TRADEOFFS IN COMMUNITY PROPERTIES THROUGH TIME IN A DESERT RODENT COMMUNITY

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ABSTRACT: Resource limitation represents an important constraint on ecological communities, which restricts the total abundance, biomass, and community energy flux a given community can support. However, the exact relationship among these three measures of biological activity remains unclear. Here we use a simple framework that links abundance and biomass with an energetic constraint. Under constant energetic availability, it is expected that changes in abundance and biomass can result from shifts in the distribution of individual masses. We test these predictions using long-term data from a desert rodent community. Total energy use for the community has not changed directionally for 25 years, but species composition has. As a result, the average body size has decreased by almost 50% and average abundance has doubled. These results lend support to the idea of resource limitation on desert rodent communities and demonstrate that systems are able to maintain community energy flux in the face of environmental change, through changes in composition and structure.

Introduction

Resource availability represents an important constraint on communities and ecosystems. It imposes a hard upper bound on the total amount of energy that can be fluxed by the constituent species and thus on the total quantity of living matter that can be supported (Hutchinson 1959; Odum 1975; Brown 1981; Blackburn and Gaston 1996; Srivastava and Lawton 1998). By assuming a steady state between resource availability and community energy use (O'Neill and Giddings 1979; Ernest and Brown 2001; Enquist et al. 2003), which is maintained by compensatory interactions among species in a dynamic environment (McNaughton 1977; Schindler 1987; Frost et al. 1995; Tilman 1996; Klug et al. 2000; Ernest and Brown 2001), it can be shown that species composition can shift to maintain a relative constancy, or homeostasis, of community energy flux (Ernest and Brown 2001).

The energy flux of a community is traditionally calculated by summing the energy use across species or across body size bins. Within a species or a bin, energy use is determined by multiplying the number of individuals by their metabolic rate, which is determined allometrically based on their average mass (Maurer and Brown 1988; Srivastava and Lawton 1998; Ernest and Brown 2001; Enquist et al. 2003). This approach makes it apparent that total community abundance (the sum of the abundances across species or bins) and biomass (which depends on abundance and mass of individuals) are likely constrained by energy supply. Because these three properties (total energy use, abundance, and biomass) typically covary in response to fluctuations in resource availability, they are often considered to be equivalent measures of a community (but see Pagel et al. 1991; Taper and Marquet 1996). Using a simple framework that shows how these three community properties are constrained by resource availability, we explore how they trade off in response to resource limitation, and why they do not represent equivalent measures of the

community.

The framework

Assuming a steady state between resource availability (R) and community energy flux (E_{tot}), driven by compensatory interactions among species, the total energy use of a community can be obtained by summing across the energy use of each individual of that community. Similarly, the biomass of a community (M_{tot}) is calculated by summing the masses of all its individuals. This is equivalent to determining energy use and biomass using total community abundance and mean values for the mass distribution by $E_{tot} = b_0 N_{tot} \overline{M^{3/4}}$ (equation 1) and $M_{tot} = N_{tot} \overline{M}$ (equation 2), where N_{tot} is the total abundance of the community, $\overline{M}$ is the average mass of an individual in the community, and $b_0 \overline{M^{3/4}}$ estimates the average metabolic rate of an individual using the exponent and normalization constant (b_0) from metabolic allometry (e.g. Kleiber 1932; Peters 1983; Calder 1984). In this case, b_0 represents the normalization constant for daily activity (i.e. field metabolic rate). $\overline{M}$ and $\overline{M^{3/4}}$ are descriptions of the distribution of body sizes among individuals in the community. This is not the body-size distribution of Hutchinson and MacArthur (1959), but the size spectrum more commonly discussed in the aquatic literature (e.g. Sheldon et al. 1972; Peters 1983; Griffiths 1986; Cyr and Pace 1993). This distribution can be described as a probability density function (*f(M)*; Figure 1). Note that $\overline{M^{3/4}} \neq \overline{M}^{3/4}$ unless all individuals in the community have the same mass.

