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Testing a Simple Rule for Dominance in Resource Competition

Jeremy W. Fox*

Department of Ecology, Evolution, and Natural Resources, Cook College, Rutgers University, New Brunswick, New Jersey 08901-8551

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ABSTRACT: Competition for limiting resources long has been considered an important factor generating community structure. A minimal model of resource competition predicts that the species that reduces the limiting resource R to the lowest level (R^*) will exclude its competitors. Whether this "R^* rule" is robust to violations of model assumptions remains largely unknown. I conducted a competition experiment with four species of bacterivorous protists in laboratory microcosms and predicted the outcome from each species' R^* value. I also examined how the outcome of competition, species abundances, and the effect of protists on bacterial density varied with productivity. Microcosms were unstirred batch cultures containing a variety of bacteria, challenging the robustness of the simplest competition models. Protists with low R^* values were less affected by competition, although competing protists often coexisted. The values of R^* can predict competitive dominance, even in the absence of competitive exclusion. Other model predictions were less robust. Contrary to expectation, densities of grazed bacteria increased with productivity, and the effect of some protists on bacterial density did not vary with productivity. Bacterial heterogeneity may account for deviations from model predictions. Further experiments should examine the conditions under which simple rules can be expected to identify dominant species.

Keywords: resource competition, protists, microcosms, productivity gradients.

Predicting which species will dominate a community, to what degree they will dominate, and why are long-standing goals in ecology (Gause 1937; Preston 1948, 1962*a*, 1962*b*; MacArthur 1957; May 1975; Tilman 1982; Grover 1997). These goals are at the heart of efforts to predict the effects of invasive species (Petren and Case 1996; Byers 2000), to relate biodiversity to ecosystem function (Tilman et al. 1997), to restore damaged ecosystems (Palmer et al. 1997), and to predict the consequences of environmental change (Ives 1995). Many ecologists considered dominant species to be the best resource competitors (Lotka 1925; MacArthur 1972*b*; Diamond 1975). Resource competition often is a logical first hypothesis because all organisms require resources to survive, grow, and reproduce.

Simple mechanistic models of resource competition imply a simple rule for predicting the equilibrial outcome of competition (Powell 1958; O'Brien 1974; Tilman 1982). The species able to reduce the limiting resource R to the lowest equilibrial level (R^*) excludes all other species (R^* rule; Tilman 1982). The R^* rule is highly successful in chemostats, both for algae competing for nutrients and bacteria competing for carbon sources (reviewed in Grover 1997). Tests of the R^* rule outside chemostats are rare, as are tests under any conditions with self-reproducing resources and/or multicellular consumers (Grover 1997). However, the competitive exclusion predicted by simple resource competition models is inconsistent with the great diversity of natural communities (Hutchinson 1961), suggesting that other factors at least partially counteract the effects of competition.

One approach to the observed diversity of natural communities is to formulate more complex competition models, incorporating factors that might promote coexistence. Models of certain factors (e.g., competition for multiple resources; León and Tumpson 1975) are fairly well tested, but models of many other factors (e.g., predators, intraguild predation, interference competition, spatial and temporal heterogeneity) are not (reviewed in Grover 1997).

However, model complexity is limited by the need for mathematical tractability and the desire for generality (Wimsatt 1987; Caswell 1988). Another approach is to ask whether the predictions of simple resource competition models hold approximately, if not exactly, in complex situations. This is an important empirical question. For instance, one popular simplification when species compete for multiple substitutable resources is to treat similar (but nonidentical) resources as a single category. Simple consumer resource models might be expected to approximately (if not exactly) predict community structure in this

* Present address: Natural Environment Research Council Centre for Population Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, United Kingdom; e-mail: jeremy.fox@ic.ac.uk.

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situation, an intuition supported by several studies (Ritchie and Tilman 1992; Sarnelle 1992; Byers 2000; but see Leibold 1989).

Here, I ask whether simple resource competition models can predict the outcome of competition among bacterivorous protists in laboratory microcosms. Although unstirred batch cultures of bacteria and protists are simpler than natural communities in many respects (e.g., lack of predators, constant environment), potential complexities in this experimental system challenge the robustness of elementary resource competition models. These complexities can be roughly grouped into three classes: resource heterogeneity, spatial heterogeneity, and interference among consumers (e.g., Van den Ende 1973; Habte and Alexander 1978; Ratnam et al. 1982; Jürgens and Güde 1994). All these complexities have analogues in natural systems.

I measured R^* values for four species of bacterivorous protists, then let them compete in batch cultures to determine whether R^* values predicted competitive outcomes. Previous protist competition experiments were motivated by Lotka-Volterra competition models and did not test competitive mechanisms (Gause 1934; Vandermeer 1969). My work is novel in the number of simultaneously competing species for which R^* has been measured and in the use of bacteria as a living resource. I repeated the R^* measurements and competition experiment at six productivity levels spanning almost an order of magnitude. Previous experiments testing the R^* rule used single-productivity levels or focused on varying the relative availabilities of two resources (Tilman 1977; Rothaupt 1988; but see Ritchie and Tilman 1992). Manipulating productivity allowed me to test other predictions of the simplest resource competition models besides those for competitive outcomes (e.g., predicted changes in bacterial density with increasing productivity). The more features of a system that a model correctly predicts, the more confident we can be that the model captures the important system variables and processes (Leibold 1999). Manipulating productivity also allows me to infer the importance of resource heterogeneity and interference, since the importance of these factors will vary with resource productivity (e.g., Habte and Alexander 1978; Tilman 1982).

Even if the predictions of the simplest resource competition models are not perfectly satisfied (as is likely to be the case), R^* values might still be useful predictors of competitive dominance. To examine this possibility, I first compare the experimental results to the predictions of the simplest resource competition models. Then, in the "Discussion," I compare the results to the predictions of more complex alternative models that incorporate various forms of resource heterogeneity or interference (see Leibold 1999 for a similar approach).

Material and Methods

Measurement of R^* *Values and Protist Carrying Capacities*

I measured R^* for *Tetrahymena thermophila* (Mating Type VII, obtained from the American Type Culture Collection [ATCC], Rockville, Md., ATCC stock 30307), *Colpidium striatum* (Carolina Biological Supply, Burlington, N.C.), *Paramecium tetraurelia* (Mating Type VII, ATCC stock 30568), and *Paramecium caudatum* (Carolina Biological Supply). I chose protists of varying body size to facilitate identification in competition trials. Bacteria served as the resource *R*. I assembled four food chains consisting of a protist and bacteria. I grew three replicates of each food chain at six different productivity levels and measured R^* as equilibrial bacterial density. I controlled bacteria productivity indirectly by varying the concentration of carbon and nutrients in the medium. I grew two bacteria-only replicates at each productivity level to determine equilibrial bacteria densities in the absence of consumers.

