Abundance and species richness in natural aquatic microcosms: a test and refinement of the Niche-Limitation Hypothesis

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Abstrtact: The Energy-Limitation Hypothesis (ELH) predicts that species richness is an increasing function of abundance. In contrast, the Niche-Limitation Hypothesis (NLH) predicts that high abundances become easier to attain as species richness increases. We tested the NLH and ELH using aquatic invertebrate communities of tropical rock pools. These rock pools span a gradient from very low density pools ($N < 200$ individuals/liter) to very high density pools ($N > 5001$). Only in low density rock pools were species richness and abundance positively related. In intermediate abundance rock pools no relationship between species richness and abundance was observed, and in high abundance rock pools the relationship between species richness and abundance was strongly negative. These patterns are inconsistent with the predictions of the ELH, but not with predictions of the modified NLH which adds carrying capacity to the model.

Abbreviations: ELH - Energy-Limitation Hypothesis, NLH - Niche- Limitation Hypothesis.

Introduction

While relationships between species richness, *S*, and abundance (number of individuals, *N*) have been documented for decades, the mechanisms behind these patterns are not fully understood. Two hypotheses, the Energy-Limitation Hypothesis (ELH) and the Niche-Limitation Hypothesis (NLH) predict that species richness and abundance positively covary. The hypotheses differ in the mechanism believed to account for the positive covariance. The ELH predicts that species richness is an increasing function of abundance (Srivastava and Lawton 1998). According to the ELH, energy (resources) limits the total carrying capacity of a habitat. Species richness is then limited by the rate at which energy enters a system, i.e., by the abundance of individuals (Wright 1983, Currie 1991, Wright et al. 1993, Rosenzweig 1995, Siemann 1998, Srivastava and Lawton 1998).

In contrast, the NLH reverses the presumed causal chain and predicts that abundance is an increasing function of species richness. The NLH posits that a more diverse habitat may have more individuals because increasing species richness facilitates greater specialization in resource use (Hutchinson 1959, Chesson 2000, Kaspari et al. 2000), permitting taxa to turn resources into individuals with greater ease, i.e., abundance is limited by the number of species in the habitat. This is based on the assumptions that members of a species pool are specialized to different parts of a resource spectrum (MacArthur 1972), and that a taxon's ability to convert resources into individuals increases with the size of the available species pool (Diamond 1970, Cody 1975). The NLH implies that the species pool can control taxon abundance by regulating the ways in which a taxon can exploit any given habitat. In this paper, we test a modified version of the NLH that incorporates the consequences of the carrying capacity of the habitat (see discussion). Consideration of carrying capacity in the model is essential. When the NLH has been modified to incorporate consequences of carrying capacity, the NLH predicts that abundance will be an increasing function of species richness up to a certain level of species richness at which further increases in species richness will have no effect on abundance (i.e., an asymptote is reached).

Determining the mechanistic relationship between species richness and abundance is of considerable importance; however, few empirical studies have attempted to disentangle the roles of niche and energy limitation. Re-

cent studies have shown that increasing the number of species in a system can facilitate higher abundance, a pattern often termed overyielding (Tilman 1999). Overyielding occurs when a multi-species mixture has higher total productivity than the most productive species in monoculture. Overyielding is thought to result from complementarity (Hooper 1998). Complementarity affects resource consumption through niche differentiation and facilitative interactions between species (Cardinale et al. 2002). Niche differentiation is thought to positively affect productivity through increasingly more specialized division of resources as species richness increases, and a subsequent increase in efficiency of resource use. Facilitative interactions between species are also thought to be a key mechanism by which species richness affects the rates of resource use that governs the efficiency and productivity of ecosystems (Cardinale et al. 2002). For example, multi-species mixtures of caddisfly larvae capture a greater fraction of resources than are caught by any one species in monoculture (Cardinale et al. 2002). However, a system with higher total abundance can also support more species (Srivastava and Lawton 1998). This occurs because species with low abundances are more likely to become locally extinct through random fluctuations in population numbers or exogenous effects than abundant species (Lande 1993).

