HOMEOSTASIS AND COMPENSATION: THE ROLE OF SPECIES AND
RESOURCES IN ECOSYSTEM STABILITY

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Abstract. A synthesis of community and ecosystem ecology should yield insights into
the role of species in ecosystem function. Concepts from these subdisciplines of ecology,
specifically species compensation and ecosystem homeostasis, can be linked by analyzing
the effect of changes in the abundance of species on ecosystem processes. Compensatory
changes in species populations in response to environmental fluctuations can maintain an
approximate steady state between rates of resource supply and resource consumption. We
predict that ecosystem-level properties, such as species richness, total population, biomass,
and energy use, will exhibit less variability in response to environmental change than will
species composition. We tested this prediction using long-term data of a desert rodent
community responding to natural environmental fluctuations and of a plant community
responding to experimental manipulations. For the rodents, species composition was twice
as variable as the ecosystem properties. This result was the same for both the analysis of
variability around the 22-yr average and the analysis of variability from one time period
to the next. For the plant communities, species composition was more variable among
treatments in most years than stem count or species richness. Using the variance ratio
proposed by J. L. Klug et al. we detected negative covariances in the rodent community,
confirming the presence of compensatory dynamics.

Key words: community ecology; competition; desert rodents; ecosystem ecology; ecosystem
homeostasis; ecosystem instability from resource competition; energy flow through ecosystems;
linking community ecology and ecosystem ecology; resource consumption; species compensation;
stability of ecosystem-level properties; winter annuals.

INTRODUCTION

Ecosystem and community ecology have separately contributed much to our understanding of ecological
systems. However, linking these disciplines has proven to be challenging (Ehrlich 1986, Huston et al. 1988,
of energy and materials among organisms affect the structure and dynamics of ecological systems, the units
of study, the nature of the important interactions, and even the fundamental currencies of these subdisciplines
have traditionally been different. While community ecology typically focuses on interspecific interactions
that affect the population dynamics of species, ecosystem ecology typically studies exchanges of energy
and materials among broad functional groups. When these obstacles are overcome, interesting insights often
result, making a synthesis between these subdisciplines an important endeavor (e.g., Carpenter et al. 1987, Vitousek 1990, Jones et al. 1994, Frost et al. 1995). Interest in the role of biodiversity in ecosystem function
has stimulated research to link ecosystem and community ecology (e.g., Naeem et al. 1994, Tilman and
of biodiversity on ecosystem function have focused on the increasing variability in ecosystem properties
with decreasing biodiversity. There is an alternative perspective that explains ecosystem stability, not
so much as a result of biodiversity, but as a result of compensatory population dynamics of interacting species.

There is a large literature on the stabilizing effect of species interactions on ecosystem processes. Most of
these studies use models of interacting populations of species to examine potential effects on ecosystems
(e.g., Austin and Cook 1974, O’Neill and Giddings 1979, Post and Pimm 1983, Watson and Lovelock 1983,
Loreau 1996, Hughes and Roughgarden 1998, Ives et al. 1999). In these models, ecosystem stability is maintained
via compensatory population dynamics of the species in the system. The difficulty of manipulating
species interactions in an ecosystem helps to explain why few studies empirically test these ideas (but see
Frost et al. 1995). In this paper we propose and test a conceptual framework that explains how compensatory
interactions among species produce ecosystem stability or homeostasis.

The framework

There is a long history in ecology of attempting to model ecosystem properties as the outcome of species
interactions. Many of the elements of our framework have been considered by others (e.g., Austin and Cook 1974, O'Neill and Giddings 1979, Frost et al. 1995). Like them, we attempt to construct a framework based on fundamental processes that operate in nearly all ecological systems: (1) resources are required for growth, maintenance, and reproduction of individuals, (2) some of these resources are in limited supply and species compete for them, and (3) no two coexisting species have identical requirements for resources and other environmental conditions. Using these longstanding and easily justified assumptions, it is possible to link ecosystem processes to the compensatory population dynamics of species.

Ecosystem homeostasis and community compensation have long traditions in their respective subdisciplines of ecology. Homeostasis describes the tendency of an ecosystem to maintain the approximate stability of certain properties, such as productivity, energy or nutrient flux, or biomass, despite abiotic environmental perturbations or changes in biotic composition (e.g., Odum 1969, Oechel et al. 1994). By definition, homeostasis is maintained by compensatory mechanisms operating within the system. Compensation is the tendency of coexisting, competing species to exhibit negative covariances in population dynamics, so that variables that reflect resource use, such as total population size or biomass, are more stable than would be expected from random shifts in species composition (e.g., Schindler 1987, Frost et al. 1995, Hooper and Vitousek 1997, Klug et al. 2000). These compensatory changes in species populations imply that resources are limiting.