This size distribution is often implicitly assumed to be stable (with the exception of seasonal fluctuations, Gasol et al. 1991). However we will show that it can and does change markedly through time (Figure 1). Shifts in this individual distribution of body sizes can result

from two distinct but non-exclusive processes. The species composition of the community can

remain the same, while the average body size of one or more species changes, or the average

body size of individuals within a species can stay the same, while the composition of the

community shifts. Both of these processes could operate simultaneously to either magnify a

change or to offset each other.

By assuming that E_{tot} does not change directionally through time we can explore how

community properties should change in response to changes in $f(M)$. This assumption does not

require that E_{tot} is a constant, but rather that there is no directional trend in resource utilization

through time and that resource availability remains a constraint on the community despite its

temporal fluctuations. To incorporate variation in resource availability we can consider E_{tot} as a

random variable with the observed mean (μ) and standard deviation (σ).

Several authors have noted the importance of $f(M)$ for community properties (Cyr and

Pace 1993; Blackburn and Gaston 1996; Srivastava and Lawton 1998), and models have been

developed to understand the relationships among community properties for specific body size

distributions (e.g. Peters 1983; Enquist et al. 2003). However the relationships between

abundance and body size in many communities does not fit these special cases. Here we use a

simple, but general, framework for the relationships among community properties, which makes

several predictions. First (from equation 1), $N = \dfrac{E(\mu, \sigma)}{M^{3/4}}$, which is to say that if the energy use

by a community varies around μ and the average energy use of an individual decreases (because

the average individual is getting smaller), then the number of individuals must increase in order

to consume all of the available resource. Specifically, this tradeoff predicts that 1) the temporal

trends of N and $\overline{M^{3/4}}$ will be opposite of one another, with the noise in the abundance trend

determined by the variability in E_{tot} and 2) the values of N and $\overline{M^{3/4}}$ should be inversely related

to one another. Because $\overline{M^{3/4}}$ is not typically measured by ecologists, we can approximate this

quantity in terms of the mean and variance of mass using the first two terms of a Taylor series

expansion (e.g. Seber 1973; for a recent examination of the use of Taylor series in allometric

studies see Savage 2004),

$$N_{tot} \approx E_{tot} \overline{M}^{-3/4} \left[1 - \frac{3}{32} \left(\frac{\sigma^2(M)}{\overline{M}^2} \right) \right]^{-1}$$
(3)

where $\sigma^2(M)$ is the variance of $f(M)$. If the second term in the expansion is much smaller than

the first term, then $N_{tot} \propto \overline{M}^{-3/4}$, and as the average mass of an individual decreases, abundance

must increase to compensate. This simplified equation appears mathematically similar to the

energetic equivalence rule (EER, Damuth 1981), which represents a static empirical pattern

relating species population density to the mass of the species. However, we are addressing a

dynamic, theoretically predicted relationship between total community abundance and average

community mass (regardless of species identity). As such these patterns cannot be directly

compared. It also follows from equation (3) that if mean body size decreases, the ratio of energy

use to biomass must increase and thus biomass must decrease (e.g. Peters 1983).

Different combinations of abundance and mass represent alternative solutions to the same

problem: how does a community utilize all of the available resource? In many cases it may be

that E_{tot}, $f(M)$, and N_{tot} all remain essentially constant at a site through time. However, here we

show that, in a desert rodent community, the average mass and metabolic rate of an individual

have decreased dramatically over the last 25 years with a concurrent, compensatory increase in

abundance, so that community energy flux has remained relatively constant.

