size n taken from a community of size N, is

$$P(x \le c) = \sum_{x=0}^{c} \frac{\binom{a_i}{x}\binom{N-a_i}{n-x}}{\binom{N}{n}} \qquad (2)$$

where a_i is the abundance of species i in a community and x is the observed number of individuals of species i (Gotelli and Graves 1996). For a given a_i, the probability $P(1)$ of observing at least one individual of species i (or any predator, in our case) is $1-P$, with c set to zero in equation (2). In this case, equation (2) reduces to:

$$P(1) = 1 - \frac{\binom{N-a_i}{n}}{\binom{N}{n}} \qquad (3)$$

In principle, any sample will fail to capture a predator if predator density lies below some minimum detectable density. To discover what that minimum density is, we ask: if the fraction of a community represented by predators is F, what is the minimum value of F needed for there to be a 95% chance of capturing at least one predator in a sample ($P(1) = 0.95$)? We denote this minimum value of F as F^*.

The probability of detecting a predator is proportional to the sample size; larger samples can detect predators at lower predator densities. The number of organisms in samples that lacked predators range from a single individual to a maximum of 25,317 individuals (mean 846.4). We estimated the value of F^* for one of the smallest pool samples, which contained only 11 individuals. Using this particular sample provides a very conservative estimate of F^* because 92.6% of the samples that lack predators are larger than 11 individuals. To calculate F^*, we set N in equation (3) to $2nV$, where V is the volume of the pool in liters, and set n to the number of individuals in the sample. Then, by varying a_i until $P(1)$ is at least 0.95, we are able to estimate the value of F^*. For a sample size of 11, the value of F^* needed to generate a $P(1) \ge 0.95$ is 21.5%. We therefore define samples that lack predators as low-predator-density (LPD) samples, representing communities in which predators account for ≤ 21.5% of the total number of individuals. High-predator-density (HPD) samples are defined as containing > 21.5% predators.

Effect of predator density on estimates of migration probability and θ

To examine the effect of predator density on the estimate of θ for the 49 pool metacommunity, we calculate separate θ values for the HPD samples and the LPD samples. To examine the effect of predators on the value of m

for pools #9, #12, and #29, we follow the same approach we describe above for determining m, except that here we perform separate analyses for HPD and LPD samples. Again, we combined the results of the Chi-square test and Wilcoxson matched-pairs test to determine the best estimate of migration probability for each pool.

Results

Community species distributions and migration probabilities

We compared the observed detritivore communities to simulated communities representing four different values of migration probability m (1.00, 0.10, 0.01, 0.001). Different values of m yield different model predictions for the number of species in a community and species relative proportions. Table 1 and Figure 1 show results for the three representative pools (#9, #12, and #29). For pools #12 and #29, the migration probability determined by comparing the results of the Chi-square and Wilcoxson tests is $m = 0.01$. However, our paired-test approach was unsuccessful in assigning a migration probability for pool #9 because the observed distribution of species relative proportions are significantly different from those of all of the simulated communities that correspond to this pool.

Metacommunity species distributions

Hubbell's neutral model performs better at predicting the mean species relative proportions of the observed metacommunity (Figure 2), although the residual variation is high. Based on the MLE analysis on all of the samples, the value of θ estimated for the detritivore metacommunity is 1.9. The corresponding neutral metacommunity distribution provides a good fit to the mean empirical values of the top 62 percent of the metacommunity ($R^2 = 0.9528$), and the curves for the observed and simulated distributions are statistically indistinguishable (Figure 2). However, the mean values of the neutral distribution do not fit the mean observed distributions of rare species. Over a third (38 percent) of the species with low metacommunity proportions (i.e., < 0.01%) were more abundant than the predicted distribution. This difference, though consistent, was not statistically significant due to the high variation in observed and predicted species proportions.

Community dynamics: variation in rank proportions

The ranked species proportions tend to be much more variable in the observed communities compared to simulated communities of identical size. To illustrate this, we plot the curves that represent the values of m that most

Table 1. Results of statistical analysis of community migration probabilities for three pools. Statistical probability values (P) represent the results of comparisons between observed and neutral (simulated) communities in ranked abundance (Chi-square test) and mean species richness S (Wilcoxson matched pairs test; WCX) for four different migration probabilities. Each pool represents a different pool size class, based on volume. The best estimate of m is indicated by an asterisk in the far right column. NA means that no estimate for m was possible.

