

## Hierarchy underlies patterns of variability in species inhabiting natural microcosms

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Relative variability of species has been shown to increase significantly with a decrease in their ecological range. Similarly, the distribution of collapse (e.g., extinctions, disturbances, population declines) magnitudes has also been shown to follow an inverse power-law form described by the  $1/f^\omega$  curve. We hypothesized that the two, possibly general, patterns associated with ecological systems share a common underlying cause: the hierarchical structure of the system itself. To test the hypothesis we used a model system of 49 natural rock pools inhabited by 40 species of invertebrates. Three measures of species variability based on changes in abundance, distribution, and persistence in individual pools conform with the postulated negative exponential curves. Correspondingly, frequency distributions of changes of various magnitudes conform to the  $1/f^\omega$  pattern. Examination of the contributions of species to the  $1/f^\omega$  pattern revealed that species low in the system hierarchy (habitat specialists in this case) are responsible for the majority of small variation events (correlations between the ecological range and position on the  $1/f^\omega$  curve range from 0.625 to 0.807 on the three measures of variability). This permits the conclusion that the two patterns are linked and constitute different expressions of the same hierarchical system structure.

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Studies on dynamics of species extinctions (and recolonizations) indicate that the frequency distribution of magnitudes of change (i.e., number of species lost or gained) fits a curve described by  $1/f^\omega$  where  $f$  is a frequency of occurrence of events and  $\omega$  is a positive scaling exponent, known as spectral coefficient, determining the curve concavity (Bak and Chen 1991, Drake et al. 1992, Cambel 1993, Jorgensen 1995, Keitt and Marquet 1996, Huxel et al. unpubl.). Such curves capture the regularity that there are many observations of small extinction events, i.e., extinctions involving a small number of species, followed by a declining number of events as the magnitude of extinction increases. This relationship is also found in the fluctuations of species and higher taxa diversity in the paleontological

record (House 1989, Raup 1991, Sepkoski 1992). Similarly the changes in species diversity (Sugihara and May 1990, Drake et al. 1992) and population abundances (Pimm and Redfern 1988, Maurer and Nott in press) over ecological time frames are described by an inverse power-law distribution.

The search for mechanisms generating the  $1/f^\omega$  pattern is the subject of current debate. An element absent from this debate is the consideration of attributes of the systems of interest. Hierarchy theory may help to include this aspect. Hierarchy theory is a collection of concepts, axioms, and models that focuses on relations among phenomena occurring at different scales or entities of different order (Voorhees 1983, O'Neill et al. 1986, Allen and Hoekstra 1992; see also Wiens 1989).

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Smaller scales or components of higher order entities are commonly referred to as lower levels (e.g., Wiens et al. 1993). One postulate of the hierarchy theory, apparently unrelated to the  $1/f^\omega$  pattern, is that processes occurring at lower levels of organization exhibit a higher frequency and greater magnitude of relative change (but much smaller absolute change) than those at higher levels of organization (Kolasa and Pickett 1989, Allen and Hoekstra 1992, Waltho and Kolasa 1994).

Because lower level components are necessarily more numerous than higher level ones, and because the curves describing the distribution of event magnitudes ( $1/f^\omega$  pattern) and the relationship between component position in hierarchy and its relative variability are similar, we speculate that these two patterns may actually be related through a common underlying cause – the underlying hierarchical structure (Fig. 1). The logical connections between abstract hierarchical conceptualization of communities and the operationalization of those abstractions to studies of multispecies systems are outlined and exemplified elsewhere (Pickett et al. 1994, Waltho and Kolasa 1994). Hierarchy theory offers a testable explanation of the  $1/f^\omega$  or inverse power-law, pattern: smaller but more frequent changes are tied to lower levels of organization (Allen and Starr 1982, Kolasa and Pickett 1989).

