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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