

 Open access • Journal Article • DOI:10.1007/S10021-005-0147-X

The Use of Discontinuities and Functional Groups to Assess Relative Resilience in Complex Systems — [Source link](#)

Craig R. Allen, Lance Gunderson, Alan R. Johnson

Institutions: Clemson University, Emory University

Published on: 28 Nov 2005 - Ecosystems (Springer-Verlag)

Topics: Resilience (network) and Classification of discontinuities

Related papers:

- [Resilience and Stability of Ecological Systems](#)
- [Ecological Resilience, Biodiversity, and Scale](#)
- [Regime Shifts, Resilience, and Biodiversity in Ecosystem Management](#)
- [From Metaphor to Measurement: Resilience of What to What?](#)
- [Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/the-use-of-discontinuities-and-functional-groups-to-assess-2me08peunz>

2005

The Use of Discontinuities and Functional Groups to Assess Relative Resilience in Complex Systems

Craig R. Allen

Clemson University, callen3@unl.edu

L. Gunderson

Emory University, lgunder@emory.edu

A. R. Johnson

Clemson University

Follow this and additional works at: <http://digitalcommons.unl.edu/ncfwrustaff>

 Part of the [Aquaculture and Fisheries Commons](#), [Environmental Indicators and Impact Assessment Commons](#), [Environmental Monitoring Commons](#), [Natural Resource Economics Commons](#), [Natural Resources and Conservation Commons](#), and the [Water Resource Management Commons](#)

Allen, Craig R.; Gunderson, L.; and Johnson, A. R., "The Use of Discontinuities and Functional Groups to Assess Relative Resilience in Complex Systems" (2005). *Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications*. 153.
<http://digitalcommons.unl.edu/ncfwrustaff/153>

This Article is brought to you for free and open access by the Nebraska Cooperative Fish & Wildlife Research Unit at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

The Use of Discontinuities and Functional Groups to Assess Relative Resilience in Complex Systems

Craig R. Allen,^{1*} L. Gunderson,² and A. R. Johnson³

¹USGS South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina 29634, USA;

²Department of Environmental Studies, Emory University, Atlanta, Georgia 29634, USA; ³Department of Forestry and Natural Resources, Clemson University, Clemson, South Carolina 29634, USA

ABSTRACT

It is evident when the resilience of a system has been exceeded and the system qualitatively changed. However, it is not clear how to measure resilience in a system prior to the demonstration that the capacity for resilient response has been exceeded. We argue that self-organizing human and natural systems are structured by a relatively small set of processes operating across scales in time and space. These structuring processes should generate a discontinuous distribution of structures and frequencies, where discontinuities mark the transition from one scale to another. Resilience is not driven by the identity of elements of a system, but rather by the functions those elements provide, and their distribution within and across scales. A self-organizing system that is resilient should maintain patterns of function within and across

scales despite the turnover of specific elements (for example, species, cities). However, the loss of functions, or a decrease in functional representation at certain scales will decrease system resilience. It follows that some distributions of function should be more resilient than others. We propose that the determination of discontinuities, and the quantification of function both within and across scales, produce relative measures of resilience in ecological and other systems. We describe a set of methods to assess the relative resilience of a system based upon the determination of discontinuities and the quantification of the distribution of functions in relation to those discontinuities.

Key words: cross-scale; discontinuities; function; resilience; scale; textural-discontinuity hypothesis.

INTRODUCTION

Resilience refers to the ability of a system to remain within a domain of attraction while exhibiting dynamic behavior (Holling 1973; Gunderson 2000). As such, it captures the richness of behavior in complex systems better than concepts such as stability. When a system is forced beyond the

boundaries of a domain of attraction, a qualitatively different pattern of behavior may emerge. It is often quite evident when the resilient capacity of the system has been exceeded and the system qualitatively changed, for example when a lake flips from a clear to turbid state. However, it is not at all clear how to measure resilience in a system prior to the demonstration that the capacity for resilient response has been exceeded.