Methods

We assessed community properties (energy use, abundance, and biomass) through time using the desert rodent community at Portal, AZ. Abundances and masses were obtained from monthly trapping and were averaged over 6-month periods from January 1978 to December 2002. For details on the site and the experimental design see Brown (1998). Individuals recaptured during 6-month periods contributed repeatedly to the total community properties and were therefore counted once for each capture. To avoid the potentially confounding effects of trophic efficiency and multiple resource use, we considered only granivorous rodents – *Baiomys taylori*, *Dipodomys merriami*, *D. ordii*, *D. spectabilis*, *Chaetodipus baileyi*, *C. hispidus*, *C. intermedius*, *C. penicillatus*, *Perognathus flavus*, *Peromyscus eremicus*, *P. maniculatus*, *Reithrodontomys megalotis*, *R. montanus*, and *R. fulvescens*. We estimated individual metabolic rates using a non-linear least squares regression between mass and rodent field metabolic rate (data from Nagy et al. 1999). Because the slope of this fit was not significantly different from the theoretically predicted 3/4 (0.79 + 0.043; West et al. 1997; West et al. 1999), we refit the data with a 3/4 slope to obtain a value for b_0 of 5.69 ($r^2 = 0.99$). Results were not different using Nagy et al.'s (1999) original ordinary least squares (OLS) regression. Desert rodents tend to have lower metabolic rates than other rodents, which may affect the value of b_0, but the scaling exponents are similar and should therefore not affect our conclusions (Hinds and MacMillen 1985).

Changes in N_{tot}, M_{tot}, E_{tot}, and $\overline{M}$ through time were characterized using power functions using non-linear least squares regression to avoid overweighting the early years of the study (Tausch and Tueller 1988). Initial parameter values for all non-linear fits were determined from OLS fits to log-transformed data, and all results were qualitatively similar using these OLS regressions. In addition, we examined temporal trends in the mass of individual species through

time using OLS regression. We only evaluated individual species trends for species that occurred in at least five six-month periods (*D. merriami*, *D. ordii*, *D. spectabilis*, *C. baileyi*, *C. penicillatus*, *P. flavus*, *P. eremicus*, *P. maniculatus*, *R. megalotis*). We also fit the relationships between N and $\overline{M}$ using non-linear least squares regression. To determine the accuracy of the Taylor approximations, we calculated the percent error of the estimates by dividing the absolute value of the difference between the real value and the approximation by the real value.

Results

During the course of the study, energy use by the community did not change directionally, but abundance increased approximately twofold and biomass decreased by about 25%. These changes resulted from a shift in the distribution of body masses with the mean mass of an individual decreasing from 73.4g in 1978 to 33.7g in 2002 (Figure 2; Table 1). In addition, the relationship between N and $\overline{M}$ was significantly negative and not significantly different from that predicted by the framework ($N_{tot} \propto \overline{M}^{-0.57}$; 95% CL: –0.97 to –0.18).

Compositional reorganization of species of different size generated the observed decrease in $\overline{M}$. Since the beginning of the study, species above the final $\overline{M}$ (33.7 g) decreased in relative abundance from 86% to 46%, while species below the final $\overline{M}$ increased from 14% to 54%. This compositional trend was dampened somewhat by the significant increase in body mass of four species during the study (*C. penicillatus*, *P. flavus*, *D. merriami*, *D. ordii*; all P values < 0.01). All other species' trends were non-significant (all P values > 0.05).

Taylor series approximations including only the first term resulted in an average error of only 2.5% (range: 1-5%); including the second term reduced this error to 0.07% (range: 0-0.5%). This demonstrates that in this system $\overline{M^{3/4}} \approx \overline{M}^{3/4}$.

Discussion

The dynamics observed in this community appear to result from combining resource limitation with a change in the average size of an individual. Resource limitation is a valid assumption in arid systems (Beatley 1969; Brown 1987; Meserve et al. 1995; Polis et al. 1998), though resource availability tends to be temporally variable. This variation in resource availability results in the observed temporal dynamics in energy use by the community (Figure 2B) as well as in the variation around the long-term trends in both abundance and biomass (Figure 2C-D).

