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Cross-scale morphology

The scaling of physical, biological, ecological, and social phenomena is 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. However, there are regular patterns of departures both from those scaling laws and from continuous distributions of attributes of systems. Those 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 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 [1–3]. Each set of processes operates at characteristic frequencies and spatial extents (i.e., occur at distinct scales in space and time) [2, 4]. 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 [4, 6] where each set is controlled by processes sufficiently different in speed and

size to introduce discontinuities (i.e., thresholds) 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.

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 adapted to the pattern. This process amplifies 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 [2, 7–10]. Independent attributes of species have been shown to be associated with discontinuous body mass patterns. These attributes include invasion, extinction (high species turnover), high population variability, migration, and nomadism, from five different taxa (birds, mammals, reptiles and amphibians, fish, and bats) in multiple ecosystems [7]. Havlicek and Carpenter [11] compared body mass distributions in a set of experimental lakes, and found that discontinuities in body mass distributions in numerous species were conserved despite changes in lake nutrient status and species composition. Allen and Saunders [12, 13] found that nomadic species have both a tendency to be large, and to be at the edge of discontinuities in body mass distributions. Allen [14] found that proximity to a discontinuity in body mass distributions was the most important factor in the success or failure of invasive species. Additionally, there is support for scale-dependent species distributions in Australian birds [15]. The abundance of species at discontinuities in body mass distributions is more variable in both time and space, which further indicates that discontinuities are “zones of transition” at the available scales of opportunity [16].

Discrete scales of resource distribution lead to discontinuous body mass distributions that correspond to the scales of available resources [17]. The

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2 Cross-scale morphology

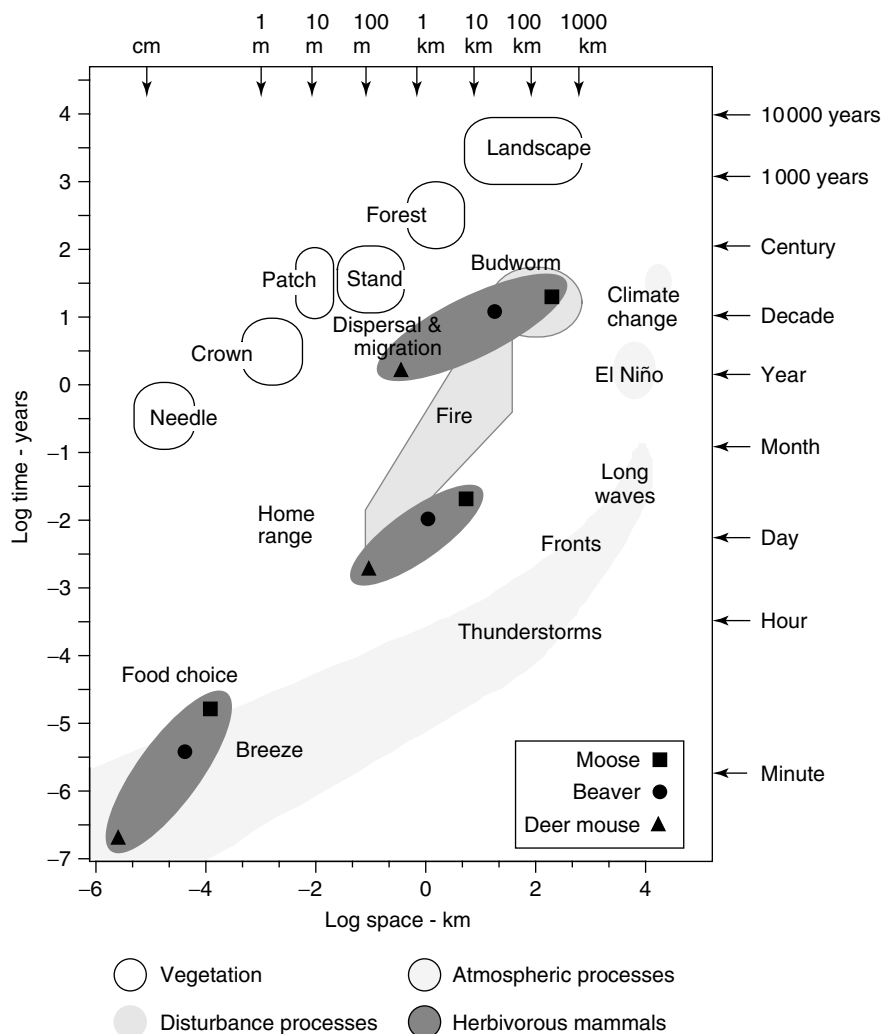


Figure 1 Time and space scales of the boreal forest, and their relationship to some of the processes that structure the forest. Processes include insect outbreaks, fire, atmospheric processes, and the recent rapid increase of CO₂ [5]. Meso-scale disturbance processes provide the linkage between macroscale atmospheric processes and microscale 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. (Source: Reproduced from *Ecosystems*, 1, 1998, 6-18, Ecological resilience, biodiversity, and scale, Peterson, G.D., Allen, C.R. & Holling, C.S., with kind permission from Springer Science+Business Media B.V.)

existence of discontinuous body mass distributions is now generally accepted, although the mechanisms that generate the discontinuous pattern is the subject of ongoing research [18]. Additionally, the distribution of functions within and across scales adds to the resilience of ecological systems [19]. The manner in which these functions are distributed within and

across the spatial and temporal scales of an ecological system ensures the continuation of function despite disturbance (i.e., cross-scale resilience). Cross-scale resilience in ecological systems is enhanced when the diversity of function within a scale, and the redundancy of functions across scales, is high [19, 20]. Furthermore, extinctions may be nonrandom in terms

of body mass distributions, and occur in a manner that conserves functions [21].

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 methods for detecting discontinuities in ecosystem attributes are poorly developed, and few standard statistics exist for the detection of patterns in univariate data. Additionally, different underlying hypotheses suggest different statistical approaches. Hypotheses suggesting there are underlying zones of attraction that vary with scale suggest the use of tests for multimodality, whereas hypotheses suggesting 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 [2] 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, n is species rank 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 between one and three give essentially the same results as the BMDI.

The gap rarity index (GRI) was introduced by Restrepo *et al.* [9], and compares actual body mass distributions with a unimodal null distribution. The null distribution is constructed from a kernel density estimator that smooths 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.* [9] maintained constant significance levels when performing analyses using the GRI, whereas Allen *et al.* [7] maintained constant power.

Standard statistical packages also provide procedures to determine modes and discontinuities. In particular, hierarchical cluster analysis (especially methods that are based upon variance reduction) and classification and regression trees are useful [22]. These procedures have the advantage of being easy to use, but have their own peculiarities. Stow *et al.* [23] proposed a discontinuity index based on the vector norm of the full assemblage of observed discontinuities, as a means to determine if size distributions are discontinuous. Xu *et al.* [24] used Bayesian hypothesis tests to test body mass distributions using nested finite mixture models. Their analysis focused upon the identification of modes, rather than discontinuities, and found consistent evidence of multiple modes in the data. Redundancy analysis, with time modeled by a principal coordinates of neighbor matrices, has been used to identify cross-scale structure in ecosystems. The approach identifies ecologically relevant scales and temporal patterns and retains the taxonomic information needed to characterize cross-scale resilience [25].

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(See also **Biomass; Diversity measures; Panarchy; Population dynamics; Demographic stochastic models; Tree morphology**)

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