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Craig R. Allen

University of Nebraska-Lincoln, callen3@unl.edu

C.S. Holling

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Craig R. Allen & C.S. Holling

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Cross-scale morphology

The scaling of physical, biological, ecological and social phenomena has become a major focus of efforts to develop simple representations of complex systems. Much of the attention has been on discovering universal scaling laws that emerge from simple physical and geometric processes. But there are regular patterns of departures both from those scaling laws and from continuous distributions of attributes of systems; these departures often demonstrate the development of self-organized interactions between living systems and physical processes over narrower ranges of scale.

Cross-scale morphology refers to morphological attributes of animals that are influenced by interaction with ecological structures and patterns at different scales. Body mass is often the attribute considered, because it correlates strongly with and integrates a broad array of a species characteristics such as energy use and home range size. Growing evidence from nature, ecological modeling, and theory suggests that **ecosystem** structure and dynamics are dominated by the influence of a small set of plant, animal, and abiotic processes [3, 6, 7]. Each set of processes operates at characteristic periodicities and spatial scales [6, 9]. Small and fast scales are dominated by biophysical processes that control plant morphology and function. At larger and slower scales, interspecific plant competition for nutrients, light, and water interacts with climate and affects local species composition and regeneration. At the scale of forest stands, meso-scale processes of fire, storm, insect outbreak, plant diseases and large mammal herbivory determine structure and succession dynamics from tens of meters to kilometers and years to decades. The largest landscape scales have geomorphological and evolutionary processes that affect structure and dynamics over hundreds of kilometers and millennia. An example for such a forested landscape is shown in Figure 1.

This, therefore, is a hierarchical representation of a nested set of variables [2, 9] where each set is controlled by processes sufficiently different in speed and size to introduce discontinuities in the distribution of ecosystem attributes. Because each set of variables controls or self organizes a persistent pattern over a particular range of temporal and spatial scales, ecological structure varies with scale and reflects the actions of the particular processes operating at a given scale.

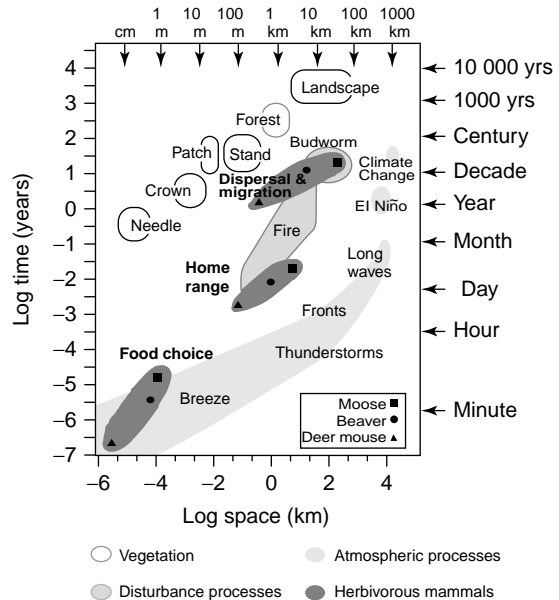


Figure 1 Time and space scales of the boreal forest, and their relationship to some of the processes that structure the forest. Processes include insect outbreaks, fire, atmospheric processes, and the rapid CO₂ increase in modern times [5]. Meso-scale disturbance processes provide the linkage between macro-scale atmospheric processes and micro-scale landscape processes. Scales at which animals such as the deer mouse, beaver and moose choose food items, occupy a home range, and disperse to locate suitable home ranges vary with their body size. Modified from Peterson et al. [10]

Discontinuous Body Mass Distributions

Because the patterns are persistent, they have the tendency to entrain attributes of other variables. If landscape patterns are persistent enough, then biological processes unrelated to the original structuring processes will become entrained by and adapted to the pattern. They could well amplify the originating pattern to provide an enhanced signature of landscape structure (*see Landscape ecology*). Hence life history and behavioral and morphological attributes of animals could all become adapted to the discontinuous landscape pattern and consequently amplify its signal.

There is a growing body of evidence for discontinuities in numerous ecological systems [1, 6, 11, 12]. Independent attributes of species have been shown to be associated with discontinuous body

mass patterns. These include invasion, extinction (high species turnover), high population variability, migration, and nomadism. Evidence comes from four different taxa (birds, mammals, herps (reptiles and amphibians), and bats) in multiple ecosystems [1]. Additionally, the distribution of function within and across scales may add to the resilience of ecological systems [10, 15].

Detection of Body Mass Patterns

The ecological and biological literature historically has been dominated by assumptions that attributes of organisms are distributed continuously, not discontinuously, and that such distributions are unimodal. The methodologies for detecting discontinuous ‘lumps’ in ecosystem attributes are poorly developed, and few standard statistics exist for the detection of pattern. Additionally, different underlying hypotheses suggest different statistical approaches. Hypotheses suggesting that there are underlying zones of attraction that vary with scale suggest the use of tests for multimodality, whereas hypotheses suggesting that there are forbidden zones suggest tests for discontinuities. All tests utilize the ranked, log-transformed body mass distributions of species from a given ecological system.

Holling [6] initially used visualization tests and body mass difference indices (BMDI) to detect structure in ranked animal body mass distributions. The index is a running average:

$$\text{BMDI} = \frac{M_{n+1} - M_{n-1}}{(M_n)^\gamma} \quad (1)$$

where M is average body mass and γ is an exponent used to detrend the data, particular for the taxon of interest. For birds, γ was found to be 1.3 and for mammals γ was found to be 1.1, with a critical value set at one or two **standard errors** above the mean of the index. Other split-moving window indices with window sizes of between one and three give essentially the same results as the BMDI. (Larger window sizes can oversmooth the data.)

The *gap rarity index* (GRI) was introduced by Restrepo et al. [12], and compares actual body mass distributions with a unimodal null distribution. The null distribution is constructed from a kernel density estimator that smoothes the observed data into the continuous null. Significance of gaps is determined by

comparing the body mass difference between species in a ranked distribution with the values generated by sampling the null distribution 10 000 times (*see Resampling methods*). Unusually large values are considered significant. Restrepo et al. [12] maintained constant significance levels when performing analyses using the GRI, whereas Allen et al. [1] maintained constant power.

Other simulation techniques also have been used to attempt to detect lumps [8] or discontinuities [13]. Manly [8] used kernel density estimation [14] to detect clumping in body size distributions. However, his test was conservative, and biased towards the detection of few modes; the corresponding probability of detecting the correct number could be small. Siemann and Brown [13] used a uniform null model and **randomization** to compare gaps (i.e. $mass_{n+1} - mass_n$) in body mass distributions to random distributions. However, their test compared gap sizes sequentially rather than testing for overall patterns.

Standard statistical packages provide procedures to determine lumps. In particular, hierarchical cluster analysis (especially methods that are based upon variance reduction) and classification and **regression trees** [4] are useful. These procedures have the advantage of being easy to use, but have their own peculiarities. Current recommendations for detecting structure in body mass patterns include use of multiple methods, and interpretation of structure based upon the convergence of multiple analyses.

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- (See also **Biomass; Diversity measures; Population dynamics; Population viability analysis; Tree morphology**)

CRAIG R. ALLEN & C.S. HOLLING