The concept of resilience currently lacks clear and reproducible measures of a system's ability to withstand internal or external shocks without changing domain and an operational measure of resilience that allows for quantification and

Received 8 October 2003; accepted 5 April 2004; published online 28 November 2005.

*Corresponding author; e-mail: callen3@unlnotes.unl.edu

†Current address: Nebraska Cooperative Fish and Wildlife Research Unit, University of Nebraska, 103 Miller Hall, Lincoln, Nebraska, 68583-0711, USA

experimental tests. We propose that the determination of discontinuities, and the quantification of function both within and across scales, produce relative measures of resilience in ecological and other systems. In this conceptual paper, we first introduce the concept of discontinuities, review some recent literature on discontinuities in complex systems, and then introduce measures for resilience based upon these concepts.

DISCONTINUITIES AND CROSS SCALE STRUCTURE

Understanding the structural attributes that contribute to resilience in human and natural systems is clearly important. We expect commonality in the mechanisms by which ecosystems, societies, economies and other complex adaptive systems maintain their structural and functional integrity when confronted by unexpected or novel events (Holland 1995; Arthur and others 1997; Allen and Holling 2002). Holling (1992) and others have proposed that complex systems can be viewed as a dynamic hierarchy with a few dominant processes operating at different, characteristic spatio-temporal scales. Through a process of entrainment these dominant processes create discontinuities in structural features of the system, resulting in, for example, aggregated patterns of animal body mass or city size. The creation and maintenance of these discontinuities and aggregations is a form of self-organization, the emergence of a predictable pattern from the internal dynamics of the system. If the presence of discontinuities is important in determining the resilience of complex systems, we would expect discontinuities to persist despite the normal dynamics of the system. Individual species may invade or go extinct, individual cities may prosper or perish, but overall the structure should be little affected unless the system is pushed beyond the limits of its resilience.

We argue, following Holling (1992), that self-organizing human and natural systems are structured by a relatively small set of processes operating across scales in time and space resulting in discontinuities in structural attributes. This occurs as key processes establish dominant temporal frequencies that entrain other processes. In ecosystems, this has most often been observed in the discontinuous distribution of body mass (Holling 1992; Allen and others 1999). In human systems, we would expect discontinuous distributions of such elements as city sizes and economic variables (Bessey 2002). Cross-scale (panarchical; Gunderson and Holling 2002) structure adds to the resili-

ence of complex systems, and discontinuities are the signature of that structure. Note that the discontinuities predicted by this theoretical perspective may be superimposed on a power-law trend, which is predicted by other theoretical frameworks (for example, Bak and others 1987; West and others 1997). The two theories are not necessarily incompatible, although at the current time, no unifying theory that incorporates both power-laws and discontinuities exists.

Resilience is not driven by the identity of any given element of the system, but rather by the functions those elements provide, and their distribution within and across scales. In complex systems, there are breaks between levels because controlling processes differ between scales, identified as discontinuities. Scale breaks in attributes of animal communities such as body masses correlate strongly with biological phenomena such as invasion, extinction, high population variability, migration and nomadism (Allen and others 1999; Allen and Saunders 2002). Economic analogues may exist in terms of changes in country GNP (the invasion of "Asian Tiger" economies in the 1980s) and in the collapse and invasion of firms. The clustering of these phenomena at predictable scale breaks suggests variability in resource distribution or availability is greatest at these states. This supports the proposition that communities structured by self-organizing dynamics will tend to maintain the pattern of discontinuities despite changes in species composition. Individual species may invade or go extinct, individual cities may prosper or perish, but overall the panarchical structure should be little affected unless the system is pushed beyond the limits of its resilience. In that case, we should observe a change in structure (at some scales) during the system's collapse, and a re-emergence of a fundamentally different structure during the subsequent reorganization at that level (Holling 2001; Gunderson and Holling 2002).