Microcosm assembly, maintenance, and monitoring followed standard protocols, with minor modifications (Lawler and Morin 1993). Microcosms were 260-mL screw-capped glass bottles containing 100 mL of medium. Medium consisted of crushed Protozoan Pellets (PP; Carolina Biological Supply) autoclaved in well water. Pellets provide carbon and nutrients to bacteria. Six different PP concentrations (0.14, 0.28, 0.42, 0.56, 0.84, and 1.12 g PP/L water) created a productivity gradient. Varying PP concentration over this range affected bacteria and protist densities in another study (Kaunzinger and Morin 1998). Sterile wheat seeds (one, two, three, four, five, or six seeds per bottle, with more seeds corresponding to higher pellet concentrations) provided an additional, slow-release carbon source. I inoculated the medium with bacteria (*Serratia marcescens*; Carolina Biological Supply) 48 h before protist addition. Forty-eight hours is ample time for bacteria to reach carrying capacity ($\sim 10^8$–10^9 bacteria/mL, depending on the PP concentration). I added protists by adding 0.3 mL of medium withdrawn from agitated, high-productivity stock cultures (0.84 g PP/L). Initial densities of protists were thus ~0.3% of carrying capacity ($\sim 10^3$–10^4 protists/mL, depending on the species and PP concentration). Because stock cultures contained a variety of bacteria (J. W. Fox, personal observation), each experimental culture also received 0.3 mL of 1.2-mm-filtered mixed medium composed of equal parts from each stock culture. Bacteria other than *S. marcescens* were thus introduced at initial densities ~8 or more orders of magnitude less than the density of *Serratia*. I maintained cultures by withdrawing 10 mL of medium from agitated cultures once per week and replacing it with fresh, sterile medium of identical PP concentration. All stock and experimental cul-

tures were kept in an incubator (20°C, 12L : 12D cycle) to control environmental conditions.

I sampled every 2–3 d using standard procedures (Lawler and Morin 1993). I agitated microcosms and withdrew 10 drops of medium (~0.3 mL) with a sterile Pasteur pipette. Sample volume was determined by weight. I counted protists using a stereoscopic microscope. If protists were numerous, I diluted the sample by weight (~10-fold to ~40-fold dilution, as necessary), subsampled from the dilution, and back-calculated to obtain density in an undiluted sample. Protists generally attained equilibrial density (carrying capacity) in 2–7 d. I calculated equilibrial density as the mean of the first three samples taken after density had stabilized.

Bacteria have much shorter generation times than protists and should attain equilibrium when protists do. I sampled bacteria from each bottle once, after protists had attained an approximate equilibrium, and counted bacteria via epifluorescence microscopy. I withdrew 0.9-mL samples from each (agitated) bottle, diluted as necessary with 3–20 mL of 0.2-μm-filtered 1% formalin, and sonicated for 45 s (Fisher model 60 Sonic Dismembrator; 20 W) to dislodge bacteria from detritus and each other. I prepared one slide from each bottle according to the method of Pace (1992). I counted bacteria in a randomly selected 0.01-mm^2 area at × 1,000 total magnification using a compound microscope equipped with a 520-nm filter and a 50-W mercury lamp. I counted multiple areas, if necessary, to obtain a total count of at least 40 cells. Measurements of natural bacteria densities typically employ greater sampling effort than used here (e.g., Pace 1992), but my level of effort proved adequate for detecting differences between treatments. I converted counts to number per milliliter. The bacterial sample from one *Tetrahymena*-only replicate failed to stain properly and was excluded from all analyses.

Competition

I grew all four bacterivores together to test whether R^* values from single-species cultures predicted the outcome of competition. I assembled four replicates at each of six productivity levels using the procedures described above. I added all four bacterivores at the same time, 48 h after bacteria.

The experiment lasted 57 d, long enough for most replicates to reach an approximate equilibrium, ensuring that the results did not reflect initial densities. Increasing *Tetrahymena* densities late in the competition experiment in some low-productivity replicates may represent sampling error (see fig. 4*c*). When food is scarce, many *Tetrahymena* individuals, and some *Colpidium* individuals, take on a narrower cell shape and increase their swimming speed ("foraging trophonts"; Fenchel 1987). *Tetrahymena* and *Colpidium* foraging trophonts are difficult to tell apart. I classified all foraging trophonts as *Tetrahymena*. Reclassifying foraging trophonts as *Colpidium* did not affect my conclusions.

I sampled protists every 2–4 d. I calculated equilibrial density for each population as the mean of the last five samples (days 42, 45, 50, 52, and 57; mean density over the entire experiment gave similar results). I sampled bacteria twice, on days 42 and 57. Bacterial densities on these days did not differ significantly (two-way ANOVA for effects of productivity, day, and their interaction on $\log_{10}$-transformed bacterial density; $P > .10$ for effects of day and day × productivity interaction), confirming that bacterial densities were stable during a time when protist densities changed little. I used mean bacterial density across the two sampling dates (arithmetic or geometric mean, depending on the analysis).

Predictions and Analyses

The simplest general model of resource competition is

$$\frac{dR}{dt} = g(R, N_1, N_2, \ldots, N_S) - \sum_{i=1}^{S} N_i f_i(R),$$

$$\frac{dN_i}{dt} = N_i c_i f_i(R) - m_i N_i, \qquad (1)$$

where R and N_i are densities of resources and consumer species i, respectively ($i = 1, 2, \ldots, S$, where S is the number of consumer species; Tilman 1982; Grover 1997). Per capita resource loss rate to consumer i, $f_i(R)$, is an increasing function of R and is converted into the per capita birth rate of consumer i by a conversion constant c_i. The functions $f_i(R)$ have minimum values of 0 when $R = 0$ and approach maximum values >0 as $R \to \infty$. The resource renewal function g can take one of several forms depending on whether the system is open or closed (Grover 1997). The key feature of any renewal function is that resource growth rate $g = 0$ when $R = T$, a maximum value. I will refer to equation (1) as the "minimal model of resource competition." I tested the predictions of the minimal model for the outcome of competition (R^* rule), the effects of productivity on equilibrial bacterial and protist densities, and the relationship between productivity and the ability of protists to reduce bacterial density (protist effect size [PES]).