Perhaps the most striking pattern in this study is the 50% reduction in the average body size of an individual. Because we do not have data on the temporal dynamics of the resource base (e.g., seed size, spatial distribution of seeds, nutrient stoichiometry), we cannot rule out these factors as potential causes of the body size shift. However, based on the natural histories of the species at the site, the observed change in the distribution of individual body sizes is likely the result of the site's long-term transition from grassland to shrubland due to a shift in historical climate patterns (Brown et al. 1997). This vegetation change has resulted in decreased inter-shrub open space, where the larger species, the kangaroo rats, are the most dominant foragers (Brown and Lieberman 1973; Rosenzweig 1973) due to their well-developed suite of anti-predator adaptations (Bartholomew and Caswell 1951; Webster and Webster 1971; Kotler 1985). An increase in shrubby vegetation will not necessarily disadvantage large species in all systems, but in this case the habitat change seems to have shifted the competitive advantage to species that happen to be, on average, smaller (e.g., *C. baileyi, C. penicillatus*; Figures 1, 2A). While this size shift appears to dominate the observed pattern at long time scales, at shorter time scales the dynamics of the system are governed primarily by intra- and inter-annual variability in energy

use by the community, presumably driven by equivalent variability in the resource supply.

These dynamics emphasize that the distribution of body sizes of individuals is an important property of the community (Peters 1983; Griffiths 1986; Cyr and Pace 1993). In this community, the important changes in $f(M)$ result primarily from changes in the mean mass of an individual (because the first term of the Taylor expansions provide good approximations). Changes in the community's average mass through time could have resulted from two distinct processes: changes in the average size of individual species or changes in species composition. In this study, both processes appear to be occurring, but in opposing directions. Of the nine species occurring at the site during at least five six-month periods, four showed increases in their average size. This increase in average body size may have resulted from decreased competitive pressure from *D. spectabilis*, the largest granivore at the site, which has steadily decreased in abundance during the course of the study (P < 0.0001, Valone and Brown 1995). However, for the entire community, average body mass decreased through time as a result of compositional reorganization. The overall effects of the compositional reorganization and the increases in masses within species (especially in *D. merriami* and *D. ordii*) on the distribution of body sizes of individuals can clearly be seen by comparing $f(M)$ between the beginning and the end of the study (Figure 1, the shift in the ~40g mode results from the increase in body mass of the two *Dipodomys* spp.).

The fact that this distribution changed substantially over ecological time scales suggests that biomass, abundance, and energy use may not be equivalent measures of community structure and function. These measures do tend to be well correlated over time (all r^2s $\geq$ 0.46), and it clearly is simpler to assume that they all approximately gauge the biological activity of the community of interest. However, previous work and the framework presented above

demonstrates that these three community properties are tied together by a fourth community property: the distribution of body sizes of individuals (Peters 1983; Pagel et al. 1991; Cyr and Pace 1993; Taper and Marquet 1996). While relative constancy in the distribution of individual body sizes may be a reasonable first assumption, our results clearly show that this is not necessarily the case. In this study the change in $f(M)$ led to each of the three traditional measures of communities behaving differently through time: abundance increased, biomass decreased, and total community energy use remained relatively constant. This supports the idea that energy represents the primary constraint on this system (Ernest and Brown 2001), and demonstrates how other properties can trade off to maintain relative constancy or homeostasis of energy flux through the community. To understand community responses to environmental change, it is necessary to understand the mechanisms that regulate these currencies, rather than assuming that they all behave equivalently.