The detection of discontinuities (scale breaks) in ecological systems has been conducted along dimensions of space and time to create hierarchies. Spatial features of vegetation structure indicate regions of self-similarity separated by distinct breaks in remnant forest patches in a landscape with substantial recent conversion to cropland (Krummel and others 1987), in the Everglades (Gunderson 1992) and urban landscapes (Hostetler 1999). Similar patterns have been found in international economic data (Summers and Heston 1991), where the variable of interest was gross domestic product per capita, measured for 120 countries over a 30-year time frame.

Insight into the resilience of panarchies can be gained from recent studies of dynamics in random networks (see Barabási 2002 or Barabási and Bonabeau 2003 for an introduction). Networks with random links between nodes lack hierarchical structure. In contrast, scale-free networks, which arise naturally in evolving networks if links are added preferentially to highly connected nodes, have a hierarchical organization of well-connected hubs radiating to less-connected peripheral nodes. Studies of the robustness of these network structures demonstrate that scale-free networks are considerably less vulnerable to random failure (via deletion of nodes or links) than their random counterparts. Thus, with respect to random perturbations, hierarchical structure promotes resilience. Such systems can have an "Achilles heel", in that they are vulnerable to a targeted attack affecting the most highly connected nodes. The world wide web is one of the clearest examples of this phenomenon—overall internet traffic is seldom disrupted by random failures in servers, but can be severely impaired by a malicious attack on a few key hubs.

Analyses of longitudinal data indicate that the hierarchical structure of urban systems is resistant to change, despite significant variability in the growth dynamics of individual cities (Bessey 2002). The pattern of discontinuities and aggregations in city size distributions of the Southwestern US region remains constant across a 100 year time horizon, despite the fact that in 1890 there were but 48 cities in the region with a maximum size of 38,000 but by 1990 there were more than 162 cities in the region with a maximum population exceeding three million (Garmestani and others 2005). Temporally discrete urban growth rates (Papageorgiou 1980) and clumping in the spatial ranges of city functions (Korcelli 1977) may provide clues into how spatially large systems, that is, national economies, "entrain" (Holling 1992) spatially smaller units, including regional and city economies, to produce stability in macrostructure but great diversity in the available growth paths (Dendrinos and Sonis 1990). These phenomena accord with the hierarchical structure that we predict contributes to resilience, but contradict the neoclassical view regarding the nature of urban economics. The generally accepted stability of urban structure is interpreted as the manifestation of a steady state condition in which a city-size distribution is affected by a myriad of small random forces (Gabaix 1999). This assumes homogeneity in underlying growth processes, that is, growth is independent of city size, which appears inconsis-

tent with the empirical data. By definition, structural patterns that promote resilience are the most likely to persist over time and be replicated across space.

CROSS-SCALE RESILIENCE MODEL

If the distribution of function within and across scales generates resilience in complex systems, the general distribution of function (that is, the behavior, affects, effects, and response to perturbation of system elements) should be unchanged by the normal dynamics of the system. Systems that do not maintain distributions of functions that contribute to resilience would be unlikely to persist. A self-organizing system that is resilient should maintain patterns of function within and across scales following the turnover of specific elements (for example, species, cities) (Gunderson 2000). However, the loss of functions, or a decrease in functional representation at certain scales will decrease system resilience. It follows that some distributions of function should be more resilient than others.

Peterson and others (1998) predict that systems with a diversity of function within scales and redundancy across scales are the most resilient. If this is so, measurement of relative resilience is simple, where discontinuities and functional group membership can be determined. Loss in function, and changes in the distribution of function within and across scales, are quantifiable, and may be incorporated into a measure of relative resilience.