Consideration of competition for limited resources in a changing environment can elucidate how species compensation can lead to ecosystem homeostasis (O'Neill and Giddings 1979, Frost et al. 1995). The Malthusian-Darwinian dynamic drives individuals to maximize their fitness, resulting in populations tending to approach the maximum size permitted by the availability of limited resources. If populations of all species maximize resource intake, then the resource use of the entire community will also be maximized, resulting in an approximate steady state between rates of resource supply and resource use. This can be stated more explicitly as:

\[ R = C_{m} = C_{1} + C_{2} + C_{3} + \ldots + C_{n} \quad (1) \]

where \( R \) is the rate of resource supply measured in units of energy or material per time, \( C_{m} \) is the total rate of consumption by all species, and \( C_{i} \) through \( C_{n} \) represent the rates of consumption of species 1 through \( n \). If \( R \) remains constant, then the \( C_{s} \) of the different species will co-vary so as to maintain the equality. The relation in Eq. 1 implies that all species share requirements for the same resources, and that as \( R \) changes, the total consumption of the community tracks those changes in resources. This, of course, assumes there is no lag in the response of species to changes in environmental conditions. This is probably a reasonable assumption for species with a high rate of increase or high dispersal ability. But it may lead to more complex dynamics when species have low intrinsic rates of increase or poor dispersal abilities.

The process modeled in Eq. 1 results in both competitive compensation and ecosystem-level homeo-stasis only if some ecological process causes or allows the abundances of the constituent species to change while the resource supply \( (R) \) remains constant or nearly so. This can occur because fewer environmental variables affect rates of productivity or resource supply than affect the abundances of species in the community. Thus, for example, rates of primary production are affected primarily by the availability of sunlight, water, and nutrients, but the abundances of individual plant species are influenced by many other variables, including competitors, herbivores, pathogens, pollinators, seed dispersers, and diverse abiotic conditions that affect many aspects of the life history. Similarly, resource availability to consumers and rates of consumption depend largely on primary production and some general features of the plant community, but the abundances of individual consumer species depend on many additional biotic and abiotic variables that represent important dimensions of their niches. So it is likely that a modest change in environmental conditions, such as a shift in temperature, pH, or salinity, or an invasion of a competitor, predator, or pathogen, may cause substantial changes in the abundance of individual species, and create the opportunity for compensatory changes in other species, without significantly altering overall productivity or resource availability. However, even if resource availability does vary with changes in environmental conditions, Eq. 1 should still hold—individuals respond to the changes in resource level and environmental conditions that lead to new and different levels of consumption and the new \( C_{s} \) will sum to the new \( R \). In other words, compensatory dynamics should still occur as the community responds to changes in both \( R \) and in environmental variables, and the covariances of the species should be more negative than if the species responded randomly. Compensation should result in less variability in community-level properties than in the abundances of individual species and the species composition of the community.

For organisms in the same taxonomic unit or functional group, \( C_{i} \), the consumption by a population of species \( i \), depends primarily on two parameters: the population size of species \( i \), \( N_{i} \), and the average body size of individuals of species \( i \), \( M_{i} \). This can be expressed as

\[ C_{i} = aN_{i}M_{i}^{h} \quad (2) \]

where \( a \) is an allometric constant (see Peters [1983] for values), \( M_{i} \) is the average body mass of the individuals in the population, and \( h \) is the allometric ex-
ponent (an approximate equality is used because the average mass raised to power $b$ does not always exactly equal the sum of the individual masses raised to that same power). The equations presented above, especially the relationship in Eq. 2, imply that compensation by competing species results in a homeostatically regulated relationship between resource supply and total resource use by the community. Eq. 2 shows that the energy use of each constituent species is a function of both the population size of a species and the average body size of an individual of that species. Some studies have shown that the distributions of abundances and body sizes among species within communities often remain relatively constant as environmental conditions fluctuate and species composition changes (May and MacArthur 1972, Brown 1975). If that is the case, the total abundance, the number of individuals of all species $N_m = \sum_{i=1}^{n} N_i$, and the total biomass, the sum of the weights of all individuals in the community $B_m = \sum_{i=1}^{n} B_i = N_m \bar{M}_i$, should track resource availability, with some variation due to differences among species in body size. Also, if the number of common and rare species remain relatively constant, then the total species richness, $S$, will tend to be approximately preserved. We will return in the discussion to consider briefly the mechanisms that may constrain the distributions of $N_i$ and $M_i$ and determine $S$ in ecological communities. For the moment, however, it is sufficient to note that Eqs. 1 and 2 imply that compensation among competing species leads to regulation of ecosystem properties: homeostasis for total resource consumption, and only limited variation in total population size, biomass, and species richness so long as productivity and resource availability remain relatively constant.