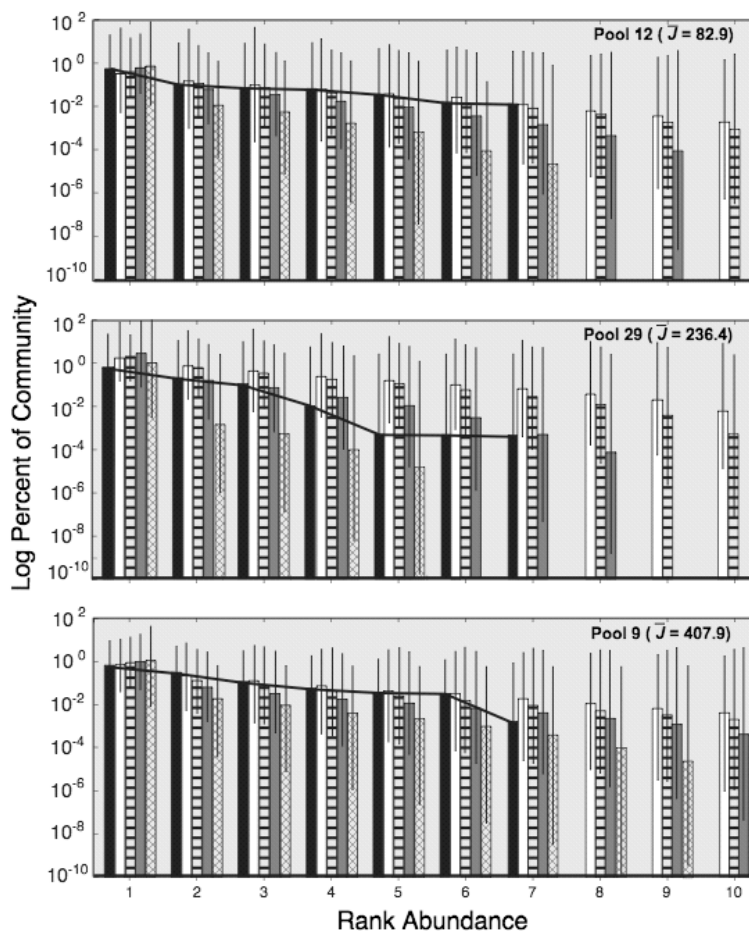| Migration Probability	Mean Observed S	Mean Predicted S	Species Relative Proportions (Chi-sq P)	Obs vs Model Mean S (WCX P)	Estimate of m
Pool 12 (volume = 2.1 l, mean community size = 236.4)					
1.000	4.75	8.78	< 0.00	= 0.02	
0.100	4.75	7.44	< 0.00	= 0.18	
0.010	4.75	5.67	= 0.50	= 0.61	*
0.001	4.75	3.00	< 0.00	= 0.18	
Pool 29 (volume = 10.7 l, mean community size = 407.9)					
1.000	3.75	9.44	< 0.00	= 0.02	
0.100	3.75	8.55	< 0.00	= 0.02	
0.010	3.75	6.11	= 0.14	= 0.12	*
0.001	3.75	3.44	< 0.00	= 0.75	
Pool 9 (volume = 27.2 l, mean community size = 82.9)					
1.000	4.63	8.00	< 0.00	= 0.03	NA
0.100	4.63	6.67	< 0.00	= 0.15	
0.010	4.63	5.22	< 0.00	= 1.00	
0.001	4.63	4.00	< 0.00	= 0.18	

Figure 1. Community proportions and probability of migration. The logarithmically transformed ranked distributions of species average community proportions is shown for each of three pools, representing different pool size classes. J = average number of individual organisms recorded for a particular pool. *Black bars*: observed proportions. Other bars are proportions for neutral communities that are identical in size to the respective pools but which vary in the value of the migration probability (m): *white* = 1.00; *striped* = 0.10; *gray* = 0.01; *crisscrossed* = 0.001. Error bars represent standard errors. Line connecting black bars is a visual aid. Natural communities frequently contain fewer species then neutral communities. Observed and simulated communities show high levels of variation in species community proportions.