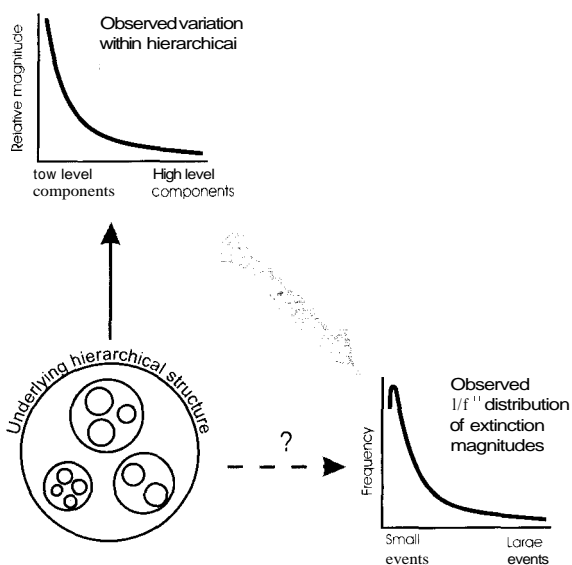


Fig. 1. Formulation of the general hypothesis and the mode of testing: the relationship among the structure of an ecological system, (ecological or spatial range: low level components – narrow distribution, high level components – broad distribution), variability of its components, and the frequency distribution of observed changes (e.g., small to large). The test consists of showing that there is a correlation between the position of the component in the hierarchy and its contribution to the  $1/f^\omega$  distribution (corresponding effect of items in one curve onto another).

We thus propose a specific hypothesis about ecological entities:

The frequency distribution of *magnitudes* of change (e.g., extinctions, recolonizations, fluctuations in abundance, contractions and expansions of ecological ranges) for any set of ecological entities is a function of and should be correlated with the position of these entities in the organizational hierarchy. Thus, lower level entities would contribute more to smaller, yet more frequent, events than the higher level entities and vice versa.

An entity can take many forms in an ecological system – it can be an individual, a population, a group of tightly interacting species, or other perceptibly integrated structures. The hypothesis stated above is anchored in the assumption that the pattern of variability is generated by predictable differences in the behavior of entities at various levels of organization (Kolasa and Pickett 1989), levels of organization which are explicitly definable in both space and time.

The test of this hypothesis is complex. Ultimately, it consists of demonstrating that the components lower in the system hierarchy are those that contribute more to the numerous small variations than the entities (system components) higher in the hierarchy. The test requires a model of hierarchical system structure based on some tangible variables. We view the habitat structure as a scaffolding populated by various species such that species occupying large portions of the habitat space are high in the hierarchy and species occupying smaller subdivisions of that space are low in the hierarchy. Here, species become components of a hierarchy and can be examined for their variability. The reason for this approach is the availability of a conceptual model and suitable data (see below). Before proceeding, we must decide how to verify species position in a so defined hierarchy of community structure and how to assess their respective contributions to the “ $1/f$ ” pattern. An alternative hierarchical community model (Sugihara 1980) could not be used as it is unclear how to determine the position of species in the hierarchy. Our strategy and procedures are presented in the Analysis section below.

## Data

### Setting

The study involved erosional rock pools formed on the fossil reef on the northern coast of Jamaica, West Indies, at the Discovery Bay Marine Laboratory. These pools are small in size (most are 20–60 cm in width and length and vary in depth from a few centimeters to no more than 50 cm). Forty nine pools were arbitrarily selected within a radius of less than fifty m (Fig. 2). The pools exhibit strong gradients of physical parameters

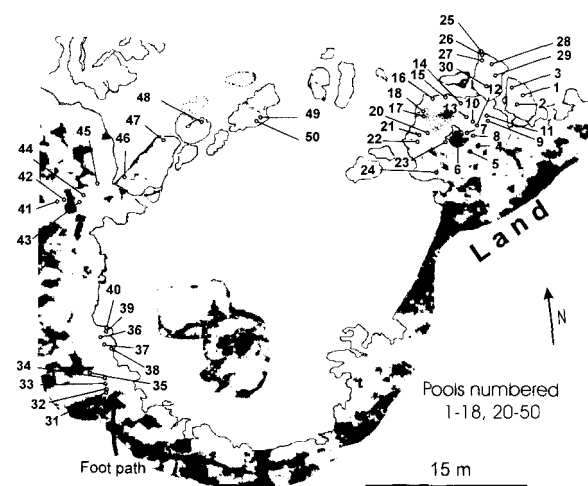


Fig. 2. Location of the rock pool communities used in the analysis. Numbers are permanent arbitrary pool identifications – detailed maps and pool photographs are available at the Discovery Bay Marine Laboratory, Univ. of West Indies, Jamaica.