While variables that index resource consumption are constrained by resource availability, there are no such constraints on species composition. Indeed, we know from experimental and nonmanipulative studies that environments that have similar rates of resource supply but differ in other conditions, such as abiotic stress or disturbance regime, can have largely nonoverlapping species compositions (e.g., Connell 1978, Pickett and White 1985, Rodriguez and Lewis 1997, Sagarin et al. 1999). The relative competitive status of each species in the community is influenced by abiotic and biotic factors that can, and typically do, fluctuate over time and space (Connell 1961, Paine 1966, Wiens 1977, Grant and Grant 1996). Differences in abiotic conditions or presence of particular predators can radically alter the outcome of species interactions, causing large shifts in relative abundance and even leading to local extinction of some species and colonization by others (e.g., Paine 1966, Chase 1996, Brown et al. 1997). In fact, Eq. 1 implies that compensatory change in the relative abundances of species is an important mechanism for ecosystem homeostasis in consumption. This leads to the empirically testable predictions that in the most simple case, if overall productivity and rates of resource supply remain relatively constant, ecosystems will maintain a relatively constant total resource consumption, total abundance, biomass, and even species richness of the competing species within a guild or functional group. Such homeostasis will be due to compensatory fluctuations, including local extinctions and colonizations, of the competing species. Since resource availability does vary, we do not expect community-level properties to be constant. We do predict, however, that as the environment changes, species composition will fluctuate much more widely than the ecosystem-level variables that reflect the utilization and allocation of limiting resources.

We used long-term data from rodent and plant communities from our study site near Portal, Arizona, USA, to explore the variability in species composition and ecosystem-level variables. Data from the rodent community gave a 22-yr record of rodent response to natural environmental variation (Brown et al. 1997). Data from the two seasonal communities of annuals gave 9- and 10-yr records of plant response to experimental removal of seed-eating rodents and ants, allowing us to compare plant response across experimental treatments where resource levels were virtually constant but differential predation had altered species composition. Since all three communities are characterized by high intrinsic rates of increase, time lags in response to changes in environmental conditions should be minimized. Using these three data sets, we tested the following predictions: (1) if species are compensatory units in ecosystems, then in response to natural or experimental perturbations species composition should fluctuate with greater amplitude than ecosystem-level variables such as energy consumption, biomass, total abundance of all individuals in the community, and species richness; and (2) covariances among species in variables, such as energy utilization or biomass, that index resource use should be more negative than expected if species fluctuations were random (Klug et al. 2000).

**Methods**

**Study area**

Data on rodent abundance since 1977 and plant species abundance since 1989 have been collected by J. H. Brown and associates at a study site 6.5 km east and 2 km north of Portal, Cochise County, Arizona (USA). The site, at elevation 1330 m, is a mixture of Chihuahuan Desert shrubland and arid grassland situated on the Cave Creek Bajada. Within the site there are 24 experimental plots, each with an area of 0.25 ha. These plots have been subjected to experimental manipulations of two guilds of seed predators: ants and rodents.

In each plot, rodents were sampled on one night each month. Annual plants were sampled biannually (spring
and late summer) on 16 permanent 0.25-m² quadrats within each 0.25-ha experimental plot. For additional details on the study site, experimental manipulations, and sampling methods see Brown (1998).

Rodent community: response to natural perturbation

We analyzed temporal variation in the unmanipulated rodent community, which has experienced substantial change in climate and vegetation (Brown et al. 1997). Over the last two decades there was a large increase of woody vegetation in apparent response to higher-than-average winter precipitation. Coincident with these shifts in vegetation and climate, the rodent community has experienced considerable turnover in species composition. Several grassland species have decreased or gone locally extinct, while several shrub-affiliated species have increased or colonized.