In nature, it is likely that both energy and niche limitation interact in a feedback loop with the upper bounds of abundance and species richness limited by the carrying capacity and elements of biotic structure (such as numbers of functional groups and evenness) and the lower bound limited by species richness being constrained by the number of individuals. One approach to disentangling the effects of energy and niche limitation is to test the model predictions across a range of communities that differ in their total abundance. While indirect, this approach to hypothesis testing is still valuable. If the relationship between species richness and abundance changes in communities with different productivity, the ability of the models to predict changes in richness will also vary.

We tested the predictions of the NLH and the ELH using aquatic microinvertebrate communities of tropical coastal rock pools. Our working hypotheses were as follows: 1) habitats with more species will have more individuals (NLH), and 2) the number of individuals in a habitat will influence the number of species that can be maintained (ELH) and may modulate the relationship between richness and abundance. Taken together, these hypotheses assume that both energy and niche limitation combine to constrain N and S (Paine 1966). In the rock pool meta-community, habitats (i.e., rock pools) can be arranged along a naturally occurring abundance gradient. This gradient can be used to test whether the relationship between abundance and species richness is the same at all levels of abundance, or whether this relationship changes depending on abundance. If the relationship changes, this indicates that N and S are interacting through more than one mechanism.

Methods

Study site and community composition

Aquatic communities in the supratidal zone at the Discovery Bay Marine Laboratory ($18^o28'$ N/ $77^o25'$ W) on the north coast of Jamaica consisting of aquatic meio- and micro- invertebrates inhabiting rock pool microcosms were chosen for this study. This site has been described in Schuh and Diesel (1995), Therriault and Kolasa (1999, 2000, 2001a,b), Kolasa et al. (1996), and Romanuk and Kolasa (2001, 2002). The dominant species are a harpacticoid copepod, *Nitocra spinipes* Boeck (present in 70% of samples), a cyclopoid copepod, *Orthocyclops modestus* Herrick (70%), an ostracod *Candona* sp. (34%), an unidentified nematode species (31%), and a *Culex* mosquito (31%). Other common species include a daphnid, *Ceriodaphnia* sp., and several fresh and brackish water ostracods. The majority of species are small benthic animals ranging from 60 µm -0.5 mm but some are plankton-like (*O. modestus, Ceriodaphnia* sp.) and swim in the water column. The full list of the taxa (69 species) identified to date includes: Turbellaria (7), Nematoda (1), Polychaeta (5), Oligochaeta (2), Ostracoda (20), Copepoda (6), Cladocera (4), Decapoda (crab) larvae (1), Decapoda (shrimps) (3), Amphipoda (1), Isopoda (1) and Insecta (18). Only the larval stages of insects, except for an occasional beetle and corixid bug, are observed in rock pools. Two hundred and thirty erosional solution pools with a maximum volume greater than 250 ml are present on the fossil reef across an area of 50 m.

Forty-nine pools were randomly chosen (Kolasa et al. 1996) and monitored yearly in late December or early January for 9 years. The pools range from 14 to 248 cm in length and 10 to 188 cm in width (mean length = 56 cm ± 35.0 SD and mean width = 32.9 ± 26.8 SD), and vary from 1-37 cm in depth (mean = 12.8 ± 8.3 SD). On average, the pools are located within 1 m of the nearest neighbor and none are separated by more than 5 m from the next nearest pool. Their elevation above sea level ranges from 1-235 cm (mean = 76.6 ± 80.1 SD) at high tide, with the tide rarely exceeding 30 cm. Seven pools are tidal (although tidal flooding is not daily), however most are maintained by atmospheric precipitation and, very occasionally, wave splash water.

Table 1. Mean, minimum (min), maximum (max), and standard deviations (stdv) of species richness (*S*) for all rock pool microcosms and for each abundance class, as well as valid *n* (number of observations) and mean number of individuals, *N*, for each abundance class. Also shown is the best-fit model for the relationship between species richness and abundance for each abundance class and the entire meta-community.