Table 2. Effect of predator density on the fit between neutral and natural communities. Statistical probability values (P) represent the results of statistical tests of the fit between observed communities with high predator densities (HPD) and low predator densities (LPD) and those of simulated communities (HPD-neutral, LPD-neutral) representing four different migration probabilities (m). When the P-values for the Chi-square test (Chi-sq) and Wilcoxson matched pairs (WCX) test are both non-significant ($P > 0.05$) we consider the corresponding simulated community to be indistinguishable from the observed HPD or LPD samples, and thus assign the matching value of m to that pool (indicated by asterisk in far right column). Otherwise we do not assign a value of m to a pool (NA). S = species richness. See Results, for details.

| Migration Probability	Mean HPD S	Mean LPD S	Mean Predicted S	Relative Proportions Chi-sq P		Species Richness WCX P		Estimate of m		
				HPD-Neutral	LPD-Neutral	HPD-Neutral	LPD-Neutral	All	HPD	LPD
Pool 12 (volume = 2.1 l, mean community size = 236.4)										
1.000	5.00	3.00	5.38	0.05	0.01	0.13	0.25		NA	
0.100	5.00	3.00	4.25	0.05	0.01	0.13	0.25			
0.010	5.00	3.00	3.00	0.02	0.00	0.06	0.25	*		
0.001	5.00	3.00	1.75	0.04	0.20	0.06	1.00			*
Pool 29 (volume = 10.7 l, mean community size = 407.9)										
1.000	4.20	3.00	7.63	0.02	0.02	0.13	0.25		NA	NA
0.100	4.20	3.00	7.00	0.02	0.02	0.13	0.25			
0.010	4.20	3.00	4.50	0.08	0.13	1.00	0.50	*		
0.001	4.20	3.00	3.00	0.07	0.18	0.13	0.75			
Pool 9 (volume = 27.2 l, mean community size = 82.9)										
1.000	5.75	3.50	6.25	0.01	0.00	1.00	0.50	NA	NA	
0.100	5.75	3.50	5.25	0.07	0.03	0.37	0.50			
0.010	5.75	3.50	4.25	0.03	0.03	0.25	0.75			
0.001	5.75	3.50	2.63	0.08	0.16	0.13	1.00			*
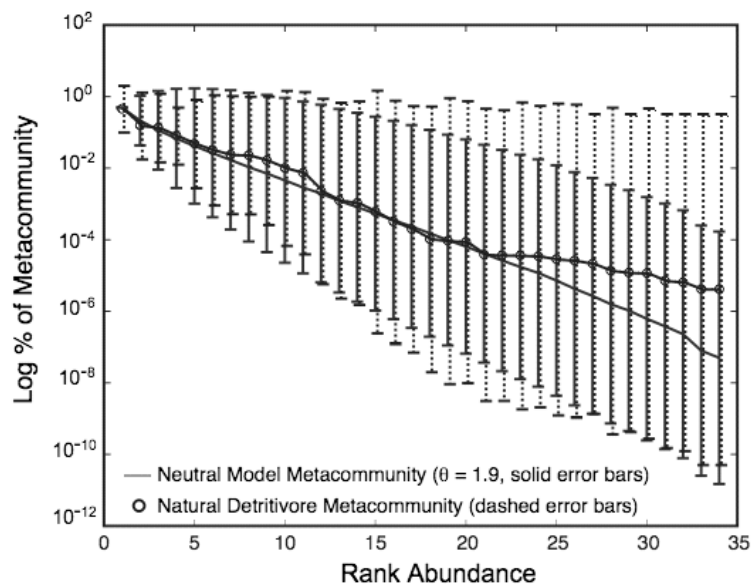
Figure 2. Metacommunity proportions. The average metacommunity proportions are shown for ranked species in a neutral metacommunity (solid line) and a natural metacommunity of 49 pools (open circles). For the neutral metacommunity, θ = 1.9 and the number of organisms J_m = 34 million. Neutral metacommunity values represent the mean and one standard deviation of 1,000 simulations (solid error bars). Natural metacommunity values represent the mean and one standard deviation of 9 collection periods (dashed error bars).