To satisfy the requirement that species must be competing for a limiting resource, we included only the granivorous species in the community: Baiomys taylori, Dipodomys merriami, D. ordii, D. spectabilis, Chaetodipus baileyi, C. hispidus, C. intermedius, C. penicillatus, Perognathus flavus, Peromyscus eremicus, P. maniculatus, Reithrodonomys megalotis, and R. fulvescens. Studies of granivorous rodents have shown that these species overlap in their resource and microhabitat use (Brown and Lieberman 1973, Brown 1975, Reichman 1975, Lemen 1978, Price 1978). While not every pair of species may compete intensely, there is the potential for some species to use resources made available by declines in other species. While organisms in other taxa, such as ants and birds, also use seed resources, evidence suggests that at Portal competition between rodents and these other organisms is much less intense than competition among the different rodent species. For example, removal of kangaroo rats resulted in compensatory increases in other rodent species, but little or no increase in granivorous ants or birds (Thompson et al. 1991, Valone et al. 1994). To eliminate differential responses to experimental manipulations, such as the removal of kangaroo rats mentioned above, we included only data from the 10 plots to which all species of rodents had equal access for the entire period (1977–1998). Rodents were sampled monthly, but data were combined into 6-mo periods, January–June and July–December, creating 43 periods for the analysis.

The values for the following variables were calculated for each month within a period and then averaged to obtain a value for the 6-mo interval:

a) Species richness ($S$): the number of species;
b) Total population ($N_{tot}$): $N_{tot} = \sum_{i=0}^{S} n_i$;
c) Biomass ($B_{tot}$): $B_{tot} = \sum_{i=0}^{S} b_i = N_{tot} \bar{M}$, where $\bar{M}$ for each species was obtained from Brown and Nicoletto (1991);
d) Total energy consumption ($C_{tot}$): calculated for each species using Eq. 2 and then summed over all species; and
e) Species composition: the relative abundance of each species.

To assess the temporal variability in these measures, we needed a standardized method to compare the univariate measures (species richness, density, biomass, energy consumption) of ecosystem response to a multivariate measure of species composition (where each axis represents the proportional abundance of a different species). The Euclidean distance (ED) equation calculates an absolute distance between points in one or many dimensions. This distance is simply a measure of the magnitude of difference between samples of interest. The ED equation can be expressed as

$$ED = \sqrt{(a_1 - a_2)^2 + (b_1 - b_2)^2 + \ldots + (z_1 - z_2)^2}$$

(3)

where $a_1$, $b_1$, and $z_1$ are values from sample 1 and $a_2$, $b_2$, and $z_2$ are values from sample 2. For the univariate measures, there is only one parameter: $a$. For species composition, each axis (i.e., each different letter) represents the relative abundance of a different species.

To examine the overall variability in the rodent community, for each variable we calculated distances for each time period from the long-term average (i.e., sample 2 in the ED equation was the 22-yr average for either species richness, total population, biomass, total energy use, or species composition). This yielded 43 distances for each variable. We divided the 43 distances for each variable by the standard deviation of the distances for that variable. This converted the distances into standard-deviation units and corrected for differences among the variables in the magnitude of the absolute values.

To examine the change from one time step to the next, we calculated the ED between consecutive time periods for each variable (i.e., sample 1 and sample 2 in the ED equation were the values for either species richness, total population, biomass, total energy use, or species composition from time periods $t$ and $t + 1$, respectively). This yielded 42 distances for each variable. As with the distances from the long-term average, we standardized for differences in absolute values among the different variables by expressing all distances in standard-deviation units.

To quantify the occurrence of compensation, we need to document the occurrence of inversely correlated population dynamics. One possible method is to look for negative correlations among species. Unfortunately, the positive semi-definite constraint on correlation matrices makes it difficult to detect negative correlations among multiple interactors (Brown et al. 2001). Instead, we used an equation proposed by Klug et al. (2000), which they refer to as the "variance ratio":

$$Var\left(\sum_{i=1}^{S} S_i\right) / \left[\sum_{i=1}^{S} (Var \; S_i)\right].$$

(4)

The variance ratio is a simplification of an equation.
that describes the variance of individual components with respect to the variance of the summed total. If the covariance among the individual components is 0 (i.e., species vary independently) then the variance ratio is 1. If the covariances among species are negative (i.e., species are compensating) then the variance ratio is <1. Using this equation, we tested for compensation among rodent species for the variables abundance, biomass, and energy use.

Plant community: response to experimental perturbation

The data on annual plants allow us to make simultaneous comparisons among replicated experimental plots. Within any given year, resource availability and other environmental conditions, except for seed predators, are replicated and therefore virtually constant across the experimental plots. The long-term experimental treatments have excluded different combinations of seed-eating animals (ants, rodents, kangaroo rats (Dipodomys), kangaroo rats and ants, rodents and ants, and unmanipulated control) on different plots. Until the mid-1990s these had major effects on the species composition of the winter annual plant community but only minor effects on the summer annual community (Brown et al. 1986, Guo et al. 1995, Brown 1998). In 1985 and 1988, the experimental manipulation applied to some plots was changed. For the purpose of this study, we only included those plots that experienced the same experimental manipulation for the entire 22 yr. Because this restricted us to small sample sizes, replicate plots were pooled to create mean values for each treatment.

