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Temporal Scaling in Complex Systems
Resonant Frequencies and Biotic Variability

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Abstract. Structure in complex systems, such as ecosystems, is scale specific, with discontinuities bounding domains within which scaling laws apply. Concordantly, changes in spatial pattern across different ranges of scale are described by different scaling relationships. The spatial aspect of scale has continued to receive considerable attention in the field of landscape ecology; however, scale has dimensions of time as well as space, and the consideration of one without the other neglects half the picture. In this chapter, we concentrate on the scaling axis of time, and describe cycles in temporal patterns in the Everglades ecosystem. We relate the temporal frequencies of ecosystem structuring processes to the interaction of animals with their environment, and describe how spatial and temporal turnover and variability in animal communities relates to variation in the availability of resources in time and space. We posit that discontinuous distributions of key structuring variables in time should be manifest as a few resonant frequencies in temporal processes. We test this idea with time series data of rainfall, evaporation, water-flow, air temperature, sea level, and fire history. The dominant temporal frequency for most data sets was the annual cycle, but secondary frequencies of 8 to 11 years were present in these data. Longer frequencies occurred at approximately decadal cycles in the water-flow and fire data, suggesting that key structuring processes are separated by an order of magnitude. Both spatial and temporal variation is observed in animal communities at discontinuities, reflecting the interplay of dimensions of space and time. The complex phenomena of migration, nomadism, invasion, and extinction are all associated with discontinuities in animal body mass patterns. Additionally, we investigate the variation in bird species abundance in relationship to their proximity to discontinuities in the body-mass distribution of this assemblage. Species whose body mass places them closer to discontinuities have population abundances that are more variable over time. These analyses support the theory that ecosystems are structured around a few keystone variables of mixed spatial and temporal dimensions.

5.1. Introduction

Ecosystems are complex adaptive systems comprised of biotic and abiotic components that interact across a wide range of spatial and temporal scales (Holling, 1986; 1992). The interactions of these components generate loosely linked hierarchical structures. For example, in a forest, leaves, stems, and trunks compose a hierarchical level of a tree. In turn, a group of trees make up a patch, and a group of patches make up a forest stand. Within a level, a key set of processes and components interact to generate characteristic behaviors and dynamics. Across levels, patterns and features change, as different keystone processes dominate across different scale domains (Holling and Gunderson, 2002).

Holling (1992) was the first to indicate the correlation between the cross-scale structures in ecosystems and the types of biotic patterns that emerge. The *Textural Discontinuity Hypothesis* proposed that body mass distributions of animal communities reflect landscape structure (Holling, 1992), and are discontinuous. The discontinuities in ecological systems derive from self-organizing interactions between biological and non-biological components at specific scales; that is, it is not appropriate simply to consider landscapes as a template upon which animals interact; rather, landscapes reflect the interactions of animals, existing landscape structures, and processes at key scales.

This discontinuous world is characterized by a small set of scale-invariant regimes, within which scaling rules apply. In the temporal domain, the small set can be measured by a few frequencies of key structuring variables. Many authors (Craighead, 1971; Davis and Gunderson, 1993; Davis and Ogden, 1994) argue that the hydrologic regime and the fire regimes are key ecological processes that determine spatial and temporal patterns, e.g. in the Everglades. The signature, or ecological legacy, of these processes is present in long lasting physical patterns upon landscapes. In the Everglades, these patterns include the distribution, size, and position of tree islands, the distribution of sloughs and features such as alligator holes, and a myriad of other structures at a variety of spatial and temporal scales (Holling et al., 1994).

The importance and prevalence of discontinuities in spatial and temporal patterns of attributes of ecological systems has been well documented (Allen and Holling, 2002). For animals residing within an ecosystem, the discontinuities in process and structure are manifest in discontinuous body mass distributions. For animals, the edges of discontinuities in body mass distributions reflect scale breaks that are analogous to phase transitions between two scales of landscape pattern. This suggests that there is greater environmental variability at the scale breaks. Allen et al. (1999) predicted that biological phenomena that are associated with greater variability would be more likely to occur at the edges of body mass aggregations and tested this model by analyzing the role of body mass pattern as a predictor of invasions and extinctions in the vertebrate fauna of the Everglades. The results supported the hypothesis; successful invaders and extinct or declining species were concentrated at the edges of body mass aggregations. Other independent biological attributes or phenomena were associated with temporal or spatial variability and occurred more often than expected at discontinuities (i.e., invasions, extinctions, migrations, and nomadism; Lambert and Holling, 1998; Allen et al., 1999; Allen and Saunders, 2002, 2006; Allen, 2006; Allan and Holling, 2002; Allen *unpub. data*).