Bacterial Densities versus Productivity. The minimal model predicts that equilibrial bacterial density will increase with productivity only in the absence of protists. Increased productivity accumulates in consumers in systems productive enough to support a consumer population (Oksanen et

Table 1: ANCOVA for the effect of different protist species combinations on the slope of the relationship between $\log_{10}$-transformed bacterial density and $\log_{10}$-transformed productivity

Source	df	MS	*F*	*P*
Species (S)	5	.127	3.331	.008
Productivity (P)	1	5.308	139.017	<.001
S × P	5	.105	2.745	.024
Error	89	.038		

Note: One *Tetrahymena* replicate failed to stain properly and was excluded. Protists failed to grow in one *Paramecium tetraurelia* replicate at 0.14 g Protozoan Pellets (PP)/L, two *Paramecium caudatum* replicates at 0.14 g PP/L, three *P. caudatum* replicates at 0.28 g PP/L, and one *P. caudatum* replicate at 0.42 g PP/L. These replicates were excluded from the ANCOVA.

al. 1981; Tilman 1982). I tested this prediction with linear regressions of equilibrial bacterial density (measured as $\log_{10}[(\text{number/mL}) + 1]$) against $\log_{10}$-transformed productivity (measured as $\log_{10}[\text{g PP/L}]$). The regression should exhibit a positive slope without protists and a zero slope (nonsignificant regression) with protists (Oksanen et al. 1981; Kaunzinger and Morin 1998). Linear regression should be a powerful test for a monotonic relationship between density and productivity, even if the relationship is somewhat nonlinear. Log transformation improved linearity and helped meet parametric statistical assumptions. To test whether protist species combinations (none, *Tetrahymena*, *Colpidium*, *P. tetraurelia*, *P. caudatum*, competition) varied in their ability to control bacteria, I conducted a one-way ANCOVA on $\log_{10}$-transformed bacterial density with $\log_{10}$-transformed productivity as the covariate. *Paramecium tetraurelia* and *P. caudatum* failed to grow in some low-productivity replicates lacking other protists. I excluded these replicates from the regressions and ANCOVA.

Effects of Productivity and Competition on Protist Densities. The minimal model predicts that without competition equilibrial protist densities will increase with increasing productivity (Oksanen et al. 1981; Tilman 1982). With competition the minimal model predicts one species will exclude its competitors at equilibrium, and the winning species' density will increase with increasing productivity just as it does when that species is growing alone (Powell 1958; O'Brien 1974; Tilman 1982; Grover 1997).

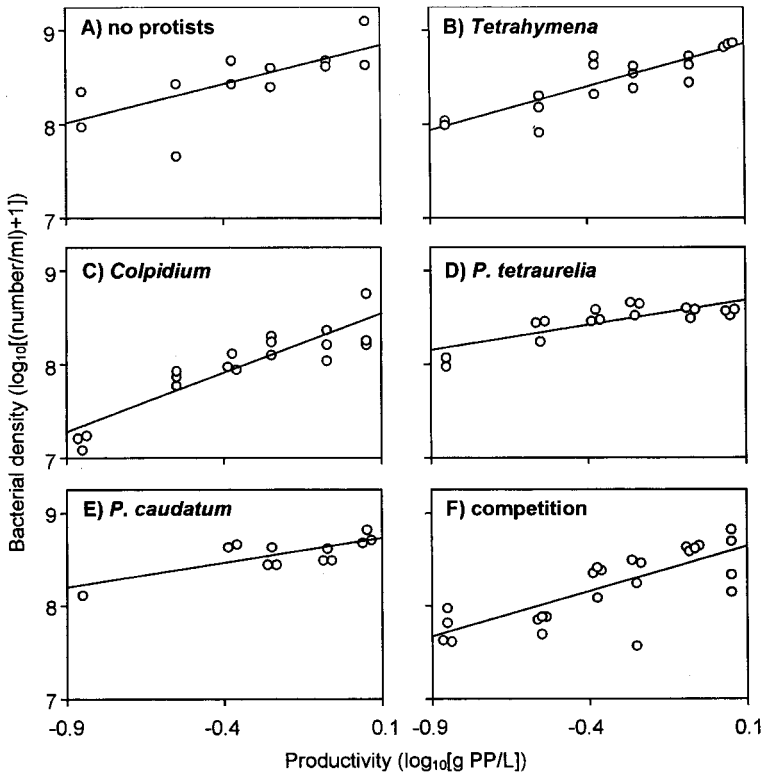

Figure 1: Linear regressions of log-transformed equilibrial bacterial densities on log-transformed productivity. Each panel corresponds to a different protist species or combination of species. Some points are offset horizontally for clarity.

Table 2: Regressions of $\log_{10}$-transformed bacterial density on $\log_{10}$-transformed productivity for different species combinations

Species	Regression	R^2	df	P
No protists	$y = 8.76 + .83x$	.51	1, 10	.009
Tetrahymena	$y = 8.77 + .92x$	.75	1, 15	<.001
Colpidium	$y = 8.43 + 1.27x$	.83	1, 16	<.001
Paramecium tetraurelia	$y = 8.64 + .54x$	.65	1, 15	<.001
Paramecium caudatum	$y = 8.67 + .52x$	.57	1, 10	.003
Competition	$y = 8.55 + .98x$	.60	1, 22	<.001

Note: Regressions illustrated in figure 1. Some replicates excluded (see note to table 1).

I tested for effects of productivity, competition, and their interaction on geometric mean equilibrial protist densities using two-way ANOVAs. Geometric means decouple means and variances. For the winning species, the minimal model predicts that only the main effect of productivity should be significant. Productivity should increase equilibrial density with or without competitors, while competition will have no effect. For the losing species, both main effects and their interaction should be significant. Productivity will increase equilibrial density in the absence of competition, while equilibrial density in competition will equal 0.

Competitive Outcomes and R*. I quantified the effect of interspecific competition on protists with a competitive effect size (CES) index in order to relate competitive outcomes to R^* values (see Sarnelle 1992; Osenberg et al. 1997; Chase et al. 2000 for discussion of effect size indices). I calculated CES for species i ($i = 1, 2, 3, 4$) in replicate j ($j = 1, 2, 3, 4$) of productivity level k ($k = 1, 2, \ldots, 6$) as

$$\mathrm{CES}_{ijk} = \frac{K_{ik} - N^*_{ijk}}{K_{ik}}, \qquad (2)$$

where N^*_{ijk} is equilibrial density (calculated as the arithmetic mean over the last five sampling dates) and K_{ik} is carrying capacity. I estimated K_{ik} as the mean of the three replicate measurements of carrying capacity for species i and productivity level k. The CES measures the ability of protists to attain carrying capacity with competitors present. Barring facilitation (which would produce CES < 0), CES varies between 0 (no effect of competitors) and 1 (competitive exclusion). Calculating CES separately for each species in each replicate makes use of all the data by treating each replicate as an independent realization of the competitive process.

The minimal model predicts that the species with the lowest R^* will exclude its competitors at equilibrium (i.e., in each bottle CES = 0 for the species with the lowest R^* and 1 for the other species). Although this prediction was not perfectly satisfied (competitors sometimes coexisted; see "Results"), R^* values might still be a useful predictor of competitive success. However, testing for an association between R^* and CES (a measure of competitive success) was complicated by dependence of R^* on productivity (see "Results"). I conducted two analyses that corrected for the dependence of R^* on productivity in different ways. First, I conducted a one-way ANCOVA on CES with productivity level as a discrete factor and R^* as a continuous covariate. I estimated R^*_{ik} as the mean of the three replicate measurements of R^* for species i and productivity level k. A positive relationship between CES and R^*, independent of productivity, would indicate that populations with low R^* are less affected by resource competition. While CES might be nonlinearly related to R^*, a monotonic relationship should show up as a significant effect of R^* on CES.