closely match the observed mean species relative proportions along side the observed values (Figure 3). We find that the proportion of the community represented by each rank in the observed communities is generally much more variable than predicted by Hubbell's model. In the simu-
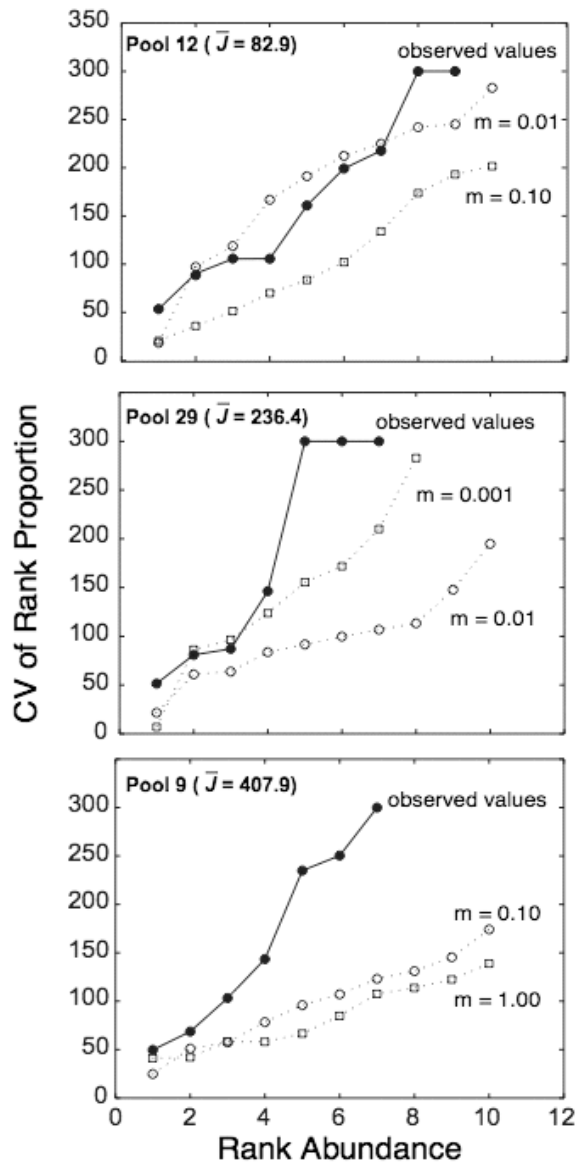

Figure 3. Coefficient of variation in species proportions. The ranked distributions of the coefficient of variation (CV) in community proportions is shown for each of three pools, representing different pool size classes (filled circles). Open symbols represent the CV of neutral communities, which are identical in size to the respective pools. Each neutral community represents the CV predicted for different values of migration probability, m, as indicated in the figure. CV values are frequently much higher in the natural communities. J = average number of individual organisms recorded for a particular pool.

lated communities, the CV of community proportion of all but the rarest species tends to increase linearly in proportion to rank. In two of the observed communities (#9 and #29), the CV increases exponentially with rank. In all cases rare species are much more variable in their community proportion than predicted by neutral models. There is closer agreement between observed and simulated communities for Pool #12 in which the simulated community with $m = 0.01$ shows good agreement in CV for some but not all species ranks.

Effects of predator-prey interactions

The influence of predators on prey species richness differed for the two prey groups. High predator densities (HPD) significantly increase mean species richness for detritivores from 2.26 to 4.25 (Wilcoxon matched pairs test, $p < 0.0001$), but the effect on algal-filterers is not significant (from 1.26 to 1.93; $p = 0.4631$). Predator density also influenced the species composition of the detritivore communities. Six detritivore species were found only in HPD samples, while two species occur only in LPD samples. In each case, the organisms limited to HPD or LPD samples represent very rare species, with average metacommunity proportions between 7×10^{-6} and 7×10^{-5}.

Predator density influences the estimate of the metacommunity biodiversity parameter, θ for the detritivores. The value of θ estimated for the 49-pool metacommunity is 1.9 when the samples are analyzed as a single set. When HPD samples are analyzed separately, $\theta = 2.6$, reflecting the higher average richness and species proportions. When only LPD samples are considered, $\theta = 1.28$. We found no statistical difference in the sizes (total individuals) of detritivore communities between LPD (mean size = 558.7) and HPD (mean size = 430.4) samples (Wilcoxson matched pairs test, $p = 0.1630$). Thus, we could not find evidence that the differences in species richness observed between samples with low and high predator densities were caused by a difference in the sizes of the samples.

For one of the three pools examined, differences in predator density affected the estimate for the migration parameter. The estimate of m in pool #12 is 0.01 when all samples are considered, but it is 0.001 when the LPD samples are analyzed separately (Table 2). However, we could not tell with certainty whether variation in predator density affected the estimates of m for pools #9 and #29 using the paired-test approach. The P-values for the Chi-square tests on LPD samples for Pool #29 suggest that this pool is characterized by lower values of m (i.e., 0.010 and 0.001) whereas the same tests for pool #9 suggest that the value of m is lower in the LPD samples (the P-value of the