Populations that exhibit higher temporal variability may be more prone to extinction than those with lower variability (Pimm, 1991). Given this and the evidence that populations situated at the edges of body mass aggregations (i.e., discontinuities) are also prone to extinction, Allen et al.'s (1999) model may be expanded upon to suggest that edge populations will exhibit higher temporal variability in abundance than populations that represent the interior of body mass aggregations. May (1973) hypothesized that as environmental variability increases, the effects of competition are enhanced and there is a greater chance that one or more species will become extinct. Furthermore, he suggested that even a small amount of environmental variability may have a dramatic effect. Thus, greater environmental variability at the edges of body mass aggregations should intensify interspecific competition. The combined effect may result in higher temporal variability of population abundances, and potentially increase the likelihood of extinction.

In this chapter, we investigate temporal aspects of the cross-scale structure of the landscape of southern Florida (USA). We first use time series analyses and other techniques to investigate the key processes responsible for structuring the Everglades ecosystem to search for discontinuities and dominant frequencies. We then analyze the avian fauna of the Everglades to determine if temporal variability in population abundance is randomly or non-randomly distributed in terms of discontinuities in the avian body mass distribution.

5.2. Methods

5.2.1. Process Frequencies

The Everglades is a well-studied and monitored ecosystem, with much available data on the biotic and abiotic components. We use multiple decade time series of hydrologic and fire data from the system to look for dominant frequencies in these key variables. Three types of hydrologic data were analyzed for temporal patterns: rainfall, stage (water level), and surface flow. Two data sets were used in the analysis of temporal rainfall patterns. Daily rainfall totals from May 1948 through December 1989 were obtained for Tamiami Ranger Station and Royal Palm Station. Daily water levels were obtained from sites designated P33, P35, P37, and P38 in Everglades National Park. Monthly summaries covering the time period January 1954 through December 1975 were analyzed. Total monthly flow data from October 1939 through 1983 under the Tamiami Trail flow section were analyzed. Area burned by month during the period 1958–1979 was used in determining fire frequencies. The analyses were conducted with the fast Fourier algorithm in the SYSTAT software for the Macintosh (Systat, 1990). For each data set the mean was subtracted from every value and the data de-trended, so that the values varied above and below zero with no overall change or trend in the mean. The Fourier analysis searches the data for multiple sine waves, and identifies the multiple wavelengths (and frequencies) present in the data set (See Box 1 for details of the Fourier technique).

Box 5.1. Fourier analysis

Fourier analyses were developed to decompose complex waveforms into simple waveforms. The Fourier analysis fits a series of sine waves of increasing frequency to a data set. The approach uses a fixed window (extent of data in time) and a variable grain to discern component patterns. The fast Fourier technique is a modification that utilizes data sets with windows that are 2^n units. The essence of the Fourier analysis is in the transform, whereby the discrete data points are transformed from a time domain to a frequency domain. The amplitude is calculated for each frequency ranging from intervals of the entire data set (one sine wave fit to the entire set) to a frequency of one-half the number of data points (wavelength every two data points). Frequencies that correlate to a large number of data points have high magnitude values. The magnitudes represent the amount of variance explained by the corresponding frequency. Statistics of mean and variance can be calculated from the magnitude values and represent the amount of noise or random behavior in the data. Dominant frequencies (that correspond to a sine wave of a given length) in the data set have high magnitude values.

5.2.2. Biotic Variability

We investigated the relationship between discontinuities in time and space and variability in biota by determining the variability in bird abundance over time in relation to discontinuities in the bird body mass distribution of the Florida Everglades sub-ecoregion (Allen et al., 1999). Species distribution and body mass estimates were determined for the avian fauna of the Florida Everglades using data collected by Allen et al. (1999). Only species that had established breeding populations in the Everglades sub-ecoregion were included. Non-indigenous species were not included. Pelagic birds were also excluded because they interact with their environment differently than other avian species (Allen et al., 1999). In all cases, adult male and female body masses were averaged to estimate a body mass for each species. Variance associated with the estimation of mean mass, which can vary in species exhibiting size dimorphism, does not have a discernable effect on determination of gaps and aggregations (Sendzimir, 1998).