Abundance Class	Number of Individuals	n	Mean S	Min S	Max S	Stdv. S	Mean N	Best-fit model
All Levels	N = 1-25,317	365	5.78	1	16	2.65	839	$y=a+bx^c$
Very Low	N<100	117	4.50	1	11	2.11	40	$y=a+b/x^{0.5}$
Low	101<N<250	67	6.17	1	16	2.65	166	$y=a+bx$
Low-Intermediate	251<N<500	48	6.47	1	14	2.65	377	$y=a+b/x^2$
Intermediate	501<N<1000	52	6.36	1	12	2.78	747	$y=a+b/\ln x$
High	1001<N<2500	54	6.66	1	13	2.58	1626	$y=a+bx$
Very High	N>2501	25	6.24	1	12	2.90	5176	$y=a+b/\ln x$

Species assemble in the rock pools along a salinity gradient, which is largely determined by elevation and exposure to the sea (Therriault and Kolasa 1999). While species composition changes along the salinity gradient, many species are euryhaline and are able to colonize and persist in freshwater, brackish, marine, and hypersaline pools. The pool communities also contain an abundant assemblage of microorganisms maintained by a range of autochtonous to allochtonous energy inputs (mangrove leaves, dead macroinvertebrates, green and brown algae). Resources, in the form of various microorganisms and detritus, are very abundant in the pools (Schuh and Diesel 1995). After desiccation and refilling, an abundant microfauna emerges rapidly. Schuh and Diesel (1995) report that 0.4-17.6 copepods ml^{-1} were counted in the detritus layer 24h after rain.

The pool communities experience desiccation (Schuh and Diesel 1995), with 17 % of pools dry on any one sampling date (Therriault and Kolasa 2001b), that, coupled with the short generation times of the organisms (between a few days and a few months), allows us to regard the annual samples as relatively independent events (i.e., the communities reassemble *de novo* from a species-pool of short-lived organisms or from inactive propagules). Pool communities are relatively isolated (Schuh and Diesel 1995), with water flowing for short periods of time between some neighboring pools during heavy rains or during high tides. There are no clear pool area effects on community density or species richness, and seasonal differences in richness and abundance are low as a result of relatively constant year round conditions in the tropics (Therriault and Kolasa 2001a, Schuh and Diesel 1995).

Sampling and statistical analysis

The procedure used to census the invertebrates has been described in Kolasa et al. (1996), Therriault and Kolasa (1999, 2000, 2001a,b) and in Romanuk and Kolasa (2001, 2002). Briefly, 500 ml of pool water was taken from a pool thoroughly stirred to dislodge organisms from its sides and bottom and to homogenize their distribution. A 100 ml dip container was used to obtain animals from a variety of locations in each pool (water surface, pool bottom, pool sides, water column); number of dips depended on pool area, shape, and depth. Samples were filtered with a 60 μm net and organisms not passing through the net were immediately preserved in 50-70% ethanol. A total of 392 samples were taken over 9 years and those with individuals (365/392) were included in the analysis. A total of 289,975 individuals were counted from all samples. Eight censuses were made of each pool over a 9-yr period: Dec. 1989, Jan. 1990, Jan. 1991, Jan. 1992, Jan. 1993, Jan. 1994, Jan. 1996, Jan 1997, and June 1997. Censuses were all made in one day.

Data were analyzed from pool communities (number of pools = 49) that range from low (*N* <100/0.5 liter) to high abundance (*N* > 2500/0.5 liter). Pool communities were grouped into six abundance classes representing the full range of naturally occurring abundances summed over all species (Table 1): very low (*N* < 100), low (101< *N* < 250), low-intermediate (251 < *N* < 500), intermediate (501 < *N* < 1000), high (1001 < *N* < 2500), and very high (*N* > 2501) abundance. Species richness, *S,* was defined as the number of species in a pool at each date. Abundance was calculated as the sum of abundances of all species in a pool and was transformed (log$_{10}$) to eliminate positive correlations between means and variances. We fitted linear, logarithmic, exponential and polynomial functions to all abundance categories to find the best-fit model for each abundance class using Table Curve 2D V3 (Jandel 1994). Interpretation of the regression equations for the abundance classes was restricted to the slope and strength of the relationship because the upper and lower bounds were artificially fixed by the data partitioning. To ensure that the use of abundance classes did not introduce a statistical error we also performed quantile regressions from the 5th to the 95th quantiles (Koenker and Basset 1978,

Cade and Guo 2000). To test whether the abundance of species rich-pools was more predictable than that of simpler pools we used the Brown and Forsythe test for homogeneity of variance in N among abundance levels at different S. This test is more robust than Levene's test and can be used in groups with unequal numbers (Statistica 1995).