Figure 4. Effect of predator density on detritivore community structure. The ranked distributions of the logarithm of species average community proportions is shown for samples with high predator density (HPD, *black bars*) and low predator density (LPD, *striped bars*). The other bars represent the logarithm of the proportions predicted for simulated communities of different migration probabilities (*m*): *white bars*, *m* = 1.00, *grey bars*, *m* = 0.001, *crisscrossed bars*, *m* = 0.01 (bottom panel). $\bar{J}$ = average number of individual organisms recorded for a particular pool. Error bars represent standard errors. Lines connecting HPD and LPD samples are provided as a visual aid. Species richness and evenness is typically higher in HPD samples. The agreement between observed proportions and simulated proportions representing different values of *m* changes with predator density
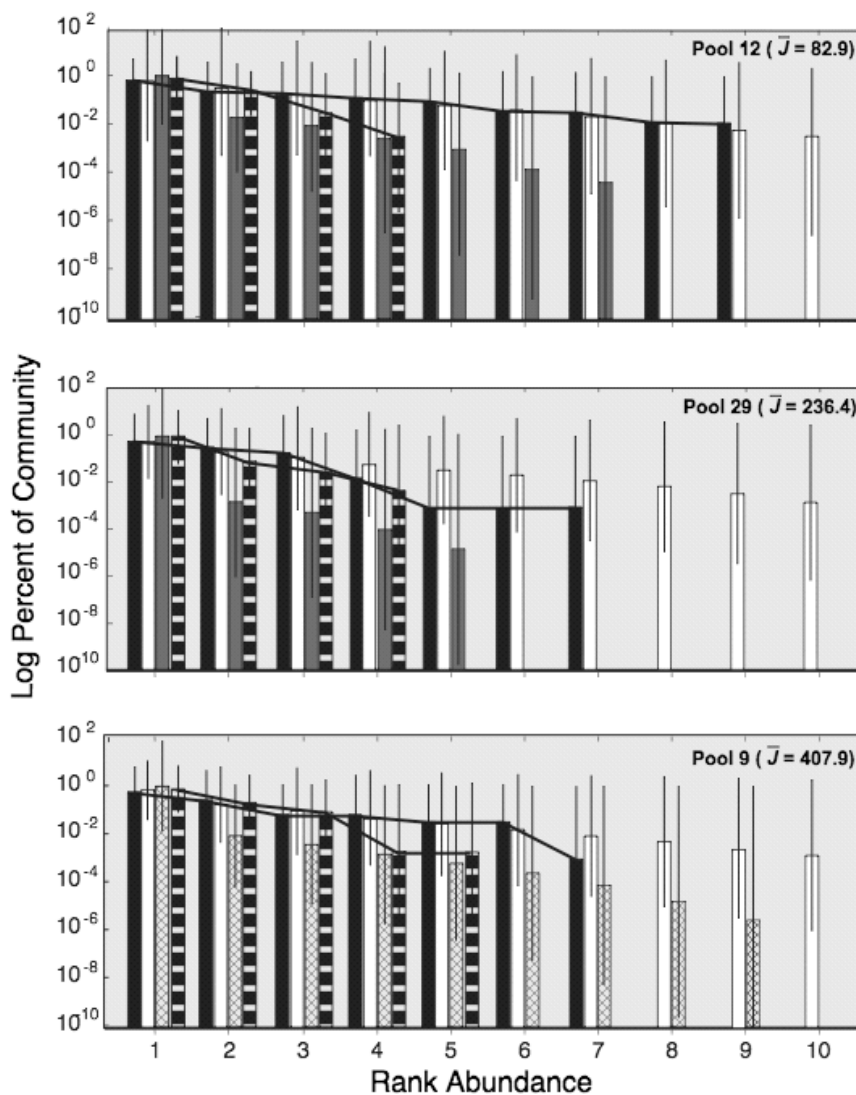
LPD samples is nonsignificant only for the lowest level of *m*). However, the evidence for how *m* is affected by predators in pools #9 and #29 is clearly equivocal.

Differences between the simulated and observed detritivore communities in species richness and evenness are less pronounced when predator densities are high (Figure 4). When predator densities are low, the numerical dominance of the most abundant species in the detritivore communities increased while the number of species decreased dramatically. In addition to increased species richness, the proportions of detritivore species in HPD samples were more evenly distributed (Figure 4). The proportion of the community represented by the lower ranks (less common species) was significantly less in LPD samples (Chi-square comparison of HPD and LPD

samples, $P < 0.00001$) for each of the three pools (#9, #12, and #29).