In the Chihuahuan Desert there are two discrete seasons for precipitation, winter and summer. Because the drought during the spring and fall kills most annual plants, there is very little overlap in the species composition of the summer and winter plant communities (Guo and Brown 1996). Because of the pronounced differences in environmental conditions and species composition, we analyzed the summer and winter communities separately. We used data from each community for 1989–1998. We excluded the 1996 winter data because a lack of winter rains resulted in essentially complete failure of the annual plant crop for that season. For the plant analyses, each year was treated as an independent unit. This allowed us to assume that resource availability was constant for all treatments. Due to the small size and homogenous topography of the study area, there is no reason to believe that, for the annual plants, there was any significant spatial variation in resource availability among the experimental plots.

Annuals were censused twice each year, at the end of the winter and summer growing seasons (March or April and August or September, respectively). In each plot, annuals were counted on 16 permanently marked 0.5 × 0.5 m quadrats. A value for the plot was obtained by pooling the values for the 16 quadrats. Replicated plots of the same granivore-removal treatment were pooled to yield an average value for that experimental treatment.

For each year we calculated the following variables for each experimental treatment:

a) Species richness (S): total number of species;
b) Total population (Nm): total number of individual stems; and
c) Species composition: the relative abundance of each species, based on the total number of stems.

Within each year, we calculated the ED among the treatments for the above variables. Since there were five treatments, this resulted in 15 distances for each variable. As with the rodent data, we standardized these distances by expressing them in standard deviation units.

Additional details of the study site, experimental design, sampling methods, and plant communities can be found in Brown 1998 and included references.

RESULTS

Rodents

Variables that reflect the response of all seed-eating rodents to environmental variation deviated only modestly from the 22-yr averages, while species composition exhibited substantial fluctuation (Fig. 1A). Variation in species richness, total population, biomass, and energy use was amazingly similar: average distances from the long-term mean ranged between 1.09 and 1.38 standard-deviation units (SDU). In contrast, variation in species composition was more than twice as high: 2.82 SDU. A similar pattern is shown when distances between consecutive time periods are used (Fig. 1B). Variation in species richness, total population, biomass, and energy use ranged from 0.91 to 1.10 SDU, while the average variability for species composition was 2.11 SDU. Plotting the deviations from the long-term average, Fig. 2 shows the relative variation among the 6-mo sample periods for ecosystem-level variables in comparison to variation in species composition. Note that the pattern of seasonal variation in abundance, biomass, and energy use was closely correlated (Table 1). Species richness was significantly correlated with total abundance but was not correlated with any other variables. Examination of the distances for each time period shows that for total abundance, biomass, energy use, and species richness most values were within two standard deviations of the mean (Fig. 2). In contrast, values for species composition were consistently higher than 2 SDU.

Examination of particular time periods with similar energy use shows that these occurred with large differences in species composition (Fig. 3). For example, during four periods energy use by all granivorous rodents varied less than 5% (Eo = 1062–1091 W) but the composition of the community was very different:
Dipodomys spectabilis went from being the first or second most abundant species in 1979–1981 to extinction in 1995; energetic compensation was provided by increases in several other species (notably Chaetodipus penicillatus, Reithrodonotomys megalotis, Perognathus flavus, and, very recently, C. baileyi).

Negative covariances provide additional evidence for competitive compensation. A variance ratio of < 1 supported the prediction that compensation occurred among these species. The ratios for biomass and energy use were 0.80 and 0.90, respectively, well within the range reported by Klug et al. (2000) as indicating the occurrence of compensation. The variance ratio for abundance was 1.80, not indicating compensation. Because of Eqs. 1 and 2 and the trade-offs among body size, metabolic rate, and abundance, however, even if compensation in resource use occurs it may not be reflected in negative covariances in abundance. This will be especially true in communities with species of very different body size where the energy used by an individual of one species is not equal to the energy used by individuals of other species.

Plants

Winter annual community.—The winter annual plants showed less variation among experimental treatments in total population and species richness than in species composition (Fig. 4A). In all nine years, species richness and total population had smaller average distances among treatments than did species composition. Interestingly, the effect of the granivore-removal treatments on species composition differed greatly among years (Fig. 5). In 1990, following a dry season and several years of high rodent abundance, there were few total plants, and large-seeded species such as Astragalus nuttallianus, Erodium cicutarium, and Erodium

![Graph showing average distance in SDU for five ecosystem-level variables during the period 1977–1998 for granivorous rodents at Portal, Arizona, USA.](image)

**Fig. 1.** Average distance in standard-deviation units (SDU) for five ecosystem-level variables during the period 1977–1998 for granivorous rodents at Portal, Arizona, USA. (A) The average distance from the long-term means. (B) The average distance between consecutive time periods. Each vertical line is 1 SDU.

![Graph showing distance from the long-term average at each of the 43 time periods for four ecosystem-level variables of rodents in comparison to variation in rodent species composition.](image)

**Fig. 2.** Distance from the long-term average at each of the 43 time periods for four ecosystem-level variables of rodents in comparison to variation in rodent species composition. The dashed lines bound the region within 2 SDU of the long-term mean.

<table>
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<th>Species composition</th>
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<tr>
<td>Species richness</td>
<td>...</td>
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<td>0.21</td>
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</tbody>
</table>

* P < 0.05 after Bonferroni correction.

![Graph showing correlation matrix for rodent community variables using standard-deviation distances from the long-term average.](image)
Fig. 3. Relative abundance of the seven most abundant granivorous rodent species during the time span of 1977–1998 for four 6-mo periods with similar energy use. The distance from the long-term average for each time period is shown for species composition and the total energy use of the community ($E_{\text{tot}}$).

texanum were much more abundant on plots where kangaroo rats or all rodents had been removed than on ant-removal or control plots. In 1993, following a wet season and two years of low rodent abundance, plant species composition was quite similar across all treatments. When data points for the average distance of each treatment from all other treatments are plotted, it is apparent that in most years values for species richness and total population were substantially less variable than those for species composition (Fig. 6). For species richness and total population, treatments were usually within 2 SDU of each other, whereas distances
for species composition showed larger deviations. The large differences in species composition among treatments within years have also been demonstrated by the multivariate analysis of Guo and Brown (1996).

*Summer annual community.*—Guo and Brown (1996) found no difference between the treatments in species composition for the summer annual community. Where our data and theirs overlap (1989–1991), we also found that the variability between treatments in species composition was not substantially greater than the variability of total population or species richness (Fig. 4B). However, beginning in 1993, differences between treatments in species composition began to appear. This trend was especially evident when the average distances for each treatment are examined (Fig. 6B). There appeared to be a gradual increase in the variability among treatments in species composition beginning in 1993. During this same time period, there was no noticeable increase in the variation (distance from other treatments) for either total population or species richness. This is shown by comparison of species composition among the different treatments in
Fig. 5. Relative (proportional) abundance on the different experimental treatments of the seven most abundant species. (A) Results for the winter annual community in the years 1990 (dry) and 1993 (wet). (B) Results for the summer annual community in the years 1992 and 1993.
1992 and 1993 (Fig. 5B). In 1992, all treatments were dominated by the same two species. In 1993, more species were abundant on the study site, and there were substantial differences among the treatments in the rankings of those species.

**DISCUSSION**

The results support the predictions based on compensation: competition for limiting resources in a changing environment leads to homeostatic properties of ecosystem-level variables linked to energy use. In response to natural perturbations, the rodent community maintained relatively stable but not static levels of species richness, total abundance, biomass, and energy use. The fact that these ecosystem-level variables were maintained within narrow limits despite the much wider amplitude of changes in species composition implies that compensatory fluctuations of the individual species resulted in ecosystem homeostasis. These results are consistent with observational data of the rodent community. Except for a brief decrease in density, biomass, and energy use in the mid-1990s, these variables have exhibited relatively modest and closely correlated fluctuations (Fig. 7). In contrast, the relative abundances of the seven most abundant species have fluctuated widely over the 20 yr (Fig. 3).

More direct evidence of compensatory dynamics comes from the variance ratios for energy use and biomass. Ratios of <1 in both cases indicates negative covariances among the species and less variability in
summer annuals are the same periods where multivariate analyses also detected no significant differences (Guo et al. 1995). This result suggests the Euclidean distance (ED) method can be used in this context to make quantitative comparisons between univariate (population density, biomass, energy, species richness) and multivariate (species composition) measures of ecosystem properties. Fourth, we have no direct measurements of total resource use for these plants. For reasons given above (see Introduction: The framework), we would expect this measure to be less variable than total population. This is especially true for annual plants, which are extremely phenotypically plastic and known to exhibit wide variation in individual size, within as well as among species, in response to local variation in resource availability and competition (Harper 1977). Therefore, the numerical compensation by the annual plants, like the changes in abundances of the rodent species, may underestimate the degree of compensation in consumption.