Second, I tested whether competitive dominants tended to have low R^* values. Even in the absence of a single linear relationship between R^* and CES across all species and productivity levels, competitively dominant species might still be characterized by low R^* values. I tested this possibility by defining the species with the lowest CES in each replicate at the competitive dominant in that replicate and used a χ^2 test to ask whether the species with the lowest R^* was the competitive dominant more often than would be expected by chance.

Table 3: ANOVAs for effects of competition (C), productivity (P), and their interaction on equilibrial protist densities

Species/source	df	MS	F	P
Tetrahymena:				
Competition	1	31.985	236.335	<.001
Productivity	5	1.215	8.974	<.001
C × P	5	2.623	19.381	<.001
Error	30	.135		
Colpidium:				
Competition	1	.296	43.484	<.001
Productivity	5	.554	81.464	<.001
C × P	5	.116	17.118	<.001
Error	30	.007		
Paramecium tetraurelia:				
Competition	1	3.212	86.452	<.001
Productivity	5	8.399	226.090	<.001
C × P	5	.469	12.634	<.001
Error	30	.037		
Paramecium caudatum:				
Competition	1	.350	2.768	.107
Productivity	5	5.790	45.801	<.001
C × P	5	.888	7.025	<.001
Error	30	.126		

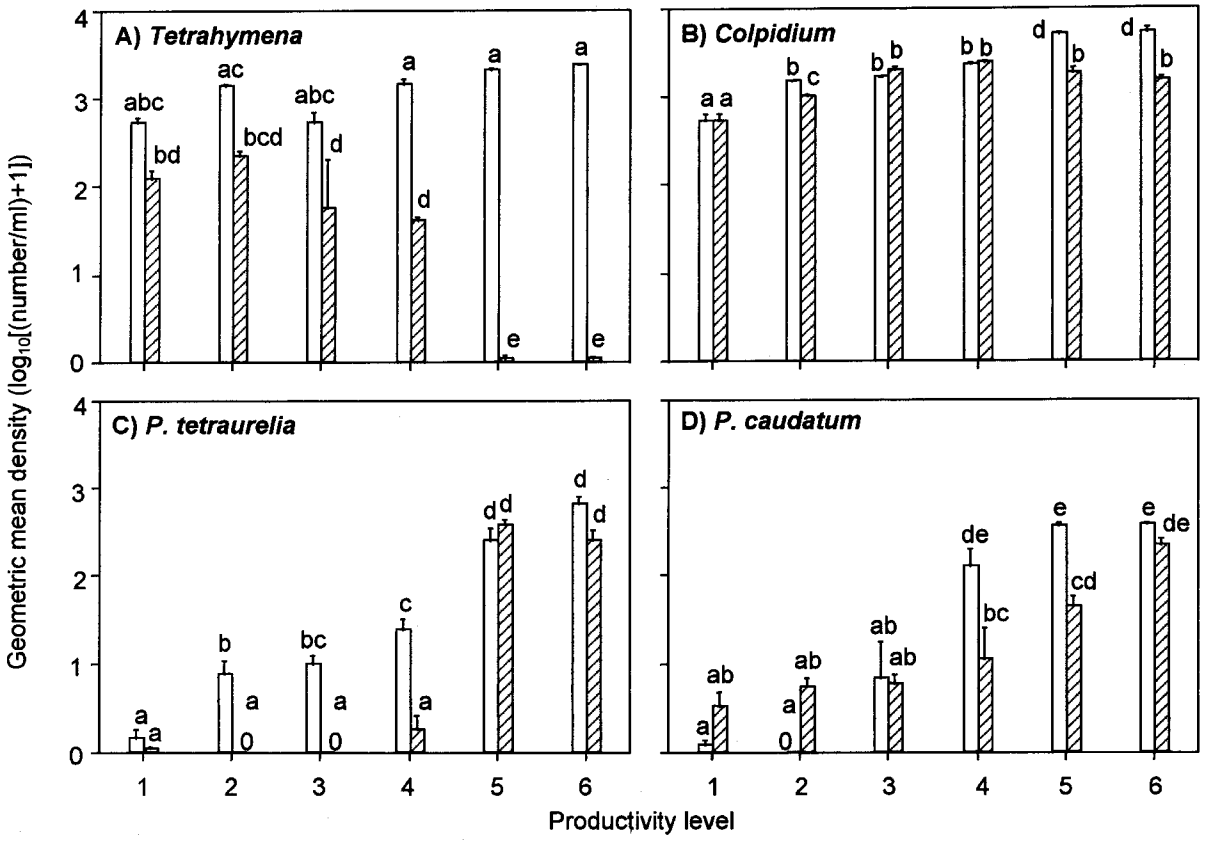

Figure 2: Effects of productivity and competition on mean densities of each protist species. Geometric mean densities (± 1 SE), with (*hatched bars*) and without (*open bars*) interspecific competition. Productivity levels *1–6* correspond to Protozoan Pellets (PP) concentrations of 0.14, 0.28, 0.42, 0.56, 0.84, and 1.12 g PP/L, respectively. Mean densities in competition are taken over the final five sampling dates. Some error bars are too small to display. Zero densities indicated by *0*. In each panel, means sharing a letter do not differ significantly in a Tukey's test ($P > .05$).

Effects of Protists on Bacteria. I quantified the effect of protists on bacteria with a unitless protist effect size (PES) index, analogous to CES. I calculated PES for each bottle containing protists as

$$\text{PES} = \frac{K_{\text{bact}} - R^*}{K_{\text{bact}}}, \tag{3}$$

where R^* is equilibrial bacterial density in that bottle and K_{bact} is bacterial carrying capacity. I estimated K_{bact} as the mean of the two replicate measurements of carrying capacity at that productivity level. The PES measures the ability of protists to reduce bacteria below bacterial carrying capacity. Barring facilitation, PES varies between 0 (no effect of protists on bacteria) and 1 (elimination of bacteria). *Paramecium tetraurelia* and *P. caudatum* failed to grow in some low-productivity replicates lacking other protists. I did not calculate PES for these replicates.

The PES should depend on productivity. The minimal model predicts PES will increase aymptotically with productivity, assuming that the system is productive enough to support consumers. The PES increases with productivity as consumers become more abundant and produce larger reductions in resource density relative to resource carrying capacity (Sarnelle 1992; Chase et al. 2000). While satisfaction of this prediction is guaranteed by satisfaction of the predictions regarding bacterial density versus productivity, failure of this prediction is not guaranteed by failure of any of the other predictions. If some predictions fail to hold, the relationship between PES and productivity may provide additional information about which aspects of the minimal model need to be modified. To test for the predicted increase in PES with increasing productivity, I regressed PES against productivity (measured as g PP/L) for each protist alone and for all four together in competition. I also conducted a regression for all data combined and used ANCOVA to test whether species varied in their ability to reduce bacteria.