Peterson and others (1998) explicitly incorporate scale and discontinuities in their model of ecological resilience. They contend that species interact with scale-dependent sets of ecological structures and processes that determine functional opportunities. At a particular ecological scale, the function of species may overlap, but they will tend to differ as species evolve to avoid interspecific competition, and this will increase diversity at a particular ecological scale. Across ecological scales, there is more overlap in ecological function because species are less likely to face competition from species that interact with the environment (for example, forage, compete, disperse, defend territories) at different spatial and temporal scales. The combination of within-scale diversity of ecological function and cross-scale redundancy (that is, reinforcement at different scales) adds to resilience (Peterson and others 1998). The function of a species loss at a particular scale can be offset by similar species that interact with the environment at a different scale (Walker and others 1999). High within-scale

diversity and cross-scale redundancy are predicted to produce ecosystems that are capable of resisting minor ecological disruptions and regenerating after major disturbances. An example is provided by the response of different insectivorous birds to different scales of spruce budworm infestations—from individual chickadees responding to small-scale infestation to flocks of crows responding to large-scale outbreaks (Holling 1988). Peterson and others (1998) model focused explicitly on ecosystems and animal species, but it is extendable to the structure of any complex system.

THE USE OF DISCONTINUITIES TO ASSESS RELATIVE RESILIENCE

The first step in quantifying function and characterizing its distribution is to delimit the spatial and temporal bounds of the system under consideration, and to select the functional attributes that will be examined. There are multiple facets to resilience in systems (Carpenter and others 2001), and no surrogate is likely to capture all the elements of resilience. Functional attributes need to be carefully chosen to reflect important or valued elements of resilience. Once the conceptual framework for the analysis has been set, appropriate data can be gathered. Such data should reflect key attributes of the system to be analyzed, for example body masses of animals (a measure that integrates numerous ecological attributes), or city sizes.

Once appropriate data have been identified, discontinuities need to be determined. A number of methods have been suggested, including null models and simulations (Manly 1996; Restrepo and others 1997), cluster analysis and split moving window boundary analysis, and difference indices (Allen and Holling 2001). Because each method has its own shortcomings and advantages, Allen and Holling (2001) concluded that the best approach is to use multiple methods and compare the resulting structures, searching for agreement among as many methods as possible. Identification of discontinuities determines the location and number of aggregations within a system. According to theory and empirical tests of that theory, a larger number of aggregations corresponds to a richer array of environmental scales available. More scales—deeper hierarchies—may or may not lead to more resilient systems.

The next step in assessing relative resilience is to determine functional groups, a non-trivial and sometimes controversial task. However, in animal

communities, many authors have defaulted to feeding guilds, defining functional groups based on what is eaten and how it is gathered. Analogous groups may be determined for other systems, such as economies (where for example, major economic inputs and outputs may be categorized) or city size distributions (where, for example, city function may be categorized by industry or other human or resource outputs). Forsy and Allen (2002) determined the richness of ecological functions within body-mass aggregations by classifying species by functional groups using both foraging strata (for example, aquatic, fossorial, terrestrial, arboreal/ foliage, bark, and aerial) and diet (herbivorous, omnivorous, insectivorous, and carnivorous). Functional group richness for each aggregation was determined by simply counting the number of different foraging strata / diet combinations present in each body-mass aggregation.

The distribution of functional groups within and across scales may be numerated in a variety of ways. The richness of functional groups within a scale (within an aggregation, defined by discontinuities) may reveal an aspect of resilience. The average number of species per functional group within an aggregation measures within-scale redundancy. Finally, the average number of aggregations for which each functional group has at least one representative measures cross-scale redundancy, another aspect of resilience.

Given this framework, changes in functional group representation (for example, presence/absence, richness, diversity) over time can be assessed to determine changes in system resilience over time. Forsy and Allen (2002) analyzed the pattern in animal body masses for the Florida Everglades ecosystem, comparing historical with likely future distributions (that is, by eliminating declining species and including breeding non-indigenous invasive species), and concluded that the similarity in the location and number of discontinuities and the richness and within- and across-scale distributions of functional groups suggested strong resilience and self-organization despite high species turnover. Similarly, different systems can be compared as to functional group membership and number of scales present to compare relative resilience across systems.