(unpubl. data) making them particularly suitable for measuring the ecological ranges of species.

### Sampling

Physical measurements (oxygen, pH, salinity, conductivity, temperature, light intensity at the pool edge, water level, and bottom of the pool) were taken using appropriate YSI or HANNA meters on several occasions between December 1989 and June 1994. Most individual variable measurements were completed within an hour. Samples of fauna were collected on eight occasions but only the first three are used in this analysis (Dec. 1989, Jan. 1990, and Jan. 1991). All sampling was completed within one day. Each sample consisted of 1 liter volume of water and sediments from a pool slightly stirred to dislodge organisms from the pool sides and from sediments and to homogenize their distribution. Organisms were caught in a 63- $\mu$ m net with a collecting container and immediately preserved in 50% ethanol. Overall 147 samples were analyzed from 49 pools.

### Community

Forty-two species were identified and counted. These species belong to a variety of freshwater and marine taxa: Anthozoa (1), Hydrozoa (1), Turbellaria (2), Nematoda (1), Polychaeta (2), Oligochaeta (1), Ostracoda (17), Copepoda (5), Cladocera (2), Decapoda (2), and Insecta (8). The total of 89 811 individuals were obtained from samples and used in the subsequent analyses. One species of copepod constituted approximately 50% of all individuals sampled.

## Analysis

The analysis consists of these steps showing in sequence that: 1) the species are in different recognizable relative positions in the organizational hierarchy of a community; 2) the position of species is associated with the patterns of variability postulated by the hierarchy theory; and 3) the position of species in the community hierarchy determines their contribution to the distribution of magnitude change described by a  $1/f^w$  curve.

Each of these steps requires the adoption of specific assumptions, methods, and calculations. These are described in the sequence of the steps above and are then followed by other methods and considerations.

### Species position

Species position in the organizational hierarchy has been determined on the basis of ecological range as suggested by Kolasa (1989, Kotliar and Wiens 1990, Waltho and Kolasa 1994). This is analogous to the use of nested geographical ranges (e.g., Patterson and Brown 1991, Cutler 1996). Two alternative measures were used to estimate the ecological range of species. One is based on species distribution, as we assume that broadly distributed species have broader ecological range with respect to many ecological dimensions (e.g., competitors, food spectra, predators, ability to cope with a fragmented landscape, and physical parameters; Maurer and Nott in press). Thus distribution in space is an indirect indicator of species overall flexibility in using its habitat mosaic. Furthermore, distribution in space determines the potential interactions with other species, with broadly distributed species having a higher probability of range overlap with most species, and with other broadly species in particular. Such species form groups which, by definition, are higher order entities in the structural hierarchy. In this study we use the number of pools in which a species occurred as a measure of distribution.

The other measure of ecological range focuses exclusively on species individual responses to physical factors. The ecological justification for this is similar to distribution with species having broad tolerance limits being at higher hierarchical levels. In fact, the two measures, distribution and ecological range, should be correlated if the underlying hierarchy is 'robust to transformation', that is, independent of the viewing perspective (Allen and Hoekstra 1992). We derive the measure of ecological range from the principal component analysis (PCA) scores in the following manner. We first obtain scores by extracting five factors using orthogonal principal component analysis on the pool parameter matrix (46 variables: multiple measurements of physical variables mentioned earlier, total variance explained by five PCA factors: 88%). Each PCA axis was considered to be a dimension of habitat space and thus useful in assessing the ecological range of a spe-