Furthermore, these results have potential implications for understanding species richness, an additional community property that appears to remain relatively constant at a site through time (e.g. Diamond 1969; Frost et al. 1995; Brown et al. 2001). Species richness is often thought to be determined by the influence of resource availability on abundance and biomass (Wright 1983; Currie 1991; Blackburn and Gaston 1996; Srivastava and Lawton 1998; Kaspari et al. 2000). However, if abundance and biomass can change in response to changes in $f(M)$ to satisfy a single energetic constraint, then it is interesting to ask whether species richness is ultimately determined by the partitioning of energy or by the more commonly considered properties, abundance and biomass (Blackburn and Gaston 1996; Srivastava and Lawton 1998). We cannot adequately address this question here due to the low variation in species richness in our system. However, it is relevant to note that species richness at Portal has not changed directionally

through time (OLS regression; S = -0.004t + 7.3; P = 0.76), despite a near doubling of abundance and a significant reduction in biomass. Clearly the idea that a fixed amount of resource leads to a fixed abundance, which leads in turn to a fixed richness, is not supported by our data.

While our approach assumes that this community is predominantly resource limited, many studies have shown that consumers can have important impacts on lower trophic levels (e.g. Paine 1966; McNaughton et al. 1989; Vanni et al. 1990; Kitchell and Carpenter 1993). Because we do not have an independent measure of resource availability, only resource utilization, we cannot rule out the possibility that higher trophic levels are regulating the dynamics of the community. However, this seems unlikely, especially given observed changes in shrub density, average rodent size, and rodent species composition, which would be expected to affect predation rates. Regardless, the predictions of the framework follow solely from the observed constancy in energy use and are not dependent on the process generating this constancy.

We have attempted to use allometric relationships to better understand general properties of communities. However, the application of allometries to communities requires knowledge of the underlying distribution of body sizes of individuals within the community (Cyr and Pace 1993). In our desert rodent community it was possible to accurately characterize aggregate community properties using only the mean mass of the community. However, in some cases the mean mass is insufficient (Cyr and Pace 1993), and the only way to determine whether or not the average mass is adequate is to assess the error on the Taylor expansions (Savage 2004). Regardless, the distribution of masses in this and other animal communities tends to be complex (e.g. Griffiths 1986; Cyr and Pace 1993) and surprisingly dynamic (Figure 1). Thus, if the distribution of masses is unknown, allometric approaches to studying communities will

inadequately reflect actual community properties and dynamics (Cyr and Pace 1993).

Our study suggests that energetic constraints are important in desert communities. Despite strong directional changes in composition and structure (Thibault et al. In press), and a 50% reduction in the average mass of an individual, energy use did not change directionally through time. By examining the dynamics of the community in the context of this constraint we can begin to understand the emergent properties of the system (abundance, biomass, etc.) and make quantitative predictions about how they can trade off to maximize use of the available resources.

Acknowledgments

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Table 1. Results of power function non-linear least squares regressions between community properties and six month period.

Variable	Exponent	95% CI	r^2
Mean Mass ($\overline{M}$)	-0.30	(-0.34, -0.26)	0.83
Energy Use (E_{tot})	-0.05	(-0.17, 0.07)	0.01
Abundance (N_{tot})	0.22	(0.06, 0.37)	0.15
Biomass (M_{tot})	-0.14	(-0.25, -0.02)	0.10

Figure Legends

Figure 1. Plot of the estimated probability density function for the mass of the granivorous

rodents at Portal, AZ in 1978 (solid gray line) and in 2002 (dashed black line). The

density was estimated using standard kernel density estimation, with a normal kernel and

a bandwidth of 5 (the optimal bandwidth for estimating normal densities for the 2002

data; Silverman 1986). This technique involves centering a normally distributed

probability density function (the bandwidth controls the width of this function) on the

mass of each individual in the community and taking the normalized sum of these

densities at evenly distributed points along the mass axis to estimate the probability

density (Silverman 1986). This technique produces results similar to those of a histogram

using a default bin-size, but these results are not sensitive to the placement of bin-edges.

Figure 2. Temporal trends in average mass (A), total community metabolic rate (B), abundance

(C), and biomass (D) from 1978 to 2002 for the granivorous rodent community at Portal,

AZ. Regression lines represent significant power function relationships to the data (non-

linear least squares).