The location of turnover in systems may also be used to assess resilience, and predict potential collapse. As has been documented for the Everglades, turnover in species composition may occur most often at the edge of discontinuities. Such change appears to be adaptive, as these edges represent scale transitions with high variability. However,

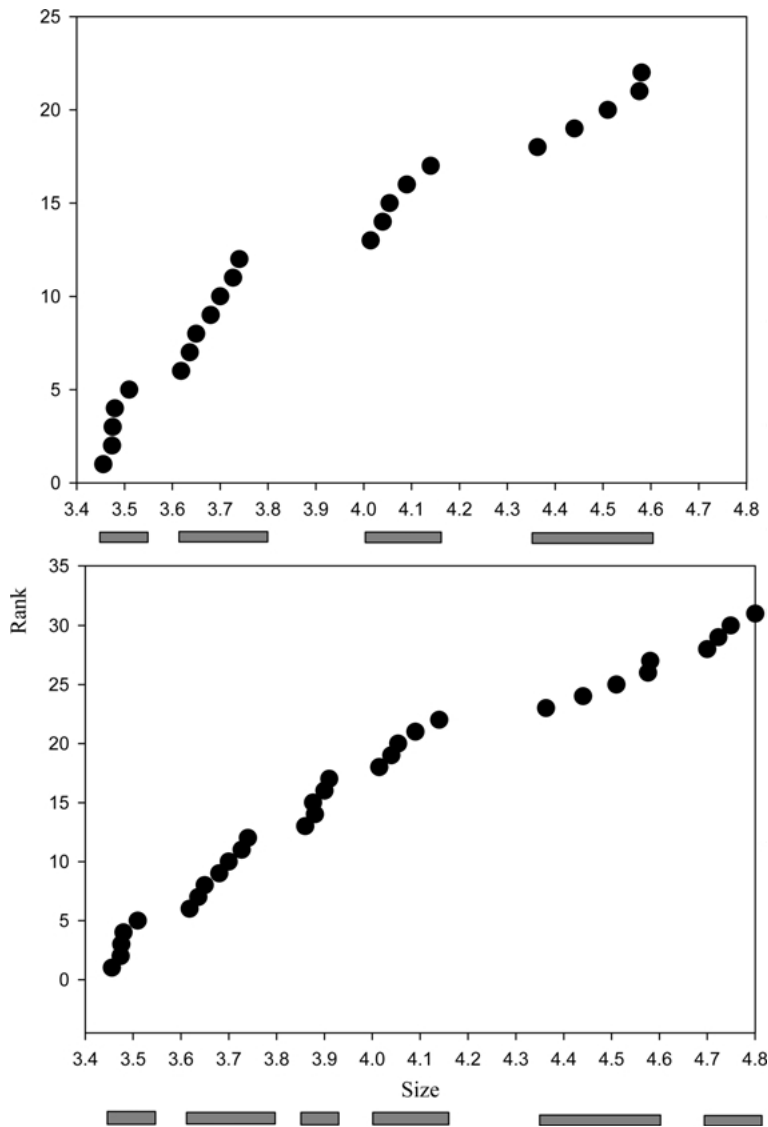


Figure 1. Two alternative discontinuous distributions differing in the number of discontinuities detected and, theoretically, the number of scales reflected. The elements of the system (for example, animal body masses or city sizes) have been ranked according to size (*y*-axis) and are shown as *dark circles*. Size is given along the *x*-axis. The *shaded bars* below the *x*-axis show aggregations; these are separated by pronounced discontinuities in the distribution.

turnover could be a sign of impending collapse. Turnover that occurs within aggregations, or turnover that substantially reduces functional representation or cross-scale redundancy, may signal loss of resilience and impending reorganization. A lack of turnover at edges may simply indicate resistance, which may or may not correspond to resilience. Likely, systems strongly resistant to turnover at scale breaks have little adaptive capacity and relatively low resilience.