ties. We then standardized the PCA scores to give each axis equal importance and thus avoid confounding effects of correlation among the measured variables on the importance of axes (Burgman 1989). To obtain the respective ecological ranges, species were 'projected' onto individual axes. This was done by replacing values in the species presence matrix with PCA score range values (max-min) found for a respective pool. Separate projections were performed for each PCA axis. Global minimum and maximum values over the whole pool system were then found for each species in each dimension. These values produced species ranges on each dimension. Estimating niche volume with all five axes was found to be inadequate (Kolasa and Drake unpubl.). Therefore we selected that PCA axis whose min-max species ranges turned out to be the best single predictor of species mean regional density ( $r^2 = 0.6070$ ).

### *Species variability*

There are several complementary measures of species variability, each providing different information and requiring a different interpretation. We evaluated the variability of three species attributes: abundance, distribution (number of sites), and local persistence (evaluated by magnitude of extinctions, i.e., the number of sites from which a species was lost compared to the last date sampled). For example, abundance characterizes mean survival, reproduction, and generation length, distribution characterizes tolerance limits and dispersal abilities, and local persistence characterizes a species' ability to resist or avoid catastrophic impacts. Note that distribution may be constant if high dispersal and establishment rates compensate extinctions. For these attributes we calculated the following parameters:

- *standard deviations* to determine frequency distribution of magnitudes of change – calculated for abundance and distribution;
- *coefficients of variation* to determine the correlation between position in the hierarchical structure and species variability; this is most appropriate when substantial differences in density exist among species (Walther and Kolasa 1994) – calculated for abundance and distribution;
- *number of pools* a species disappeared from one date of sampling to another (local extinction events). While species disappearances may not represent true extirpation of the species from the pool, they represent the number of instances in which the abundance was so low as to be indistinguishable from extinction (ecological extinction). The reappearance of a species may represent either a re-colonization or a recovery from extreme rarity. For pure convenience, we treat these events as extinctions (and colonizations) while recognizing that this is not necessarily the case. Note that, unlike in the case of whole faunas, extinction here is a species attribute. Changes in site occupancy

are often used to characterize species variability (e.g., Maurer and Nott in press), especially when presence-absence data are of interest.

We have examined the correlations between these measures of species variability and the measures of their ecological range. This analysis aims to determine whether the system in question conforms to the prediction from hierarchy theory concerning the link between structural levels and component variability (Fig. 1), a link which is a precondition for the main test of the hypothesis.

### *Hierarchical position vs frequency distribution*

This relationship cannot be examined directly. In order to determine whether there is a good correspondence between component behaviors underlying the two curves shown in Fig. 1, we first produced histograms of extinctions and standard deviations of range and abundance with approximately 20 intervals (often known as frequency spectra of variance). We then re-coded each species according to the frequency class of its standard deviation, SD, or the magnitude (number) of extinctions. For example, if a species SD for extinctions was  $0 < SD_{ext} < 1.1$ , then that species would be in the left-most 'class 1'. Similarly, if a species range SD was  $2.0 < SD_{ran} < 2.2$  (i.e.,  $0.2 \times 11$ ), the species would be in the eleventh class from the left, 'class 11'. Finally, we regressed the ecological range against these re-coded measures. This procedure would detect whether species that are low in the system hierarchy, and thus relatively variable, tend to contribute to the low end or high end of the  $1/f^\omega$  curve for variability in abundance, range, and persistence (as evaluated by the number of local extinctions). If such species contributed significantly to the high end (many small events or changes), the hypothesis would be accepted.