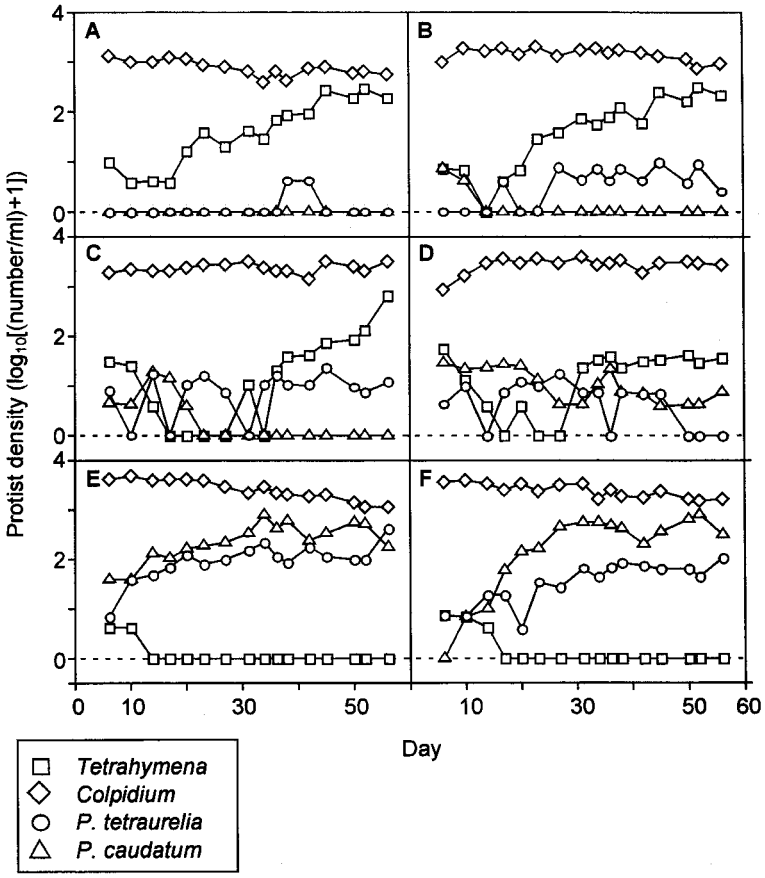

Figure 3: Population dynamics in competition. Each panel shows dynamics from a single representative replicate. *A–F*, Productivities of 0.14, 0.28, 0.42, 0.56, 0.84, and 1.12 g PP/L, respectively.

Results

Bacterial Densities versus Productivity

Equilibrial bacterial density increased with productivity whether or not protist consumers were present (table 1; fig. 1). The slope of the relationship varied between protists (significant interaction term; table 1) but was always positive (table 2; fig. 1). *Colpidium* exhibited the lowest R^* at every productivity level (fig. 1).

Effects of Productivity and Competition on Protist Densities

Competition, productivity, and their interaction all had highly significant effects on most species (table 3). All protists increased with productivity when growing alone, although the increase in *Tetrahymena* was not significant (table 3; fig. 2). In competition, multiple species coexisted, and most cultures reached an approximate equilibrium (figs. 2, 3). *Colpidium* was the most abundant species (figs. 2, 3). Competition reduced *Colpidium* density only at high productivity (fig. 2*B*). At low productivities, *Tetrahymena* coexisted with *Colpidium* at moderate densities, while the *Paramecium* spp. persisted at very low densities, if at all (fig. 2; fig. 3*A*, 3*B*). *Paramecium tetraurelia* became extinct (absent from at least the last five samples) in three of four replicates at 0.14 g PP/L, all replicates at 0.28 and 0.42 g PP/L, and two of four replicates at 0.56 g PP/L. *Paramecium* spp. replaced *Tetrahymena* at high productivities (fig. 2; fig. 3*E*, 3*F*). *Tetrahymena* became extinct in three of four replicates at 0.84 and 1.12 g PP/L.

Competitive Outcomes and R*

Colpidium exhibited the lowest R^* at every productivity level (fig. 1) but never excluded all its competitors (fig. 2). Although the R^* rule did not strongly hold, we can still ask whether R^* values remained good predictors of competitive success.

ANCOVA revealed a highly significant positive rela-

tionship between CES and R^* (table 4; fig. 4), indicating that populations with low R^* were less affected by competition. The strength of this relationship varied with productivity (significant interaction term; table 4). CES increased significantly with increasing R^* at low and intermediate productivities but was unrelated to R^* at the two highest productivity levels (table 5; fig. 4).

I excluded data for *Paramecium caudatum* at the two lowest-productivity levels from the ANCOVA because these treatments yielded aberrant CES values. *Paramecium caudatum* failed to persist in any replicate when growing alone at 0.28 g PP/L (CES undefined). *Paramecium caudatum* also failed to persist when growing alone in two of three replicates at 0.14 g PP/L, and CES values calculated using the single remaining replicate were outliers (range: -0.7 to -26). At low productivity, *P. caudatum* persisted at very low density, if at all, and so measurements of *P. caudatum* density were affected by stochastic extinctions and large sampling errors. The CES is a scaled ratio of densities and is asymmetrical about 0 (range: $-\infty$ to 1). When densities are low, small absolute changes in the data (e.g., due to sampling error) will produce large changes in CES, particularly when CES < 0. Several other CES values <0 probably also represent sampling error. These other negative CES values were less extreme than those for *P. caudatum*, so I included these other negative values in the ANCOVA. Deleting all negative CES values from the ANCOVA or setting all negative values to 0 did not affect the conclusions.

Alternatively, we can ask whether low R^* values identify the competitive dominant at each productivity level more frequently than would be expected by chance. *Colpidium* had the lowest R^* at every productivity level and had the lowest CES in 16 out of 24 replicates (*Colpidium* dominated all replicates at the lowest four productivity levels). The observed association between low R^* and low CES is highly improbable by chance alone (table 6). The association remains significant if data for *P. caudatum* at 0.14 g PP/L are included in the analysis (with these outliers included, *Colpidium* dominated 12 replicates).

Effects of Protists on Bacteria

The PES was not related to productivity when all data were considered together (linear regression, $R^2 < 0.01$, $F = 0.085$, $\mathrm{df} = 1, 86$, $P = .772$). The relationship between PES and productivity varied between protist species combinations (significant species × productivity interaction term in ANCOVA; table 7; fig. 5). The PES was unrelated to productivity for *Tetrahymena*, *Colpidium*, and all four species in competition but increased with productivity for *P. tetraurelia* and *P. caudatum* (table 8; fig. 5). As with CES, negative PES values are not scaled the same way as positive values and probably represent sampling error. Setting negative PES values equal to 0 does not change the direction or statistical significance of any effects (not shown).

Table 4: ANCOVA for effect of productivity (g PP/L), R^* (bacteria/mL), and their interaction on competitive effect size

Source	df	MS	*F*	*P*
Productivity (P)	5	.334	2.587	.032
R^*	1	4.567	35.348	<.001
P × R^*	5	.607	4.697	.001
Error	76	.129		

Note: Data for *Paramecium caudatum* at the two lowest productivity levels excluded. See text for details.

Discussion

The experimental system used here, although simpler than any natural community, is one of the most complex systems in which the R^* rule has been tested. Despite this complexity, the R^* rule remained an excellent predictor of competitive success at low and intermediate productivities. The core assumptions of the minimal model probably describe a key competitive mechanism in this system. However, factors not included in the minimal model produced deviations from its predictions.

The minimal model captures several important features of this system. When grown alone, protist densities increased with productivity, and protists reduced bacterial density (figs. 1, 2). Protists competed when grown together, and R^* values predicted competitive outcomes at low and intermediate productivities (although the R^* rule did not strictly hold; figs. 2–4). The simplest explanation for these data is that protist growth rates are at least partially a function of the availability of a shared, finite bacterial resource, which is the core assumption of the minimal model.

The minimal model predicted competitive outcomes better at lower productivities. This success may reflect the variance in competitive ability between species at different productivities. At low and intermediate productivities, *Colpidium*'s R^* values usually were several times smaller than those of its competitors. Proportionally large differences in R^* translated reliably into large differences in competitive success (fig. 4*A*–4*D*). At high productivities, the gap in R^* between *Colpidium* and other species was proportionally smaller, and R^* values were unrelated to competitive success (fig. 4*E*, 4*F*). The predictive failure of R^* values at high productivities did not reflect a lack of competition at high productivities. The CES varied sig-

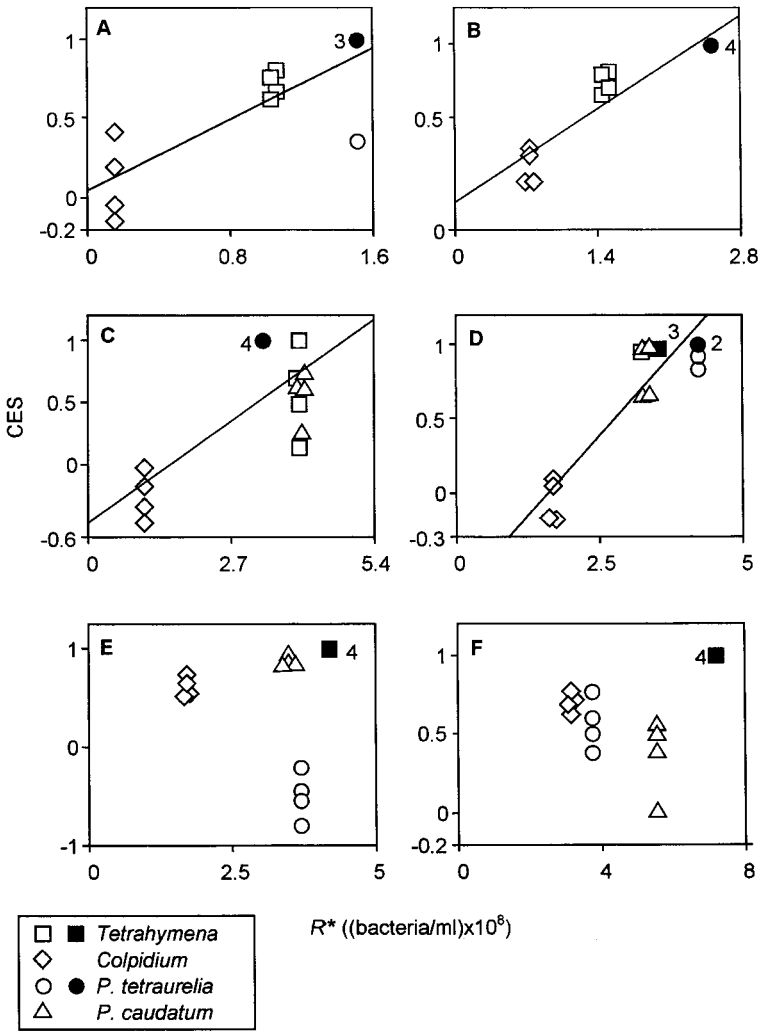

Figure 4: Competitive effect size (*CES*) versus R^*. *A–F*, Plot CES versus R^* at productivity levels of 0.14, 0.28, 0.42, 0.56, 0.84, and 1.12 g PP/L, respectively. Solid lines are significant linear regressions; nonsignificant regressions are not shown (see table 5 for regression equations). Filled symbols represent two to four identical data points, as indicated. Some points are slightly offset horizontally to improve clarity.

nificantly between productivity levels (table 4) but not because CES declined with increasing productivity (fig. 4).

Interestingly, having the highest R^* value appeared to be associated with a greatly elevated probability of extinction (fig. 4*A*, 4*B*, 4*D*–4*F*). This was true even at high productivities, where having the lowest R^* value did not lead to competitive dominance (fig. 4*E*, 4*F*). The explanation for this pattern is unknown.

While some predictions of the minimal model were at least approximately satisfied, others were not. The minimal model incorrectly predicted that the density of grazed bacteria would be independent of productivity, PES would increase with productivity, and the protist with the lowest R^* would exclude all competitors. The data generally deviated from minimal model predictions in the same direction in different treatments, suggesting that the deviations were due to qualitative features of the system not captured by the minimal model. Bacterial density increased with productivity for all protist species combinations (fig. 1), and PES was unrelated to productivity for three of five protist species combinations (fig. 5). A successful modification of the minimal model should make more accurate predictions without invoking species-specific factors, while retaining the core assumption that consumer growth depends on a shared, finite resource. Comparison of the results with those of similar studies (see "Comparison with Other Studies") suggests that bacterial heterogeneity and/or interference may explain deviations from the minimal

Table 5: Linear regressions of competitive effect size on R^* for different productivity levels

Productivity (g PP/L)	Regression	R^2	df	P
.14	$y = .04 + 5.62 \times 10^{-9}x$	.68	1, 10	.001
.28	$y = .15 + 3.59 \times 10^{-9}x$	.87	1, 10	<.001
.42	$y = -.48 + 3.06 \times 10^{-9}x$	.54	1, 14	.001
.56	$y = -.69 + 4.30 \times 10^{-9}x$	.82	1, 14	<.001
.84	$y = .55 - 1.56 \times 10^{-10}x$	<.01	1, 14	.929
1.12	$y = .35 + 6.21 \times 10^{-10}x$	.14	1, 14	.154

Note: Regressions illustrated in figure 5. Some replicates excluded (see note to table 4).

model. However, comparison with the predictions of alternative models (see "Alternative Models") indicates that the simplest models of bacterial heterogeneity fail to predict all of the results.

Comparison with Other Studies

My results are typical of protist microcosm systems where the taxonomic and structural homogeneity of the bacterial resource is not tightly controlled. Densities of bacterivores and bacteria typically increase with productivity when grown together (Balčiūnas and Lawler 1995; Morin 1999; Diehl and Feißel 2000). Bacterivore competition studies find a mixture of competitive exclusion and coexistence (Gause 1934; Vandermeer 1969; Balčiūnas and Lawler 1995). Cochran-Stafira and von Ende (1998) found a positive relationship between bacterivore competitive success and the ability to reduce total bacterial density, although Balčiūnas and Lawler (1995) found the opposite.

Results of these studies suggest an important role for bacterial heterogeneity, but a definitive test would manipulate heterogeneity experimentally. Hairston et al. (1968) grew one to three *Paramecium* spp. on all possible combinations of one to three edible bacterial species and found that increasing bacterial diversity prolonged protist coexistence. However, Hairston et al. (1968) did not measure R^* values or bacterial composition. The desired edible species were reinoculated periodically and therefore probably persisted for the length of the experiment, but it is unclear whether other bacteria also were present. It also is unclear from the data of Hairston et al. (1968) whether increased bacterial diversity produced coexistence or merely delayed exclusion.

Perhaps the strongest evidence for the importance of bacterial heterogeneity comes from the contrast between my results and those of Kaunzinger and Morin (1998; see also Kaunzinger 2000). Their experiments involved less resource heterogeneity than mine but were otherwise extremely similar to my single-species (R^*) experiments. Experiment 1 of Kaunzinger and Morin (1998; hereafter, KM1) eliminated all bacteria except *Serratia marcescens* with antibiotics, save for one contaminant found almost entirely at the two highest productivity levels (C. Kaunzinger, personal communication). The KM1 also lacked wheat seeds and used filtered PP medium, eliminating particles to which bacteria adhere. The KM1 found that densities of bacteria and *Colpidium*, and PES, varied with productivity as predicted by the minimal model (Oksanen et al. 1981), in contrast to my results.

Experiment 2 of Kaunzinger and Morin (1998; hereafter, KM2) included contaminant bacteria and PP particles like my experiments. In that experiment, both bacterivores and total bacteria increased with productivity. Interestingly, when contaminant bacteria were excluded from the analysis, KM2 also conformed to minimal model predictions (Kaunzinger 2000). Kaunzinger (2000) suggested selective consumption of *Serratia* or competition between *Serratia* and contaminant bacteria could explain the results of KM2. Resource competition between vulnerable and invulnerable bacteria contributed to deviations from the minimal model in another system (Bohannan and Lenski 1997). However, neither the presence of more or less vulnerable bacteria or resource competition among bacteria can explain all of my results by themselves (see "Alternative Models").

Alternative Models

Comparison with Hairston et al. (1968) and Kaunzinger and Morin (1998) suggests that resource heterogeneity alters competitive interactions and the response of the entire community to productivity. Can simple models incorporating resource heterogeneity explain my data? Here, I compare my data to predictions from heterogeneity models simple enough to make predictions independent of parameter values. Parameter estimates are difficult to obtain, and detailed, parameter-heavy models are unlikely to provide general insight into the consequences of resource heterogeneity for species coexistence and trophic structure.

Possibly, bacteria might be modeled as a number of resource populations of varying edibility. Bacterial cell size

Table 6: χ^2 test for whether the competitive dominant in each replicate has the lowest R^* more often than would be expected by chance

Outcome	Observed	Expected	χ^2	P
Dominant has lowest R^*	16	6.67	18.09	<.001
Nondominant has lowest R^*	8	17.33		

Note: Some replicates excluded (see note to table 4).

Table 7: ANCOVA for effects of different species combinations on the slope of the relationship between protist effect size and productivity (g PP/L)

Source	df	MS	*F*	*P*
Species (S)	4	.947	12.351	<.001
Productivity (P)	1	.209	2.725	.103
S × P	4	.314	4.097	.005
Error	78	.077		

Note: Some replicates excluded (see note to table 1).

varied within bottles (J. W. Fox, personal observation), and cell size affects edibility (Fenchel 1987). Variable edibility could explain coexistence if each protist can outcompete the others for some portion of the bacterial assemblage, assuming the bacteria do not compete among themselves (León and Tumpson 1975). However, if all bacteria are edible, this mechanism incorrectly predicts bacterial density will not increase with productivity (and PES will increase with productivity) with multiple protist species present (Abrams 1993; food webs 4 and 5 in his fig. 2).

Possibly, some bacteria were completely invulnerable, either due to large cell size or by occupying a refuge (attachment to surfaces or one another; Jürgens and Güde 1994). This mechanism explains how bacteria increased with productivity, with protists present, which might explain why PES was sometimes independent of productivity (Abrams 1993). However, invulnerable bacteria cannot explain protist coexistence (Abrams 1993; Scheffer and deBoer 1995; Abrams and Walters 1996).

Different bacteria might compete for a shared limiting resource (e.g., Hansen and Hubbell 1980) so that the microcosms effectively contain three trophic levels (bacterial resource, bacteria, protists) rather than two. Adding resource competition among bacteria to the alternative models described above does not by itself yield model predictions more in line with the data (Phillips 1974; Abrams 1993). However, resource competition among bacteria creates the potential for a trade-off among bacteria between

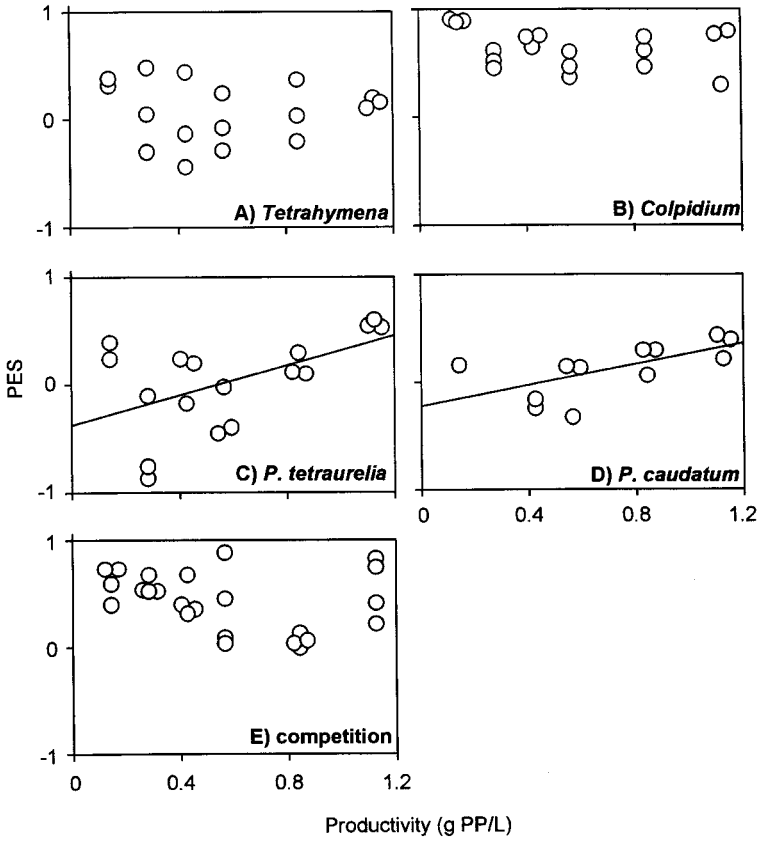

Figure 5: Protist effect size (*PES*) versus productivity for different species or combinations of species. Solid lines are significant linear regressions; nonsignificant regressions are not shown (see table 8 for regression equations). Some points are slightly offset horizontally to improve clarity.