APPLICATION

Consider a pair of sets of attributes of a complex system, for example distributions of body masses or regional city sizes (Figure 1). In both cases, the distributions are discontinuous. In the first case, three discontinuities and four aggregations have

been identified while in the second case five discontinuities and six aggregations have been identified. The functions of the individual elements are identical in both distributions. Which is more resilient? The first case shows a clear separation between distinct size classes, which may represent strong hierarchical organization. The second case more nearly approximates a continuous rank-size distribution, which may indicate that hierarchical controls are less developed. If this interpretation is correct, we would expect the first system to be more resilient to random perturbations, but perhaps be more vulnerable to a targeted attack.

Second, consider sets of attributes from three systems where the identical number of discontinuities have been identified, and the same kinds of functions are represented, but the distribution of functions differs (Figure 2). Which system is more

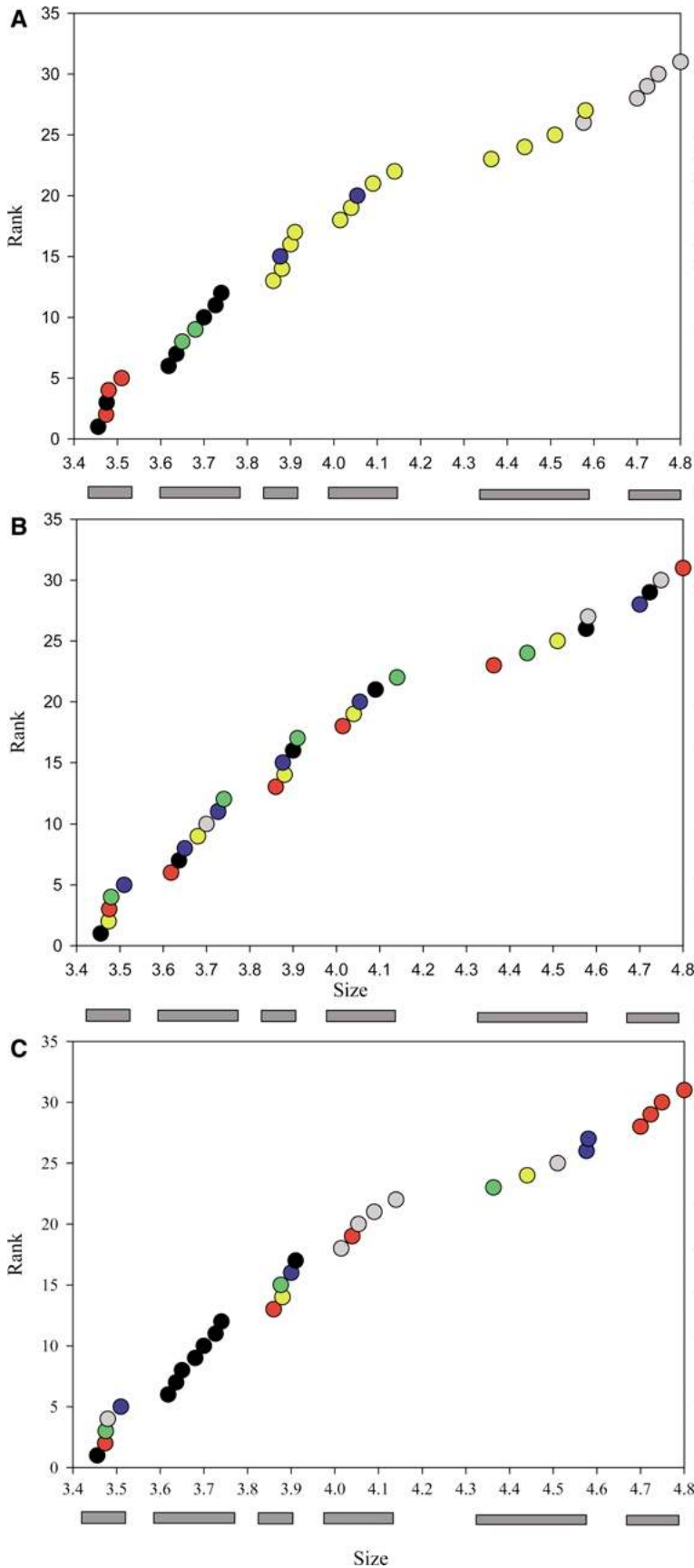


Figure 2. Three alternative discontinuous distributions identical in the number of discontinuities detected, the number of elements at each scale, and the number of functional groups present but differing in the distribution of functional groups both within and across scales. Different functional groups are represented by different colors. The elements of the system (for example, animal body masses or city sizes) have been ranked according to size (*y*-axis) and are shown as *dark circles*. Size is given along the *x*-axis. The *shaded bars* below the *x*-axis show aggregations; these are separated by pronounced discontinuities in the distribution.

Table 1. Comparison of Metrics Relevant to Assessing the Relative Resilience of the Three Distributions shown in Figure 2

Aggregation	Fnct1	Fnct2	Fnct3	Fnct4	Fnct5	Fnct6	Richness	Evenness	Diversity
Distribution 1									
1	2	3	0	0	0	0	2	0.375984	0.6730117
2	5	0	0	0	2	0	2	0.334229	0.5982696
3	0	0	4	1	0	0	2	0.279554	0.5004024
4	0	0	4	1	0	0	2	0.279554	0.5004024
5	0	0	4	0	0	1	2	0.279554	0.5004024
6	0	0	0	0	0	4	1	0	0
Distribution 2									
1	1	1	1	1	1	0	5	0.899127	1.609438
2	1	1	1	2	1	1	6	0.976463	1.747868
3	1	1	1	1	1	0	5	0.899127	1.609438
4	1	1	1	1	1	0	5	0.899127	1.609438