## **Results and discussion**

We found significant correlations between measures of species variability and their ecological range (Fig. 3, Table 1). This finding supports the first premise that species located at lower levels in the habitat (or system) hierarchy are relatively more variable. Indeed, such species should be and usually are more variable in absolute terms for other reasons such as selective extinctions of narrowly distributed species with large population fluctuations (e.g., Glazier 1986). The mean rate of extinction conforms less to the expectations than the two other measures of variability. It is possible to attribute this particular result to the coarse resolution or lower sensitivity of this measure compared to the others. Changes in abundance necessarily precede changes in presence or absence (cf. Rahel 1990) while changes in distribution express and gauge two pro-

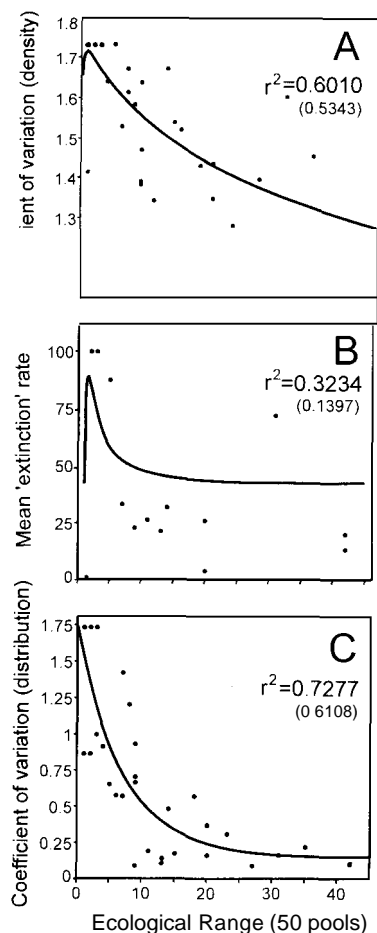


Fig. 3. Relationship among species relative variability and their ecological range. As the relationships are purely empirical, we report their form for the record. **A)** coefficients of variation in species abundance (two outliers were removed from the analysis), fitted equation:  $y^{0.5} = a + b(\ln x)^2$ , standard error of the fit 0.1119,  $F = 54.22$ . **B)** mean 'extinction' rate, fitted equation:  $y = a + b \ln x/x^2$ , standard error of the fit = 21.24,  $F = 18.16$ . **C)** coefficients of variation in range measured as the number of pools occupied, fitted equation:  $y = a + b x^{-0.5}$ , standard error of the fit = 0.3301,  $F = 49.44$ . Linear regressions were also highly significant but explained less variance ( $r^2$  values shown in parentheses).

Table 1. Correlations among the relative measures of species variation and the compound measure of ecological range. The compound measure of range is a product of distribution in rock pools and PCA scores based on physical parameters for the single most important axis (see text for the criteria of choice). Because hierarchy theory suggests a negative curvilinear relationship between the variation and position of the component in the hierarchy but provides no specific mathematical model, determination of the pattern remains, by default, empirical. The best fitting function was in all cases  $y = a + b x^{0.5} \ln x$ , indicating that the nature of the relationship does not change from one measure to another.

Variable	$r^2$ of the best fitting line (linear fit in parentheses)	Probability	Coefficients
Coefficient of variation in density	0.4795 (0.4887)	0.00020	$a = 1.63115$ $b = -0.07105$
Mean 'extinction' rate	0.2946 (0.2636)	0.00110	$a = 64.2226$ $h = -8.25707$
Coefficient of variation in distribution	0.6565 (0.6108)	0.00000	$a = 1.05662$ $b = -0.26126$

cesses: local disappearances and regional expansion through dispersal and establishment.

The shape of the curves is in general agreement with the expectations of hierarchy theory as outlined earlier and the curvilinear fits are better than linear ones, although not significantly so. The first premise of the hypothesis test is thus satisfied.