Results

Species richness ranged from one to 16 species (mean $S = 5.78 \pm 2.65$ SD; Table 1) and abundance ranged from pools with only one individual to 25,317 individuals per 0.5 liter (mean $N = 839 \pm 1776.07$ SD). Intermediate levels of species richness were encountered most frequently (mode = 7). Species richness did not differ significantly for 5 out of the 6 abundance classes ($p > 0.311$). Species richness was only significantly different between the very low abundance class and the higher abundance classes ($p < 0.0001$).

To determine if the predictions of the NLH, that higher abundances become easier to achieve when more species are present, apply to aquatic rock pools we regressed abundance on species richness. Abundance positively correlated with species richness ($p < 0.0001$, $n = 365$; Fig. 1). Abundance was best predicted by $N = -0.4206 + 2.004 - 7.287^{.1995}$, with an explained variance of 14%. A nearly identical relationship occurs when only the 36 most common species are considered, ruling out mathematical artifacts potentially introduced by the addition of rare species which would inflate S values ($r = 0.372$, $r^2 = 0.139$, $p < 0.0001$, data not shown). The ELH also fits the data from aquatic rock pools: Species richness

was best predicted by $S = 6.8308 + 7.864 - 2.4348^{-6.8308}$, with an explained variance of 18% ($p < 0.0001$, n = 365).

Grouping the communities into six abundance classes (see Table 1) and using species richness as the independent variable (NLH), revealed a gradient of patterns in species richness-abundance relationships (Fig. 2A-F), with strong positive relationships for low abundance habitats and strong negative relationships for high abundance pools (Fig. 3). At very low, low, low-intermediate, and intermediate N levels the relationship between species richness and abundance is positive or absent *(very low $N < 100$, r = 0.611, p < 0.0001 Fig. 2a; low $101 < N < 250$, r = 0.245, p = 0.045 Fig. 2b; low-intermediate $251 < N < 500$, r = 0.077, p = 0.599 Fig. 2c; intermediate $501 < N < 1000$, r = 0.082, p = 0.575 Fig. 2d).* Analysis of the relationship between species richness and abundance for high N and very high N classes indicated a switch to a negative although insignificant correlation at the high N level, and a strong significant correlation at the very high N level *(high $1001 < N < 2500$, r = -0.145, p = 0.294 Fig. 2e; very high $N > 2501$, r = -0.755, p < 0.0001 Fig. 2f).* These differences show that while abundance correlates with species richness, the relationship shifts along the abundance gradient from a strong positive correlation at very low N to a strong negative correlation at very high N (Fig. 3).

To test whether the abundance of species-rich pools was more predictable than that of simpler pools, we used the Brown and Forsythe test for homogeneity of variance in N among abundance levels at different S. The null hypothesis of homogeneity of variances was rejected for the very low (F=7.3, p < 0.001), low (F=317.86, p < 0.001),
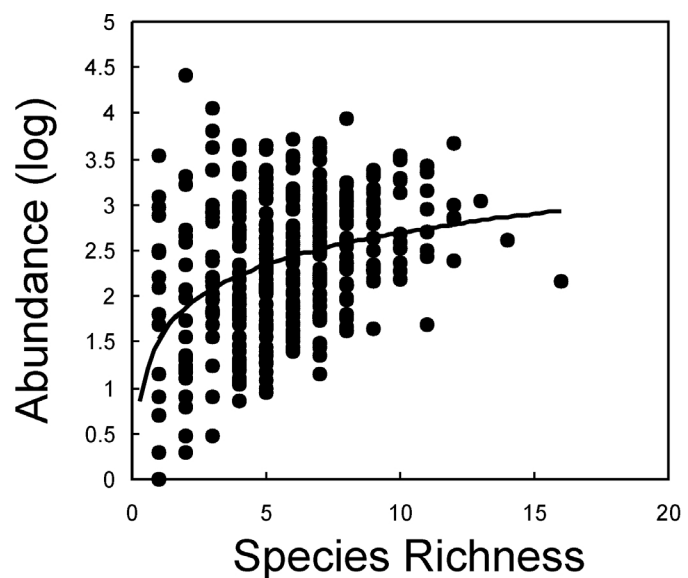