5	1	1	1	0	1	1	5	0.899127	1.609438
6	1	1	0	1	0	1	4	0.774466	1.386294
Distribution 3									
1	1	1	0	1	1	1	5	0.899127	1.609438
2	7	0	0	0	0	0	1	0	0
3	1	1	1	1	1	0	5	0.899127	1.609438
4	0	1	0	0	0	4	2	0.279554	0.500402
5	0	0	1	2	1	1	4	0.744234	1.332179
6	0	4	0	0	0	0	1	0	0

Table 2. Summary Comparison of Metrics Relevant to Assessing the Relative Resilience of the Three Distributions shown in Figure 2

	Average richness	Average evenness	Average diversity	Within-scale redundancy	Cross-scale redundancy
Dist'n 1	1.83	0.26	0.46	2.67	1.83
Dist'n 2	5	0.89	1.59	1.03	5.00
Dist'n 3	3	0.47	0.84	2.79	3.00

resilient in this case? This example lends itself to quantification. Following the approach of Forsy and Allen (2002) we can determine redundancy in functional groups across scales. Forsy and Allen (2002) counted the number of aggregations where at least one member of a given functional group was present in the first distribution and compared this to the number of aggregations where it occurred in the second distribution. In their analysis, they found that within each body mass aggregation, there were large changes in species composition and functional group membership. However, the tests comparing the mean functional group richness in body mass aggregations pre-invasion and post-invasion were not significantly different for each taxonomic group or for all of the groups combined. Forsy and Allen (2002) concluded that both distributions were strongly self-organizing and likely similarly resilient.

A number of specific metrics may be used to compare the distributions shown in Figure 2. First, it is possible to simply enumerate the number of aggregations present. Second, the number of functional groups (richness) present within each aggregation (scale) can be determined, and indices of evenness and diversity (Table 1). These indices of functional richness, evenness and diversity can be averaged across aggregations (Table 2). Functional redundancy can be represented as the average number of species within each functional group in an aggregation (within-scale redundancy) and the average number of aggregations at which each function is represented (cross-scale redundancy) (Table 2). For this example, Distribution 2 is expected to reflect the most resilient system, as average within-aggregation richness, evenness and diversity are all higher than in Distribution 1 or 3,

and it possesses the greatest cross-scale redundancy (Table 2).