There is strong evidence from the literature that these results are not simply artifacts of our methodology or system. The results from this study are supported by similar observations in other systems. These have shown that while species composition may vary dramatically in response to natural changes in or experimental manipulation of environmental conditions, these fluctuations tend to be compensatory, so that relatively constant values of ecosystem-level variables are maintained (e.g., Copeland 1965, Schindler 1977, Chapin and Shaver 1985, Prins and Douglas-Hamilton 1990, Frost et al. 1995, Kelt 1996, Tilman 1996, Wardle et al. 1999). The generality of such homeostatic processes is evidenced by their occurrence in different habitats (e.g., desert, temperate rain forest, grassland, tundra, lakes, oceans) and in different kinds of organisms (e.g., perennial plants, annual plants, rodents, megarbivores, phytoplankton, zooplankton), lending credence to the assertion that homeostasis is a general property of communities and ecosystems.

While we propose that homeostasis is indeed a general property of ecosystems, we do not claim that homeostasis should occur in all circumstances. Our framework has several inherent assumptions. First, resources must be limiting. Our model is based on the assumption that organisms occur in a resource-limited environment, so there is a competitive pressure to utilize all available resources. Compensation is unlikely to be observed if, for example, a guild of species is under strong top-down control so that it is limited by predation rather than resource availability (Carpenter and Kitchell 1993). Second, for energy use and related community-response variables to remain constant, resource availability must also remain constant. In a resource-limited environment, we expect energy use and ecosystem variables to track fluctuations in resource availability. In our study, while energy-related variables were less variable than species composition, they

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The community properties than would be expected just from the variation in the individual components.

The response of plants to experimental manipulation also suggests that species compensation results in homeostasis of ecosystem-level variables. Three things are noteworthy. First, different environments created by selectively removing certain kinds of seed predators had large effects on species composition only in certain years (winter annuals: 1989, 1990, 1992, 1994, and 1997; summer annuals: 1993, 1994, 1995, and 1998). Just because the same press gravirole-removal experiments were maintained across all years, the effect of selective predation on particular plant species was mediated by other environmental conditions, resulting in different species composition on different treatments. Second, not only were the standard-deviation distances among treatments consistently greater for species composition than for species richness and total population, but also the deviations in the latter two variables were relatively constant, between one and two standard deviation units (SDU) in nearly all years and both communities. For the summer annual community, the low variability in species richness and total population is especially remarkable given the increasing difference in species composition between treatments over time. Third, the sample periods (1989–1992) where our analyses showed no significant difference among treatments for species composition of ecosystems.
were by no means constant. Fluctuations in primary production and food resources probably caused the peaks and troughs in rodent abundance, biomass, and energy use that we observed over the 22 yr of the study (Fig. 7). As stated above, however, even when resources vary individual species are responding not only to changes in resources but to changes in many other environmental variables, resulting in higher variability in species composition than in ecosystem-level properties. Temporal fluctuations in resource availability also affected the plant community, but they did not affect the present analysis because we made comparisons among experimental treatments within the same season. Third, communities are open systems. When environmental changes occur, it is likely that they will be detrimental to the resident species. Compensation will be more likely to occur if new species, better able to cope with the new conditions, have the potential to colonize from some regional species pool. In the present study, the role of colonization is indicated by the fact that only one rodent species, Dipodomys merriami, was present in every monthly census since the beginning of the study and only two species were present in every 6-mo period. If Portal (Arizona, USA) were a closed system with no access to species from a regional pool, compensation would have been limited to reciprocal shifts in abundance among the few species that were able to avoid local extinction.

There is a growing body of literature exploring the role of “functional redundancy” in ecosystem stability (e.g., Walker 1992, Naeem et al. 1994, Morin 1995, Naeem and Li 1997, Tilman et al. 1997). However, species compensation does not necessarily imply functional redundancy. While some of the compensating species may already be present in the community when environmental conditions change, the limited residence time of any one rodent species in our system means that much of the compensation must be due to immigration from the species pool. Similar patterns are seen for the annual plants although the seed bank might substitute in part for the regional pool in providing a source of new species able to exploit the new environmental conditions. While we do not specifically address whether most compensation occurs from changes in relative abundance among the species coexisting at the site or from local extinction and compensating colonization from the regional pool, our data do suggest that this is an important question for further research. Most studies of functional redundancy have occurred in systems where exchange of species with the regional pool is restricted, making it impossible to assess the importance of the regional pool in maintaining ecosystem function (e.g., Naeem et al. 1995, Naeem and Li 1997, Tilman et al. 1997, Wardle et al. 2000, but see Wardle et al. 1999). However, whether compensation is accomplished mainly by colonizers or residents, it does not change the fact that compensation depends upon the unique characteristics of each species that affect their interactions with the local environment, including competition with each other. Redundancy implies that species are functionally identical. Compensation requires that species be complementary and overlapping in their resource requirements but different in their environmental tolerances.