competitive ability and ability to sustain or withstand predation. Large-celled, less vulnerable bacteria often replace small-celled, vulnerable taxa in the presence of bacterivores (Jürgens and Güde 1994), although I did not observe substantial differences in bacterial cell size between bottles with and without protists. Less vulnerable taxa should become increasingly dominant as productivity and protist density increase (Leibold 1996). Bacterial compositional turnover along the productivity gradient might explain how densities of protists and bacteria increase with productivity (Leibold 1996). However, for most parameter combinations, this "keystone bacterivory" model predicts PES will decline with productivity since consumers in very productive habitats merely shift prey composition toward less edible taxa, rather than reduce total prey abundance (Leibold 1996; Chase et al. 2000). I found PES either increased with productivity or did not vary, depending on the protists present (table 8; fig. 5). Bacterial turnover can result in PES declining (or unchanging) with productivity if protists have a much higher conversion efficiency for more resistant bacteria, as might be expected if resistant bacteria are much larger than vulnerable bacteria (Abrams 1993; Leibold 1996). However, lack of an obvious effect of protists on bacterial cell size argues against this possibility. The consequences of bacterial compositional turnover for protist coexistence are unclear. The coexistence of multiple bacterial taxa within each productivity level (different taxa at different levels) might explain protist coexistence (e.g., web 19 in Abrams 1993), but the possibility deserves further theoretical study.

Intra- and interspecific interference among protists, due to collisions or toxin production (Gause et al. 1934; Curds and Cockburn 1968; Habte and Alexander 1978), can explain correlated increases in consumer and resource densities with increasing enrichment (Gatto 1991). Protist densities in the R^* experiments failed to respond to productivity increases beyond 0.84 g PP/L (fig. 2, *open bars*), consistent with self-limitation at high-protist densities. However, density-dependent consumer death rates cannot explain the coexistence of several consumers on one resource.

In summary, simple alternative competition models explicitly incorporating resource heterogeneity or interference generally modify some predictions of the minimal model in the desired way, but none of the simplest alternatives captures every feature of the data (although the keystone bacterivory model cannot be entirely ruled out). This is not to say that bacterial heterogeneity is unimportant. Comparison with other studies strongly suggests an important role for bacterial heterogeneity (and possibly for interference at high productivities). Rather, examining the predictions of the simplest models incorporating heterogeneity or interference suggests a lower bound on the amount of detail required to explain every major feature of the system. A more complicated model, possibly incorporating both invulnerable bacteria and a variety of edible bacteria, would be necessary to explain all the results.

Table 8: Linear regressions of protist effect size on productivity for different species combinations

Species	Regression	R^2	df	P
Tetrahymena	$y = .10 - .03x$	<.01	1, 15	.900
Colpidium	$y = .74 - .16x$	.08	1, 16	.246
Paramecium tetraurelia	$y = -.37 + .70x$	.28	1, 15	.028
Paramecium caudatum	$y = -.23 + .49x$	.40	1, 10	.027
Competition	$y = .56 - .23x$	.08	1, 22	.180

Note: Statistically significant regressions illustrated in figure 5. Some replicates excluded (see note to table 1).

Caveats

The evidence for a relationship between competitive outcomes and R^* should be treated cautiously because CES values from the same replicate may not be independent. A weak effect of competition on some populations might necessarily imply a strong effect of competition on other populations. Nonindependence will inflate the statistical significance of the relationship between CES and R^*. However, the relationship between CES and R^* at low to moderate productivities is quite strong and its statistical significance is unlikely to be artifactual (tables 4, 5; fig. 4). The χ^2 analysis avoids any problems with nonindependence and reinforces the broad conclusion of the ANCOVA: R^* values predict competitive dominance at low and intermediate productivities (table 6).

The evidence for resource heterogeneity and/or interference should be treated cautiously for at least two reasons. First, inferring process from pattern is never certain because many processes generate the same patterns (Cale et al. 1989). The experimental design limits but does not eliminate this problem by ruling out many alternative mechanisms of coexistence (e.g., predation). However, other mechanisms besides those considered here may have contributed to the results. For instance, protists appear to aggregate around patches of high bacterial density (J. W. Fox, personal observation), potentially leading to coexistence (Hanski 1981). Second, lack of a relationship between PES and productivity for some species might reflect insufficient statistical power (partly due to the unbalanced experimental design). Conclusions also depend on the range of treatment levels used. Interestingly, equilibrium densities of *Paramecium tetraurelia* (and, to a lesser degree, *Paramecium caudatum*) increased rapidly at intermediate and high productivities (fig. 2, *open bars*), and both species

exhibited higher PES values at higher productivities (table 8; fig. 5). *Paramecium tetraurelia*'s R^* values also appear to level off at high productivities (fig. 1). *Paramecium tetraurelia* and *P. caudatum* may be approximately described by the minimal model, with R^* values too high to maintain substantial populations at low productivity.

Conclusions and Future Directions

Rather than providing a definitive explanation for the results, the comparisons with other studies and models provide direction for future research. Repeating these experiments with different, controlled bacteria combinations, while technically challenging, would reveal if or how much bacterial diversity is necessary to convert a homogeneous, minimal model system to a system better described by an alternative model incorporating bacterial heterogeneity. Understanding the conditions governing model applicability (e.g., how much resource diversity is required to convert a homogeneous, minimal model–type system to a donor-controlled system [Strong 1992]?) acknowledges ecological variability while preventing community ecology from becoming a collection of special cases (MacArthur 1972*a*; Kareiva 1989).

Simple rules for dominance may apply, at least approximately, in many circumstances. A small but increasing number of experiments indicates that R^* values are useful predictors of dominance, even in environments too heterogeneous to permit exclusion of subdominants (this study; Grover 1997; Byers 2000). However, mechanistic experiments measuring effects of competition on population densities remain to be conducted in most systems (Grover 1997). We need more controlled, mechanistic experiments in a variety of systems to determine when simple rules of thumb can be expected to correctly identify dominant species.

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