All species within the community were ranked in order of log transformed body mass, and the data were examined for discontinuities with the Gap Rarity Index (GRI) (Allen and Holling, 2002). The GRI compares observed body mass distributions with a unimodal null distribution that is produced by a kernel density estimator, which smoothes the observed data into a unimodal continuous null. The observed distribution of body masses is compared with values generated from sampling the null distribution 10,000 times. Unusually large gap values are considered significant and determine the location of discontinuities. Discontinuities bound aggregations of species with similar body masses, which perceive and interact with their environment at the same, or very similar, domains of scale. The results were confirmed with Cluster analysis based on variance reduction (Ward option; SAS Institute, Inc., 1999).

Population abundances were determined for Everglades birds using Breeding Bird Survey (BBS) data (Breeding Bird Survey, 2005). Three BBS routes were selected from the Everglades (Flamingo, Homestead, and Pinecrest) and abundances were recorded over a 5-year period (1999–2003) for each route. We used the same species list for each route; however, the same birds were not always recorded on each route or year. For each species, the coefficient of variation (CV) was determined for each route over the 5-year study period. Distance to edge is a measure, in terms of log body mass units, of how far a species is to the edge of a discontinuity in the overall body mass distribution of Everglades birds. Those species directly on the edge of an aggregation (located at the edge of a discontinuity) have a distance to edge of zero. For "interior" species, the distance was measured to the closest edge.

We used a mixed model, blocking by BBS route, for the regional analysis of temporal variability in population abundance. In our model, CV was the dependent variable and distance to edge, aggregation, and the edge-by-aggregation interaction were fixed effects and BBS route was a random effect.

5.3. Results

5.3.1. Process Frequencies

5.3.1.1. Rainfall

Rainfall data from January 1949 through December 1988 exhibited four resonant periodicities. The complex pattern of rainfall can be decomposed into waveforms with cycles of 1 year, 3 months for the daily and monthly data, and a longer-term 6–11-year cycle for annual rainfall (Table 1). The dominant period is the annual cycle, characterized by a summer wet season and winter dry season (Hela, 1952; Thomas, 1970; MacVicar and Lin, 1984). Summer rainfall is mainly a result of convective thunderstorms associated with the daily sea- and land-breeze cycle (Hela, 1952; Bradley, 1972; MacVicar and Lin, 1984). The generation of convective thunderstorms is related to the annual variation in heat budget associated with the earth's orbit. During the fall, winter, and spring months (November through April), rainfall is associated primarily with the passage of cold fronts (Hela, 1952; Bradley, 1972; MacVicar and Lin, 1984). The multiple-year cycle had significant peaks of approximately 11, 5, and 3 years, like the dominant frequencies reported for

TABLE 5.1. Summary of Fourier analyses of time series data.*

			Frequencies (yr)		
Data set	Length (yr)	Resolution	1°	2°	3°
Rainfall	39	Day	1	0.25	0.3
	39	Month	1	0.25	0.3
	44	Year	6	8	11
Stage	22	Day	1	7	3
		Month	11	1	3
Flow	44	Month	1	8	22
Pan evaporation	22	Month	1	11	5
Temperature	22	Month	1	5	0.5
Fire	22	Month	11	1	5

*The length of time and resolution of data are given for each data set of rainfall, stage, flow, evaporation, sea-level temperature, and fire sizes analyzed. For each data set, the primary (dominant), secondary, and tertiary frequencies of from each Fourier analyses are given.

south Florida by Thomas (1970) and Isaacs (1980). These inter-annual variations have been attributed to the degree of tropical storm activity (MacVicar, 1983), or to influences from the El Niño Southern oscillation (ENSO; Rasmussen, 1985; Ropelewski and Halpert, 1987). The 3–4-month cycle evident in the data is less well understood. This cycle is evident as the bimodal summer peaks of rainfall. Thomas (1970) and MacVicar (1983) attribute the summer depression to a combination of two processes. During the late summer months, convective activity may decrease due to feedback dynamics of changing albedo, lapse rates, and heat budget after the freshwater system is full of water (Gannon, 1978). The latter peak may also be a result of the increased frequency of tropical storms and hurricanes in August and September that add to rain during these months (Gentry, 1984).

5.3.1.2. Surface Water

As with the rainfall data, the dominant frequency in the water level data is the annual cycle, although the presence of multiyear cycles in the surface waters (levels and flows) suggests fluctuation over longer frequencies. For example, the monthly water level data indicates the presence of three cycles; the strongest cycle is about 11 years, with smaller ones at frequencies of 1, 7, and 3 years (Table 1). The monthly water flow data vary on frequencies of 1 and 8 years, with minor frequencies of 22 years. The effects of water management are included in this analysis. The period in the early 1960s of extremely low flow was when the Tamiami Trail was closed while the S-12 structures were completed. The period of regularity in the 1970s through early 1980s was when the minimum flow regime was in effect. Flows greater than 3×10^8 m^3 per month occur on the long-term frequencies (22+ years). The 3.2×10^8 m^3-month break seems to correlate with the 9-year return interval. The 2.3×10^8 m^3-month break is roughly observed on the 5-year cycle;

the 1.5×10^8 m^3-month, the 3-year cycle; and the smallest break seems to correlate with an annual cycle. These correlations are approximate; certainly high flows don't occur every 9–10 years. The data indicate distinct periodicities, with dramatic annual and decadal cycles, that appear to correlate with distinct volumetric groupings.