Our results also have implications for the role of species richness in ecosystems. The ecosystem-level variables considered include not only measures related to resource consumption but also species diversity. Taken together, Eqs. 1 and 2 demand precise compensation in energy use and less precise but bounded homeostasis of total abundance and biomass. These relations place no such limits on species richness. So how and why does species richness show little variability? We will not attempt a definitive explanation here, but will make two points. First, a large literature indicates similar distributions of “importance” among coexisting species, irrespective of taxonomic group or habitat (e.g., MacArthur 1957, Preston 1962, Williams 1964, Whittaker 1970, May 1975, 1986, Tokeshi 1990). “Importance” is typically measured in terms of relative population size, but sometimes in terms of other currencies, such as cover, biomass, and resource use. Note that when these are summed across all species they become the ecosystem-level variables that we expect to exhibit homeostasis. The seeming homeostasis of species richness is another manifestation of the general pattern of division of resources among coexisting species, and therefore of the various measures of “importance.” While several theories have been proposed (MacArthur 1957, Preston 1962, Williams 1964, Sugihara 1980, Tokeshi 1990), there is still no generally accepted explanation for this pattern.

The second point concerns the relationship between species diversity and ecosystem processes. Recently, several investigators have examined the effect of either natural or manipulated variation in species richness, and found that it is positively correlated with such ecosystem properties as drought resistance and stability of biomass, productivity, and energy or nutrient flux (e.g., Tilman and Downing 1994, Naeem et al. 1996, McGrady-Steed et al. 1997, Naeem and Li 1997). In effect, this approach treats species richness as the independent variable and the ecosystem-level property as the dependent response. Our results suggest an alternative perspective: that species diversity is one of those properties of ecosystems that tend to be homeostatically regulated. Despite fluctuations in the environment, the species in a community collectively tend to consume all available resources and thereby to maintain the relative stability of ecosystem processes. They do this through compensatory population dynamics, which include not only shifts in relative abundance but also colonizations that compensate for local extinctions. Most of the studies cited above were performed on systems where species richness was controlled, either in closed experimental units or in other coloni-
zation-limited systems. Our study suggests that in open systems where species composition is able to vary in response to environmental changes, fluctuations in relative abundance and local colonization/extinction events are mechanisms that maintain a relatively constant number of species so long as the supply of limited resources remains relatively constant and the environmental changes do not exceed the tolerances of the species in regional pool.

To show the links between species-level and ecosystem-level phenomena it is necessary to adopt currencies that are common to both population and community ecology on the one hand and ecosystem ecology on the other. Variables, such as total population, biomass, and cover, reflect the utilization of limited resources by a community. These currencies do not provide precise measures of energy or material resource use, primarily because of variation among individuals and species in body size. More precise estimates can be obtained using empirically derived allometric equations that describe the relationship between metabolic rate and body size. Because requirements of individual organisms for inorganic compounds (e.g., N, P, K) and other materials (e.g., essential amino acids and vitamins) have virtually the same allometric scaling exponents as metabolic rate (e.g., Peters 1983), this approach could be extended to investigate the role of species in other regulating ecosystem processes, such as nutrient cycling.

While progress in linking community and ecosystem ecology is being made, there is still much to be done. In this study, we have attempted to build on an existing set of literature that proposes ecosystem stability is the result of interspecific competition among species in a resource-limited environment. While our model is highly simplified, the empirical results suggest that this avenue of research may be very productive. We think that continued research based upon the fundamental currency of energy and upon basic biological principles can be very useful in linking community and ecosystem ecology.

ACKNOWLEDGMENTS
Special thanks to A. Ernest, E. Siemann, J. Parody, F. Smith, E. Charnov, M. Huston, J. Haskell, M. Molles, B. L. Li, and E. Toulson for discussion and helpful suggestions. The Portal Project has been supported by NSF grants, most recently DEB-9707406. S. K. M. Ernest was supported by these grants and by NSF DGE-9553623.

LITERATURE CITED


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