We have also found that the distributions of the three measures of change (abundance, extinctions, and range) exhibit a  $1/f^\omega$  trend (fitted by a linear equation of the form:  $\ln y = a + b \ln x$ ; Fig. 4). The equation fit for population density (not shown in the figure) is lower than that those for extinctions and changes in distribution (range). This is an artifact which results from log transforming the standard deviations in order to create a sufficient number of frequency classes. Non-transformed data fit the  $1/f^\omega$  curve with an  $r^2 = 0.9700$  ( $p < 0.000001$ ,  $N = 40$ ) indicating complete conformity with the expected signal. The spectral coefficients ( $\omega$ ) for all three measures of variability significantly differ from random ( $\omega = 0$ ) indicating a degree of organization (Hastings and Sugihara 1993). Specifically, the values of these coefficients range between 0.6331 for variation in distributional range and 2.119 for non-transformed standard deviations of density. These values correspond to white to red noise range in the temporal frequency spectra of variance discussed by Steele (1985) and Steele and Henderson (1994). It is unclear, however, if there is a connection between the patterns described by Steele and the patterns observed in the rock pools. The difference between the two types of pattern relates to the representation of scale: in the time series analysis scale is varied by increasing time intervals among data values used for calculation of variance while in our analysis the scale is defined by the magnitude of species attributes (persistence, distribution, abundance). Taylor (1961) has found that in collections of species variance is often related to the population mean by a power law such that variance is proportional to a fractional power of the mean. The frequency distribution of variance we observe appears to have the same qualitative properties, with abundant species ex-

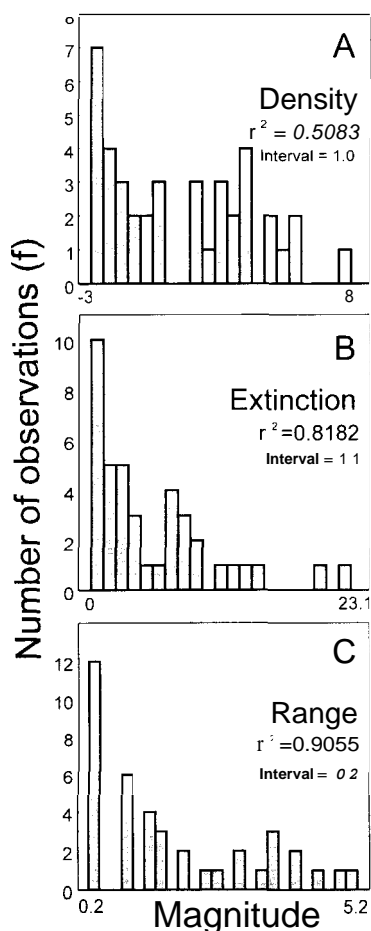


Fig. 4. Frequency distributions ( $f$ ) of the magnitude of change for: **A)** standard deviations of density (log transformed), **B)** the number of local extinctions per species, and **C)** standard deviations of distribution (occupancy) in the system of pools. All frequency distributions conform to the  $1/f^m$  curve fitted by  $\ln y = a + b \ln x$ . Correlations ( $r^2$  values), interval size, and the first and last values (Magnitude) for frequency classes are shown on the graph.

hibiting larger variance. Taylor's finding appears to indicate that higher level entities (broadly distributed species) exhibit larger absolute variability in space. Our observations complement this by showing larger absolute variability of such species in time as well.

The correlation between the position in the hierarchy, adequately represented by the distribution in pools (i.e., occupancy of), and the frequency classes of variability measures to which species contribute constitutes the ultimate test of the hypothesis. This correlation is statistically significant for all three criteria (Fig. 5, Table 2). Interestingly, this relationship is approximately linear, unlike the relationships between the range and measures of variability. This is expected if the underlying assumptions as to the origin of the two patterns are correct. The relationship among the rela-