5.3.1.3. Pan Evaporation and Temperature

Pan evaporation rates (depth of water lost to the atmosphere over a given time period) vary at multiple cycles. The most significant periodicity in both data sets was the annual cycle. Significant multiyear periods of 11 and about 5 years were also observed in both data sets, although the peaks were not as significant as the annual cycle. A cycle of about 6 months was also present.

5.3.1.4. Fires

The periodicity of fires in the Everglades exhibit the same multiyear frequency (11 years) as the stage and flow data (Gunderson and Snyder, 1994). Significant spectral peaks were measured at return intervals of 11 and 1 years with minor peaks at a 5–6-year interval. Although the periodicities of fires are similar to the flow and stage the phases are different. The years of high fire activity and size (early 1960s and early 197s) are years of low water level and low flow. Fire sizes during the 22-year period from 1959 though 1979 ranged from 10^2 to 10^8 m^2. Fire patterns indicate at least two classes of fires occurred in Shark Slough: more frequent smaller fires and less frequent large fires. Fires above this size may be a result of many factors, including inability of humans to control or contain fires over a given size, or perhaps a less frequent combination of climatic conditions that would support the fire to burn over a broad area and longer time frame. The larger fires burn over longer time periods than the smaller ones.

5.3.2. Biotic Variability

The body mass distribution of the birds of the Everglades sub-ecoregion was discontinuous and distinct aggregations of body mass were detected with both statistical methods used (Allen et al., 1999). The Breeding Bird Survey provided abundance data for 84 of 106 birds in the Florida Everglades species list. Of those 84 species, many were only present at one or two of the three study routes.

Significant edge ($p = 0.010$) and aggregation effects ($p = .003$) were present. Species with the greatest variation in population abundance over time tended to have body masses that were relatively closer to discontinuities than species with body masses that placed them in the interior of body mass aggregations (Fig. 1). There was also a significant interaction between edge and aggregation ($p = 0.002$), suggesting that the exact nature of the relationship between distance to discontinuity CV varies with body mass aggregation.

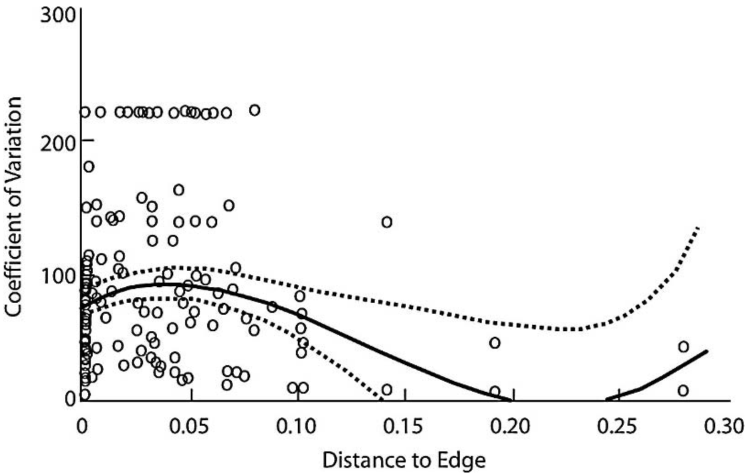

FIGURE 5.1. Coefficient of variation (CV) in relation to distance to edge (DE) of a body mass aggregation in log body mass units for Everglades birds. Solid line represents fitted polynomial ($CV = 72.6 + 835.14 * DE - 12202.63 * DE^2 + 30855.42 * DE^3$), dashed lines represent upper and lower 95% confidence limits, respectively. CV in abundance increases as distance to edge decreases.