Figure 1. Abundance ($\log_{10}$) increases with species richness in rock pool microcosms ($n = 365$). Data are shown from 49 pools over 9 sampling dates. Pools with no individuals (that were dry at the time of sampling) are not plotted. The equation for the plotted regression line is given in Table 1.
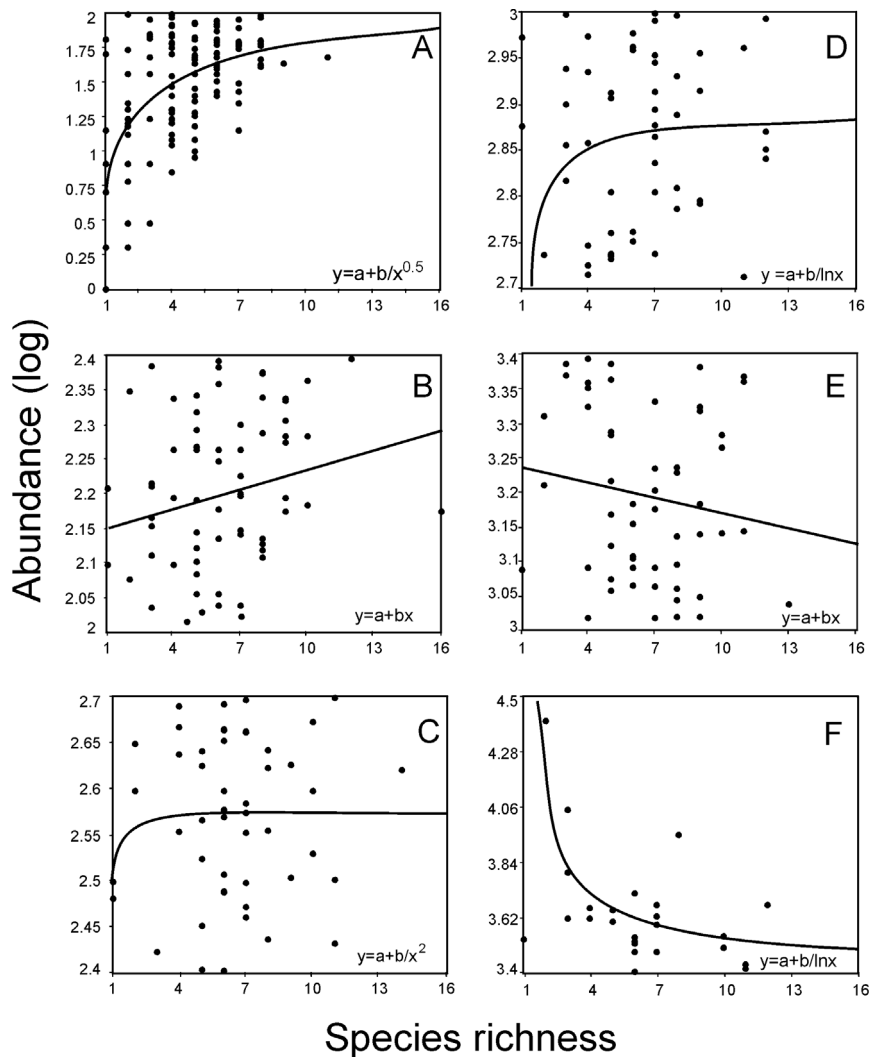
Figure 2. Abundance (y-axis) increases with species richness (x-axis) for low abundance habitats (A, B) and decreases with species richness in the very high abundance habitat (F). Abundance classes: (A) very low (B) low (C) low-intermediate (D) intermediate (E) high (F) very-high. Best fit regression models are shown as determined by Table Curve 2D V3 (Jandel 1994).
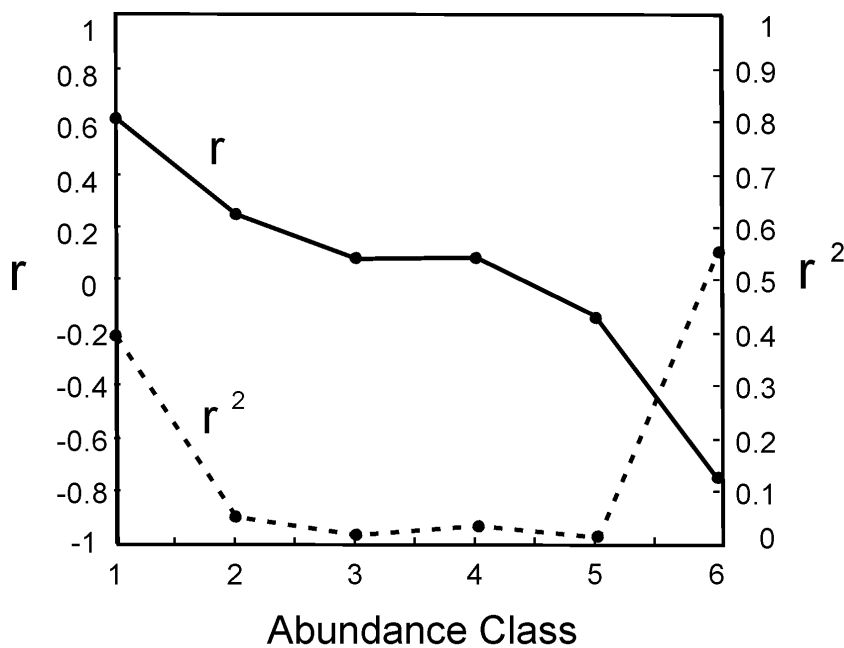
Figure 3. As abundance increases, the trend (left x-axis = R) shifts from positive correlations at low levels of abundance (x-axis abundance classes 1-4) to negative correlations at high levels of abundance (abundance classes 5-6). The explained variance of the species richness-abundance relationship (right y-axis = r^2) is high at the extremes of abundance, i.e., very low (1) and very high (6) abundance.