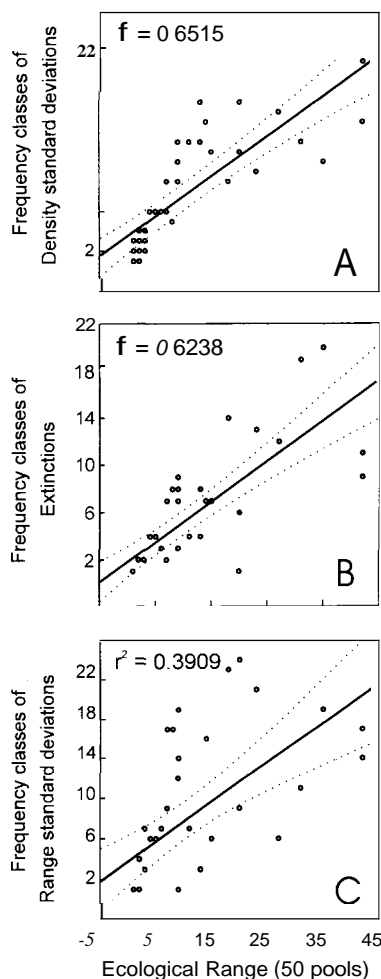


Fig. 5. Relationship between the ecological range and the frequency classes of magnitudes of change obtained for: **A)** extinctions, **B)** density (based on standard deviations), and **C)** shifts in the distribution (based on standard deviations). Frequency classes are determined from histograms shown in Fig. 4 (explanation in text).

tive measures of variability and the classes of absolute variability is weaker but sufficient (Table 2) to link the two types of curve shown in Fig. 1 (Correspondence arrow). The only exception is relative extinctions which were not significantly correlated with the corresponding magnitude classes. They were however correlated with variation in range and abundance ( $r^2 = 0.672$  and  $0.209$ , respectively).

The realization that the relative variability of components or entities (species in our system) and the distribution of variability magnitudes are linked has major implications for modeling, interpreting and investigating complex systems. For example, in food web analysis, patch dynamics or community models one would have to appropriately and differently scale parameters for habitat specialists versus generalists in order to account for the dramatic differences in their behaviors.

Table 2. Correlations among absolute measures of species variation and the compound measure of range (A–C) and among relative variation and classes of absolute variation (D–E; cf. the Correspondence arrow in Fig. 1). The compound measure of range is a product of distribution in rock pools and PCA scores based on physical parameters for the single most important axis (see text for the criteria of choice). The absolute classes of variation are based on standard deviations.

Variables	$r^2$ of the best fitting line	Probability	Coefficient beta
A. Standard deviation of density and compound range	0.184032	0.012734	0.002326
B. Total extinctions and compound range	0.541366	0.000001	0.263376
C. Standard deviation in distribution and compound range	0.297329	0.001032	0.752268
D. Frequency classes of standard deviations and coefficients of variation in density	0.17470	0.007281	–0.41797
E. Frequency classes of standard deviations and coefficients of variations in range	0.17198	0.00799	–0.41471

While we conducted this test using an aquatic, multi-species system, the relationship between the component position in the hierarchy (or more generally system scaling), component variability, and the relative component contribution to the distribution of system change (e.g., extinctions) may have much broader application. If our hypothesis is correct and structural hierarchy is the underlying factor behind the “ $1/f$ ” pattern, we may be able to describe differences among systems in terms of shape (spectral coefficient) of the curve relating entity position in the hierarchy and entity contribution to change.

Furthermore, an intriguing possibility emerges. If our results do in fact originate from a hierarchical organization, then the paradoxical difference between the observed power spectra and theoretically generated power spectra (Sugihara 1995) might be easier to explain. Natural data sets appear to be redshifted, that is, variability increases at larger time scales, whereas theoretical models produce spectra shifted in the opposite direction, towards ‘blue’ (Cohen 1995). Significantly, the models studied by Cohen (1995) lack one important aspect of natural systems, the hierarchical structure. It is thus possible that redshifted power spectra, first reported by Steele (1985), are also due to hierarchical organization. To verify this hypothesis one would need to demonstrate that species operating at higher levels of habitat structure do experience larger fluctuations but only at time scales larger than those of habitat specialists.

The rock pool system discussed herein is shown to be a dynamical system at various spatial and organizational scales. We believe that this is true of all ecological systems. Thus, the hierarchical approach taken provides a new means of comparing various such systems across scales. Comparisons of disparate systems may also provide insights into the relationship between hierarchy theory and the ubiquitous phenomenon of power-law scaling in ecological systems. The relationship between the hierarchical structure and the position of species in that structure, which we demonstrate, may

provide critical information on the assembly processes and differences between disparate systems which vary in complexity (such as coral reefs, tropical forests, and agroecosystems).

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