Discussion

We tested the ability of Hubbell's zero-sum neutral model to predict the distribution of species proportions in a metacommunity of 49 pools, and in the communities of three individual pools. Our results did not agree with the predictions of Hubbell's neutral models. Specifically, levels of variation in species abundances are generally higher than predicted. The observed variation influenced estimates of the migration parameter *m* and the biodiversity parameter, θ. The effect of variation on the agreement between simulated and observed communities is most apparent in Figure 3, which shows that the CV in the fraction of a community represented by each species rank often

deviates strongly from the variation predicted by neutral models.

At the community scale, the neutral theory proposes that variation in species proportions and species richness arises through variation in community size and dispersal limitation. This proposal is based in large part on the assumption that species richness is controlled by resource levels. By contrast, the niche-assembly view considers species richness to depend on additional factors, such as disturbance, fluctuating environments, and predator-prey interactions (Cornell and Lawton 1992, Chase 2005). In our study, the richness and evenness of detritivore communities are greater in samples with high predator densities. This indicates that natural variation in predator densities, and the proportion of the metacommunity that supports high predator densities, can influence the community and metacommunity species patterns of prey. Previous studies indicate that variation in abiotic factors such as salinity also influence community patterns in our study system (Therriault and Kolasa 1999, Romanuk and Kolasa 2002). Thus there is evidence that several deterministic processes influence the distribution and abundance of species in our system. This is not to say that random processes such as dispersal do not contribute to the observed community patterns. But the neutral dynamics of Hubbell's models do not adequately predict the observed level of variation. In our system, the probability of successful migration depends on the local conditions within each pool. Local conditions can fluctuate in both biotic (i.e., predator density) and abiotic (water chemistry, pool volume) factors, causing the probability of *successful* migration to change over time. This variation in the effective migration rate can override or obscure the influence of random processes. But again this depends on local conditions. An interesting potential side effect of high predator densities is that by reducing the intensity of competition of their prey, predators may actually allow random processes such as dispersal to play a stronger role in prey community structure. The closer fit of simulated community proportions with those of observed community proportions in HPD samples (Figure 4) supports this hypothesis.

The level of variation of the simulated communities is governed by the rate of species turnover, which is determined by the disturbance parameter, D. We lack data on the rate of turnover, and therefore used a conservative estimate of $D=10$ percent. Using a higher level of disturbance might improve the fit between the observed and simulated communities in CV. However, it would also increase the variation in species relative proportions, degrading our already tenuous ability to assign a specific value of m to each community. This issue underscores the

problem of parameterizing neutral models with empirical data when communities contain small numbers of species. The pools in our study average less than 7 detritivore species, and similar numbers are typical of community studies. Better techniques for estimating m are needed to evaluate the ability of neutral models to predict species patterns.

At the metacommunity scale, the variation in species proportions is quite high. The standard errors for the observed metacommunity indicate that the level of statistical independence among the samples is higher than predicted. The observed level of variation at the metacommunity is at odds with the assumption of neutral theory that metacommunities are in dynamic equilibrium, and are characterized by slowly changing species abundances (Hubbell 2001, McGill 2003, Chave 2004). In addition, we see evidence that Hubbell's model does not adequately describe the mean relative abundance of rare species: 38% of the observed metacommunity is more abundant than predicted by Hubbell's neutral model (Figure 2). The consistent lack of a decline in the metacommunity proportions of rare species suggests that the pattern is biologically meaningful. For example, spatial variation across the landscape in the biotic and abiotic conditions of the pools may enhance opportunities for less competitive species, increasing their abundance at the metacommunity scale over that expected by neutral theory. On the other hand, the higher observed proportions of rare species may also reflect sampling error associated with the difficulty of detecting species of low abundance. The probability of detecting the individuals of a species in a sample increases with species abundance, creating a positive bias in the mean species proportion of multiple samples. Thus several factors may contribute to the observed pattern of the rarest species.

Our results suggest that the community assembly processes described by Hubbell's algorithms are insufficient to account for the assembly process in the natural system we studied. For example, the greater than expected variability of rare species is compatible with predictions of hierarchy theory (Waltho and Kolasa 1994, Kolasa and Li 2003). There are of course other modeling approaches based on neutral theory (e.g., Caswell 1976, Bell 2000). By focusing specifically on Hubbell's approach, our analysis does not evaluate the usefulness of all neutral models. It appears that the primary reason for the inadequacy of Hubbell's approach is that the probability of survival is not constant as required by his models, but depends on species characteristics and the biotic and abiotic conditions of each pool. We show that differences in survival can influence estimates of the migration

probability of the pools and estimates of the fundamental diversity parameter, θ. Our analysis of predator effects suggest that the procedure necessary for assigning the survival probability of species is more complex than a simple random assignment.

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