and very high N level (F=67.8, p < 0.0001). Thus, for rock pool microcosms, species-rich habitats had a more predictable N than species-poor pools.

Discussion

Our results offer a strong argument against the traditional species richness-abundance interpretation, i.e., that richness is simply determined by abundance (see Srivastava and Lawton 1998). Specifically, the fact that species richness is unrelated to N at the low-intermediate, intermediate, and high abundance levels and strongly negatively correlated with N at the very high abundance level (Fig. 2b-f) is inconsistent with the view that richness is a positive function of total community abundance.

The NLH predicts that species richness and abundance should covary as a result of greater specialization and thus more efficient resource use in more diverse communities (Diamond 1970, MacArthur 1972). However, the predictions of the NLH (before incorporating carrying capacity, K, see below) were only consistent with the patterns observed in 50% (184 of 365) of communities, i.e., low abundance pools (Fig. 2A-B). Species richness may facilitate higher abundance in low abundance communities (Fig. 2A-B), but at very high abundances species richness appears to fail to facilitate further abundance, possibly by pushing it to near the carrying capacity of the habitat (Fig. 2F). Once this is accomplished, no additional increases in abundance are possible (Fig. 1). Between these extremes of abundance, there was no relationship between species richness and abundance (Fig. 2C-E), which may reflect a mutual cancellation of the effects postulated by NLH and ELH. A modification of the NLH incorporating consequences of the carrying capacity, K, provides a possible explanation for these patterns.

If adding species unlocks the resources and makes them available to the community, it is expected that an increase in the overall number of individuals would be observed. However, such an increase is unlikely to follow a concave-up trend as a function of S (Kaspari et al. 2000) because increasing the number of species will lead to an increasingly higher efficiency of resource use such that, at some value S (S_c) the community carrying capacity will be reached. Subsequent increases in S above S_c would accord no further benefits. This relationship can be represented as community abundance (D), i.e., combined abundance of all species:

$$D = \sum_{i=1}^{S} \varepsilon(K - D_{i-1}) \qquad (1)$$

where K is the carrying capacity of the environment occupied by the community, S is the number of species, and ε is the efficiency of resource extraction.

The following hypothetical situation illustrates the behavior of this relationship. Suppose that the first species to arrive, S=1, uses somewhere between 0 and 100 units (K) of the total energy available, that is 50 units on average. Addition of a second species, S=2, increases the community resource use one step further which makes additional forms of energy available. This increase can take values anywhere between no improvement (50 units of resources used previously available but now shared by two species, i.e., a direct competitor for the same resources) up to maximum use of 100 units (S=2 represents a species occupying a new niche). On average, an additional increase would be 25 units - thus 75 units would become available for the two species. Adding a third species, S=3, however, can only increase the resource use the remaining 25 units (100-75). Thus, the third species is likely to make a smaller contribution to an increase in resource availability than the second, which is about 12.5 on average for the community. Should the newly added species change the efficiency of resource extraction, ε, of the current community members, the curve describing the changes in D (Fig. 4) will become steeper or shallower depending on whether the effect is positive or negative, respectively. At some value of S (S_c) this increase in resource use will become asymptotic. In this example, where species are utilizing 50% of the available energy on average, the number of species where an asymptote is reached is, S_c = 6 (Fig. 4).

The model presented above predicts that in situations where the NLH applies (a) abundance will be a positive decelerating (convex-up) function of richness, S and (b) individual densities of species will on average decline in spite of the overall growth of community abundance (abundance compensation). The differences between Kaspari et al. (2000) predictions and this model are solely a result of the introduction of the community carrying capacity as a constraining factor in the Niche-Limitation Model. Why this system is different from ant communities (Kaspari et al. 2000) in which niche-limitation may be stronger at higher densities (rather than lower abundances for this community) is unclear.

We suggest that energy and niche limitation may interact in aquatic microcosms, in support of Paine (1966). That abundance itself can modulate the relationship between species richness and the number of individuals in a community makes intuitive sense. Resources limit the number of individuals and the numbers of species as habitats reach a carrying capacity. At low levels of abundance,
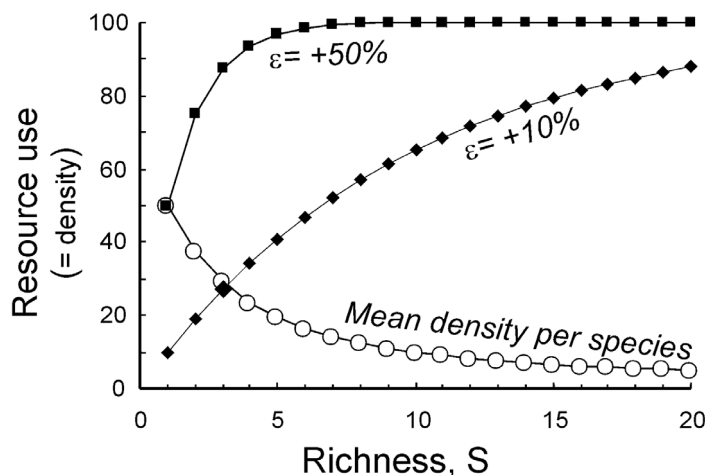
Figure 4. The general relationship between S and resource use expected from the Niche-Limitation Hypothesis (community species abundance is assumed to be proportional to resources used) described by Equation 1. The two increasing trends show the expected total abundance assuming an increase in efficiency of resource use (for two scenarios: 10% and 50% efficiency increase) with each added species, given the remaining resources to be unlocked in the assembly process. The third curve (circles) shows the mean species abundance for the 50% efficiency model. These trends remain qualitatively constant over a wide range of ε in unlocking resources by additional species. If adding species fails to unlock the additional resources, D as a function of S remains a straight horizontal line.

increases in species richness may act to remove resource limitations by increasing the total range of accessible resources in the community. Adding more species should result in only a modest improvement in abundance compared to one that is possible when the whole community is still far from its carrying capacity. In contrast, high densities are likely to be a function of already high efficiency of resource use in aquatic microcosms. A negative relationship between species richness and abundance in very high abundance pools may be a result of higher probability of sampling pools fluctuating around carrying capacity, with a significant number of pools experiencing temporary population crashes. Such crashes would occur as a result of either exceeding carrying capacity or small variations of environment (Lande 1993). Another possible factor is the effect of predation in species-rich pools. Abundances in species-rich pools were also more predictable than species-poor pools for 3 of the 5 abundance classes (very low, low, and very high abundance), as predicted by recent experiments (McGrady-Steed et al. 1997, Naeem and Li 1997). These three abundance classes were the same classes that showed significant relationships between species richness and abundance. This suggests that not only does species richness facilitate higher abundances in pools with low N and constrain abundance in pools with very high N, richness may also increase the predictability of N.

In summary, the joint predictions of the Energy-Limitation Hypothesis and the Niche-Limitation Hypothesis that abundance and richness positively covary was only supported in low abundance rock pools. In rock pools with intermediate abundance there was no relationship between species richness and abundance, and in rock pools with very high abundances the relationship between species richness and abundance was strongly negative. This pattern of results is inconsistent with the ELH but not with the modified NLH that incorporates carrying capacity into the deductive process.

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