CONCLUSION

We have derived metrics for assessing resilience useful especially when comparing among systems or within a system through time. Simple null models can be used to compare actual distributions from random distributions in the absence of comparable systems. Forsys and Allen (2002) demonstrated the utility of quantifying changes in functional groups for scenario analysis of possible futures in the South Florida vertebrate fauna. Tests of these metrics will best be made by analyzing systems that have collapsed as compared to systems that have not collapsed when challenged by similar perturbations.

Resilience is a systemic measure. Carpenter and others (2001) state that resilience measures differ in two important ways from indicators: they apply to the entire system and they focus on variables that underlie the capacity of the system to provide ecosystem services. Can measuring body mass or city size or other variables assess overall system resilience or state? Animals, or city sizes, encompass a wide-range of scale. If these variables reflect cross-scale structure, and are entrained by key processes, the answer is yes.

ACKNOWLEDGEMENTS

This manuscript was improved by comments from E. Bennett and two anonymous reviewers. The South Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement among the USGS-BRD, the South Carolina Department of Natural Resources, Clemson University, and the Wildlife Management Institute. Support was provided to C. R. Allen by the James S. McDonnell Foundation 21st Century Research Award/Studying Complex Systems.

REFERENCES

- Allen CR, Forsys EA, Holling CS. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems* 2:114–21.
- Allen CR, Holling CS. 2001. Cross-scale morphology. In: El-Shaarawi AH, Piegorsch WW, Eds. *Encyclopedia of environmetrics*. Chichester, UK: Wiley. p 450–2.
- Allen CR, Holling CS. 2002. Cross-scale structure and scale breaks in ecosystems and other complex systems. *Ecosystems* 5:315–8.
- Allen CR, Saunders DA. 2002. Variability between scales: predictors of nomadism in birds of an Australian Mediterranean-climate ecosystem. *Ecosystems* 5:348–59.
- Arthur WB, Durlauf SN, Lane D. 1997. *The economy as a complex evolving system II*. Reading (MA): Addison-Wesley.
- Bak P, Tang C, Wiesenfeld K. 1987. Self-organized criticality: an explanation of 1/f noise. *Phys Rev Lett* 59:381–4.
- Barabási A-L. 2002. *Linked: the new science of networks*. New York: Perseus Publishing.
- Barabási A-L, Bonabeau E. 2003. Scale-free networks. *Sci Am* 288:60–9.
- Bessey KM. 2002. Structure and dynamics in an urban landscape: toward a multiscale view. *Ecosystems* 5:360–75.
- Carpenter S, Walker B, Anderies JM, Abel N. 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4:765–81.
- Dendrinos DS, Sonis M. 1990. *Chaos and socio-spatial dynamics*. Berlin, Heidelberg, New York: Springer.
- Forsys EA, Allen CR. 2002. Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem. *Ecosystems* 5:339–47.
- Gabaix X. 1999. Zipf's law for cities: an explanation. *Quant J Econ* 3:739–67.
- Garmestani A, Allen CR, Bessey KM. 2005. Time series analysis of clusters in city size distributions. *Urban Studies* 42:1507–1515.
- Gunderson LH. 1992. *Spatial and temporal dynamics in the everglades ecosystem with implications for water deliveries to Everglades National Park*. Dissertation. Gainesville, USA: University of Florida.
- Gunderson LH. 2002. Resilience in theory and practice. *Annu Rev Ecol Syst* 31:425–39.
- Gunderson LH, Holling CS. 2002. *Panarchy: understanding transformations in human and natural systems*. Washington (DC): Island Press.
- