A community ecology perspective on variability in complex systems: The effects of hierarchy and integration

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ABSTRACT

The question of whether organization and degree of integration of ecological communities are related in a predictable manner to patterns of variability in abundance as well as to patterns of environmental variability is important for theoretical and practical reasons. However, a quantitative answer to this question is difficult as no single measure of organization and variability gained widespread acceptance. Ecological communities exhibit hierarchical structure and that structure can be interpreted as an index of integration and organization. Constituents of such communities show patterns of variability amenable to power spectrum analysis (often abbreviated as $1/f^\nu$, where $\nu$ is the power exponent characterizing contribution of events of different magnitudes to the overall pattern of variability). I postulated that richer, and thus more hierarchical communities, should gravitate further away from white noise (random) than simple communities. Also, I postulated that communities in more stable physical habitats will also show pattern of variability indicative of complex, multiscale organization.

In this paper I analyze the data from natural microcosms to test the above hypotheses. The data span a time series of abundance data for over 70 species of invertebrates occupying 49 supratidal rock pools in Jamaica. These rock pools have many attributes of general ecological systems.

The analyses led to a number of findings. First, I established that richer communities have some attributes of higher integration by finding that they are more resistant to periodic 'invasions' (return of species previously present). Second, variability of the physical environmental variables, whether at small or large scales, was within the typical range observed in other studies, with power spectrum exponents close to 1. Third, the variability of component populations differed consistently with theoretical expectations. Specifically, physically more stable pools contained communities whose power spectrum exponent was higher than those in physically variable pools. The same was true for species-rich as compared to species-poor pools. These observations mean that variability is more episodic in pool communities with higher organization and lesser external perturbation levels, with overall variability declining. Fourth, variability of biotic components was substantially different from variability of the environmental variables, suggesting that the physical environment may be a constraining but not necessarily the driving force. I further suggest that different exponents should characterize communities at different stages of development and self-organization.

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Patterns of variability constitute an important facet of ecological systems. Examples abound. Variability of populations affects their persistence or impact on other species or abiotic environment. Variability in species composition informs conservation and management strategies. Variability in distribution of species ties with homogenization of faunas and florae and impacts of invaders (Rahel, 2000). Variability in ecosystem processes determines long-term patterns of environmental modifications, microclimate, and has many other consequences.

For a few decades ecologists entertained the view that variability of ecological systems may have causal links to their complexity. While originally this view appeared as the complexity–diversity hypothesis (May, 1973), in recent years it reappeared in the new form and focused on the connection between complexity and variability (Tilman, 1999). The new formulation spawned exciting research but has not yet provided definitive answers. Most of this research focused on two kinds of variability in communities, the variability of aggregate properties such as combined abundance or biomass and the variability of populations of constituent species (e.g., Tilman, 1996). Considerable empirical support has accumulated for the reduction of variability of aggregate community descriptors with the increasing species richness (e.g., Romanuk and Kolasa, 2002; Lhomme and Winkel, 2002).

Analyses of variability of individual species in a community show a range of responses. Some studies reveal no (McGrady-Steed and Morin, 2000), others a weakly positive one (Tilman, 1996), and still others a negative relationship (Kolasa and Li, 2003; Romanuk and Kolasa, 2002). Relevant in this context is the finding by Gonzalez and Descamps-Julien (2004) that random fluctuations of environmental parameters stabilize aggregate community properties. Surprisingly, this incarnation of complexity–stability research was rather ‘simple’ on the complexity side. Complexity notion widely adopted by ecologists reduces in practice to the number of species (Haydon, 1994) or, occasionally, to the number of functional groups (McGrady-Steed and Morin, 2000) or trophic levels (Duffy, 2002). Stability of ecosystem processes received also some attention in addition to the structural descriptors such as biomass or combined community abundance mentioned earlier. While process oriented, it falls within the category of aggregated measures of variability (cf. Loreau et al., 2001). Within the field of ecology, however, other aspects of complexity and its relationship with stability and variability drew limited attention. A recognition that complexity involves more than a number of different components is a good starting point that has been promulgated for a couple of decades by T. Allen, his collaborators and a few others (e.g., O'Neill et al., 1986; Ulanowicz, 1997) within a broad conceptual approach called hierarchy theory. For the purpose of this paper, I will suggest that multispecies systems organize into hierarchical structures (Kolasa and Waltho, 1998; Kolasa and Romanuk, 2005) and that such organization may have a defining influence on our understanding of the relationship between complexity and variability and, indeed, on the patterns one expects and detects.

For many natural systems, with some implicit hierarchical structure or self-organization, power law describes the state of complexity they can achieve without some major collapse (Li, 2002). Accordingly, power spectrum analysis offers a preferred method of variability analysis (Keitt and Marquet, 1996; Halley and Kunin, 1999). Earlier, we have verified that a metacommunity of aquatic invertebrates inhabiting supratidal rock pools exhibits a link between hierarchical and power spectrum (Kolasa et al., 1996). In particular, we found that species categorized as occupying low positions in the hierarchy of habitat use contribute to numerous small changes in the system properties such as local extinction patterns, fluctuations in distribution, or variability in population densities. Details of the hierarchical interpretation of multispecies communities appear in several papers (Kolasa and Strayer, 1988; Kolasa, 1989; Kolasa and Waltho, 1998; Kolasa and Romanuk, 2005). The recognition of a linkage between hierarchical structures and patterns of variability (cf. Hogg et al., 1989) represents the first step into various aspects of community organization and their dynamic properties. One such aspect that clearly involves more than the number of different components and their topology is system integration or the overall interdependence of parts (cf. Li, 2000).

Intuitively, ecologists recognize system integration as an important dimension but little work has explicitly focused on the examination of general effects integration has on various aspects of system structure and performance. I have identified elsewhere (Kolasa, 2005) a variety of phenomena ecologists often study under different names but which fit the concept of integration. More importantly, I argued that the hierarchy of systems reveals itself as a function of integration. However, probability and magnitude of perturbation modulates the relationship between the two in a fairly specific manner (Kolasa, 2005). Without going into more details, it suffices to say that one could expect more integrated hierarchical systems to perform differently than those with less integration (Hogg et al., 1989).

Intuition and recent work (Kolasa, 2005) offer guidance as to which systems are likely to be more integrated and hierarchical. Specifically, an analysis of interactions between the size of system subunits, probability of disturbance, and degree of system integration indicates that a complex system can persists when:

1. its integration increases and, as it does so;
2. the size of the subassembly or subsystem decreases.

In other words, integrated systems perform generally better in assembling themselves or in coping with perturbation. Yet, this improvement in performance requires greater differentiation of their components and greater modularity of interactions among them. In the process of differentiation and compartmentalization of interactions, their structure develops deeper hierarchy and greater complicatedness (in the sense of possessing more elementary components). Evaluation of these system attributes requires a proxy measure. A number of correlates might serve this purpose. For example, higher differentiation of system components translates in greater degree of specialization, interdependence, and ultimately requires greater organization.
These general observations can be applied to multispecies systems. A species-rich community that shows low aggregate variability (variability in the total biomass or abundance of all species combined) would represent a hierarchical and integrated system in contrast to one that has few species and show considerable aggregate variability.

The logic of this paper can be summarized as follows. Variability of ecological systems is important. Variability and complexity link forms a perspective on organization of ecological systems. The complexity aspect involves hierarchical structure. The hierarchical structure can vary in its depth, complicatedness, and integration. These aspects of structure should correlate predictably with the patterns of variation. Patterns of variation most appropriate for examination of such effects involve frequency distribution of magnitude of changes. Specifically, I hypothesize that a more hierarchical and more integrated systems will display a greater range of changes, with fewer large changes and many more small changes compared to systems that are less integrated, less hierarchical, and more affected by environmental variability (extraneous noise). In terms of spectral exponent \( \omega \) (\( =\beta \) or \( \gamma \) in some papers) used to characterize frequency distribution of event magnitudes (for instance, size of the avalanches, earthquakes, or neuron firings and often referred to as 1/f noise), these expectations should translate in higher absolute values of the exponent. For comparison, the exponent of 0 is characteristic of the ‘white noise’ seen in many chaotic systems (Halley, 1996). Brown (or red) noise has a slope equal to −2, and the pink noise, often associated with self-organized criticality, has a slope of −1. Power spectrum analysis has been applied to a variety of problems involving ecological variability and the results range from \( \omega \sim 1 \) to \( \omega > 2 \) (e.g., Keitt and Marquet, 1996; Solé et al., 1997; Cuddington and Yodzis, 1999). Furthermore, existence of 1/f noise could be used as a mechanism for extrapolating from small-scale measurements to make large-scale predictions (Denny et al., 2004).

I approach the hypotheses by taking several steps. Initially, I show that expectations are different between community models based on random distribution of resources (broken stick model) and distribution of resources constrained by habitat hierarchy. In the next step, I analyze patterns in power spectra observed in natural communities. Here I contrast communities along two independent but potentially overlapping dimensions: community integration and community hierarchy. I use proxy measures to identify community integration and hierarchy. I assume that communities with lower rates of species turnover are more integrated. I further assume, consistently with the hierarchical model of community structure (Kolasa, 1989) and subsequent research (Kolasa et al., 1996), that communities with larger number of rare species have deeper hierarchy. These criteria allow for discrimination of integrated communities and hierarchically structured communities from their opposites.

2. Data and methods

Depending on the analyses I used simulated or empirical data. These are described in the sections below.

2.1. Conceptual models and simulated data

As posited earlier, randomly and hierarchically structured communities should differ in distribution of perturbation magnitudes (DPMs). To illustrate the nature of the difference I have analyzed DPMs in two simulated communities. In one, the distribution of abundances resulted from applying the broken stick procedure (Raup, 1991) to the total community abundance. In the other, abundance for individual species and hence the size of possible perturbations, was produced using a blend of the hierarchical habitat-based model (HBM; Kolasa, 1989) and random process identical to that used in the broken stick model. Here, species were assumed to operate simultaneously at three levels of habitat resolution, with the population costs increasing in proportion to habitat size and habitat fragmentation. Since the effective habitat fragmentation increases with the level of resolution, concurrently with shrinking of habitat size, an expected abundance of a species declines as a product of both—the degree of fragmentation and of the habitat size decline.

I have simulated approximately 50 communities of each type and compared their DPMs by fitting the power function of the form \( y = ax^b \), where the coefficient \( b \) corresponds to the spectral exponent \( \omega \) in 1/f convention (i.e., in 1/f\(^\nu\)).

2.2. Empirical data

The following data sets were used in this chapter:

1. Long-term variation in species abundance: This data set comprised 10 annual population census numbers for 75 species in 49 natural rock pool communities and covered the period from December 1989 to January 2001.

2. Short-term variation in selected physical variables characterizing three rock pools (identified in our earlier publications as no. 3, 16, 38; cf. Therriault and Kolasa, 2001): This data set consisted of 150 records of temperature, oxygen concentration, turbidity, and chlorophyll concentration taken at 30 s intervals in each of the three pools. The data were obtained by YSI DataSonde 6600 and a 650 Data Logger in January 2004. Additional data were compiled from long-term observations spanning a period of 10 years (1989–1999) and three sets of 24 h values recorded every 2 h.

In this study I used data on a rock pool metacommunity of aquatic invertebrates located around a small cove near the grounds of the Discovery Bay Marine Laboratory, on the Northern coast of Jamaica (Fig. 1). The system comprises a set of 49 coastal rock pools that are formed primarily by rain erosion on fossil reefs (Kolasa et al., 1996, 1998; Romanuk and Kolasa, 2002). The pools are on average ~60 cm \( \times \) 30 cm, have a mean depth of 13 cm and mean volume of 15 l. On average the rock pools are located within 1 m of the nearest neighbor and none is separated by more than 5 m from the next nearest rock pool. Their elevation above sea level is 1–235 cm (mean ~8-0 cm) at high tide, with the tide rarely exceeding a 30 cm range. Seven of the 49 rock pools are tidal, although tidal flooding is not daily, but most are maintained by atmospheric precipitation and occasional wave splash water. The rock pool inhabitants comprise over 70 species of invertebrates.
represented by over 300,000 individuals. Ten annual censuses were conducted to record composition and abundance of species in individual rock pools. Population size change for individual species in each pool was calculated as an absolute value of the difference in $N$ between two adjacent dates. These values of change were then combined together in one series whose power spectrum was fitted the same equation used for the models. Normally, a fast Fourier series transform is applied to spectral analysis (Keitt, 2000; Solé et al., 1997). However, the data I analyzed here do not form a true time series but are a scrambled collection of short time series.

2.3. Habitat variability

In order to analyze community behavior in variable and constant environment, I used an index of habitat variability (Therriault and Kolasa, 2000a). The index represents principal component analysis scores that combine standard deviations of field measured variables: oxygen concentration, temperature, pH, and salinity—all of known significant ecological complexity.
importance to aquatic organisms living in the rock pool system (Therriault and Kolasa, 2000a). The raw data consisted of multiple measurements of the above variables taken between January 1996 and January 1999 in the rock pools from which community data originate. At most times the physical measurements were taken on the same or within a couple of days of biological sampling.

2.4. Calculating the power spectrum exponents

For both the biotic and abiotic data I have obtained difference between two consecutive measurements. The distribution of difference values (e.g., Fig. 2) was then organized into 20 or more intervals using Statistica, ver. 6.0, Distribution Fitting module. Intervals with zero observations were not used. Finally, a power function of the form \( y = ax^b \) was fitted using TableCurve2D, ver. 4. Temporal trends in the data might increase the frequency of large values at the expense of small values of differences between the time steps. Thus, whenever a trend in the original data was present (for example, temperature may have kept increasing or decreasing during the time of record taking), a second-order polynomial was fitted to the raw data and the analysis was conducted on the residuals. The procedure assured that all comparisons are made on trend-free data. The analyses were conducted for physically variable and physically stable pools as well as species-rich and species-poor pool communities. The groupings were accomplished by sorting pools according to their physical variability index (Therriault and Kolasa, 2000a) and mean species richness, respectively, and assigning 24 or 25 pools to one category and the remainder to the contrasting category.

3. Results

Spectral exponents found for simulated data set varied in qualitative agreement with the expectations. The broken stick model produced a much lower value than the hierarchical model (Fig. 3), which confirms that ‘structured’ systems tend to have higher exponents.

Rock pool invertebrate communities have different characteristics in physically variable and physically stable pools. The rate at which communities are invaded and the degree to which they retain species can be seen as an indicator of community integrity and stability. In the set of more stable pools, increasing habitat variability leads to the reduction of number of successful ‘re-invasions’ by species periodically excluded from a local community (Fig. 4a) but this relationship broke down in pools classified as variable (Fig. 4c). The relationship between mean local richness and cumulative richness over 10 censuses retained similar slope but was noticeably weaker (\( r^2 = 0.840 \) versus 0.603) in the physically variable pools (Fig. 4b and d).

Given the effects of habitat variability on composition and turnover of species in individual rock pools, it is reasonable to expect differences in the patterns of variability in abundance of species between these two habitat categories. Subsequent analyses reflected this fact (Table 1). Furthermore, species-rich communities were invaded less effectively than species pool communities as evidenced by regressing mean richness against invasion rate (invasions per species) (\( y = ax^b \); \( r^2 = 0.435, F = 36.2, n = 49, p = 0.0000 \)). A significant negative linear relationship persisted between mean richness and invasion rate even when the species availability (difference between the cumulative \( S \) and observed \( S \)) was factored out (\( r^2 = 0.201, p > 0.006 \)). The reduction of invasion rate by biodiversity, \( S \), has also been observed in other systems such as in experimental grassland communities (Kennedy et al., 2002). Importantly, this result would be expected if richer

![Fig. 3 – Power spectra of two models of communities, the broken stick (dashed line, solid circles; adj. \( r^2 = 0.999, F_{stat} = 20051.3 \)) and hierarchical model (continuous line, open circles; adj. \( r^2 = 0.992, F_{stat} = 3456.1 \)). The hierarchical model produces fewer large perturbations and many more small ones.](image)

| Table 1 – Differences in biological power spectra among physically stable, and physically variable, species-poor and species-rich pool communities |
|-------------------------------|--------|-----------|---------|----------|--------|
| Data set                      | n      | Adj. \( r^2 \) | Coefficient \( a \) | Coefficient \( -b (=v) \) | \( F \) statistic |
| Stable pools                  | 1527   | 0.991     | 8.98    | 3.096    | 1570.6 |
| Variable pools                | 1773   | 0.972     | 2.30    | 2.741    | 388.2  |
| Species-poor                  | 1688   | 0.978     | 3.58    | 2.814    | 546.1  |
| Species-rich                  | 1612   | 0.994     | 2.37    | 3.250    | 3032.4 |

Coefficients and other parameters are for \( y = ax^b \) fitted to frequency distributions of populations changes (PDMs) for all species in pools in one of the three categories.
communities were also more organized and integrated. Thus, I treat this result as a proxy indicator of higher integration of species-rich communities.

The analysis of the power spectra for the two subsets created using the criterion of habitat variability showed a good fit of the power equation and a weak signal postulated by the hypothesis expressed as a higher absolute value of \( v \) in physically more stable pools (Table 1). When the pool communities are split into groups of high and low \( S \), the high \( S \) group has \( v = 3.25 \) as compared to \( v = 2.81 \) for ecological complexity 3 (2006) 71–79

![Graphs showing differential effects of physical variability of habitat in natural microcosms on community level phenomena such as invasions and species turnover.](image)

**Table 2 – Spectral exponents associated with variability of physical parameters in several natural rock pools**

<table>
<thead>
<tr>
<th>Pool id or data type</th>
<th>Turbidity (NTU)</th>
<th>Oxygen (% saturation)</th>
<th>Temperature (°C)</th>
<th>Chlorophyll (µg/l)</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>−1.844</td>
<td>−0.958</td>
<td>−0.784</td>
<td>−0.722</td>
<td>−1.077</td>
</tr>
<tr>
<td>16</td>
<td>−1.350</td>
<td>−0.823</td>
<td>−0.790</td>
<td>−0.670</td>
<td>−0.908</td>
</tr>
<tr>
<td>38</td>
<td>−2.739</td>
<td>−1.179</td>
<td>−0.259</td>
<td>−0.662</td>
<td>−1.210</td>
</tr>
<tr>
<td>Tap and sea water mix (sal = 5%)</td>
<td>n/a</td>
<td>−0.703</td>
<td>−0.997</td>
<td>−0.668</td>
<td>−0.789</td>
</tr>
<tr>
<td>Mean (excl. tap and sea mix)</td>
<td>−1.978</td>
<td>−0.987</td>
<td>−0.611</td>
<td>−0.685</td>
<td>−1.065</td>
</tr>
<tr>
<td>Diurnal variation (( \Delta t = 2 ) h)</td>
<td>−0.553 ± 0.195</td>
<td>−1.321 ± 0.101</td>
<td>(for five pools)</td>
<td>(for five pools)</td>
<td></td>
</tr>
<tr>
<td>Annual variation</td>
<td>−1.715</td>
<td>−1.075</td>
<td>−0.85</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Frequency distribution of turbidity variation in tap/sea water mix showed two values only, which is insufficient for calculation of the exponent. For comparison, spectral exponents for a mixture of filtered tap and sea water (salinity = 5%) are added as well as spectral exponents for diurnal and inter-annual variation in temperature and oxygen. For the diurnal spectra data differences between adjacent measurements were used; the measurements were taken on three separated days every 2 h and results are shown for five randomly selected pools. The inter-annual differences were calculated from annual means. Blank cells imply insufficient data.
species-poor group (Fig. 5). This result conforms to the expectation that high biodiversity (high $S$) communities, being more hierarchical and more integrated, should show a greater frequency of small variations, with relatively rare larger variations. Similarly, communities in physically stable pools have larger $\omega$ values than those in physically unstable pools. In such unstable pools, biotic variability is likely to be partly driven by the physical variability and, because physical variables are characterized by lower $\omega$ values, some reduction of $\omega$ values should occur in biotic variables.

As observed earlier, the physical variability exhibits a pattern different from that observed in biotic variables. The spectral exponents tend to fluctuate around $\omega = 1$, with somewhat lower values for oxygen and chlorophyll concentrations and higher values for turbidity (Table 2). Turbidity, with its higher values, does not constitute an anomaly because it appears to have arisen from the crab movement, a biological factor. At the larger time scales these variables show a similar pattern, with $\omega$ ranging from 1.321 for temperature measured at 2-h intervals to 0.850 for inter-annual differences among temperature means, 0.553 and 1.075 for respective oxygen data (Table 2) and 2.019 for desiccation frequency. The magnitude of absolute differences between adjacent measurements appears to stabilize within hours. For example, an analysis of temperature shows that differences increase from approximately 0.005 at 30 s intervals to 0.85°C at 2 h intervals to only 0.97°C at annual intervals—a pattern consistent with climatic regime of the area.

Overall, the world of microcosms exhibits a trend of spectral exponents increasing with the presumed increase in importance of biotic organization (Fig. 5). The highest exponents are associated with systems having the lowest presumed physical forcing and systems with the highest level of biotic differentiation (those with the highest richness and presumed deepest hierarchy and highest integration), respectively.

### 4. Discussion

The main finding of the analysis is a gradient of spectral exponents increasing from purely physical processes to situations progressively dominated by biological interactions and structure (Fig. 5). This gradient is consistent with the theoretical expectations illustrated earlier by the contrast between the broken stick and hierarchical model simulations (Fig. 3).

The relatively high $\omega$ (black noise; Schroeder, 1991) in physically stable and species-rich communities bears similarity with other natural phenomena such as earthquakes or floods, characterized by rare large or catastrophic events. This similarity does however imply that communities in physically stable and species-rich pools vary less, most of the time, than other communities. It also implies that, occasionally, such communities undergo radical restructuring. The results reported here converge with the conclusions of the modeling approach taken by Cuddington and Yodzis (1999). They also found black noise to be conducive to long-term population persistence.

The spectral exponent values found in rock pool meta-community differ substantially from other biological processes observed at very coarse scales of taxonomic and geologic resolution. Sole et al. (1997) examined patterns of family extinctions over a period of 150 myr and found $\omega$ approaching 1, which they took as evidence of self-similarity (self-similarity occurs when $1 < \omega < 2$). The data at their disposal do not represent, however, functional and integrated local communities. As such they are more likely to reflect a compound signal produced by adding multiple and unrelated scales of variability rather than a signal typical of organized system. Organized, integrated systems are generally believed to attain some degree of internal stability (Choi et al., 1999) or steady state but may also be more vulnerable to perturbation exceeding their typical adaptive range (Kolasa, 2005). In other words, high $\omega$ is consistent with the expectations that complex systems exhibit reduced variability relative to simpler systems of the same type.

Alternatively, high $\omega$ may be seen as indicator of more complex and organized systems. Communities in physically stable pools and species-rich communities are more likely to represent such systems when compared to communities in physically unstable and species-poor communities, whose composition and population variability appear dominated by the physical environment.
By contrast, generally lower values of the spectral exponent exhibited by the physical variation at short-term (min) and long-term (years) scales make the assumption of strong coupling between physical variability and biotic less plausible. Most of the values found here lie within the middle of the range reported by others and reviewed in Cuddington and Yodzis (1999). Furthermore, biological variability has no obvious explanation in physical variability suggesting that the specific patterns of biotic variability are induced by biotic aspects of community organization. Experimental evidence into the self-generated community richness (Therriault and Kolasa, 2000b) further supports this inference. It is possible, and in some cases certain, that biotic variability influences physical variability (e.g., oxygen, pH, turbidity). However, variability of abundance of individual species is unlikely to result a synchronous variability of these variables that respond to an aggregated behavior of lower trophic levels (algae). Thus, while not fully independent of biological activity, oxygen, pH, or chlorophyll concentrations can have an impact on individual species comparable to the impact of other environmental variables such as light, temperature, or salinity.

The results obtained in this study may be useful to the interpretation of the effects of environmental forcing on populations and communities as initially discussed by Steele (1985) in the context of differences between marine and terrestrial systems. Here, some rock pools share salinity and all share aquatic medium with the marine systems. At the same time, their small size makes them more responsive to the local climate to share that aspect with the terrestrial systems. Interestingly, \( \omega \) values of physical variables are on average ‘pink’ (-1) by contrast to \( \omega = 2 \) in marine systems (Steele, 1985) but the values of biotic components correspond to ‘black’ noise, with \( \omega \gg 2 \).

Values of spectral exponents collected in Table 2 must be treated with caution, however, because of the statistical approach used in this paper. These exponents depend to some degree on the number of intervals chosen to find frequencies. However, irrespective of the choices made during their calculations, the exponents are always much lower than those found for the biotic variables and show are range reported by others (e.g., Denny et al., 2004). Thus, while quantitative results might change under a different analytic protocol, the meaningful differences between the biotic and abiotic variations would persist.

Finally, this tentative and yet encouraging analysis suggests further lines of investigation. The obvious one is calculation of spectral exponents separately for each community. Such an analysis would permit a direct test of the effects of physical environment, system productivity, and community structure on patterns of variability.

In conclusion, this pilot analysis shows the patterns of variability summarized by the spectral exponent of the 1/f expression change consistently with the assumption of hierarchical organization of multispecies assemblages. As system organization and complexity increase, so does the exponent. This change implies an increase in the episodic nature of major perturbations or system restructuring and greater system stability during the intervening periods.

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