5.4. Discussion

Temporal patterns in the hydrologic variables of water level (stage) and flow reflect dominant frequencies resulting from the interplay between the faster dynamics of the atmosphere (such as daily thunderstorms and seasonal storms) and the longer-term dynamics in vegetation, atmosphere (such as ENSO), and sea level (Fig. 2). These analyses support the theory that ecosystems are structured around a few keystone variables of mixed temporal (and spatial) dimensions. The dynamics of these variables are separated by about an order of magnitude; from months to years to decades, which reflect discontinuous patterns that result from the interactions within and among hierarchical levels in time. The discovery of discontinuities in the temporal frequencies of structuring processes are an important step in understanding how discontinuities in spatial and temporal parameters affect landscape structure and dynamics, and ecological and evolutionary processes such as evolution, adaptation, assembly, and competition.

Discontinuities are present in animal body mass patterns as well as the periodicities of processes. We do not attempt to make a mechanistic link between dominant process frequencies and discontinuities in the body mass distributions of vertebrates in the Everglades ecosystem. A strong link such as that would be extremely compelling. Importantly, though, temporal variability in bird population abundance is non-randomly located in terms of body mass distributions, and is highest at discontinuities in the body mass distribution of the birds of the Florida Everglades.

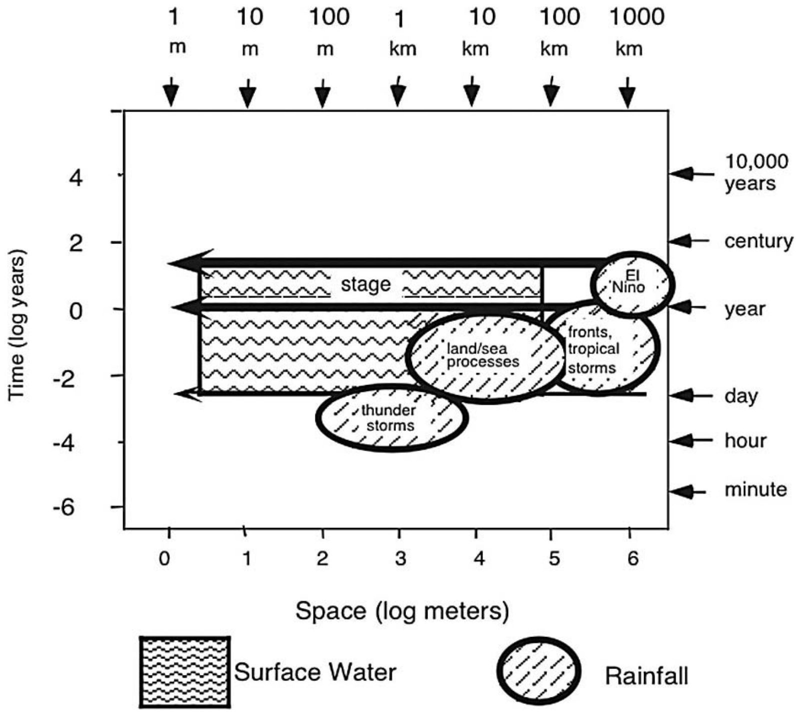

FIGURE 5.2. Temporal frequencies in key ecosystem processes of water stage and flow in the Everglades. Dominant frequencies are depicted by horizontal lines with arrows; with the 1-year cycle (middle line), decadal cycle (top line), and monthly cycle (bottom line). Each of these corresponds to different scales of processes, indicated by the ellipses in the diagram.

Prior research has provided evidence that populations that are more variable are more prone to extinction (Pimm, 1991). Because species near discontinuities in body mass distributions are more prone to decline in the Everglades ecoregion (Allen et al., 1999), this analysis links population variability with that decline. Discontinuities in body mass distributions may be associated with greater resource variability in time and space and higher environmental variability may increase the effects of competition and the possibility that one or more species become extinct (May, 1973).

The most important structuring processes of the Everglades exhibit pronounced temporal periodicities at multiple scales. The body mass distributions of the vertebrates of the Everglades are discontinuously distributed (Allen et al., 1999), with aggregations of species theoretically corresponding to the dominant temporal scales of structure, process and resource distribution upon the landscape. Additionally, abundance in birds whose body mass places them closer to discontinuities is more variable than in birds whose body mass places them farther from those discontinuities, theoretically reflecting higher resource variability to be found at scale breaks, areas of transition from one scale to another. Many investigations in ecology, and landscape ecology in particular, are concerned with process and pattern. However, in almost all cases such analyses default to analyses of spatial patterns upon landscapes. Partially this is due to the relative lack of long-term data sets, but it is also driven by GIS technologies that make spatial analyses so simple. The analyses we report are based on temporal variation; in frequencies of processes and changes in abundance over time. However, landscape ecology in particular and ecology in general will take a giant leap forward when spatial and temporal aspects of process and structure are analyzed simultaneously.

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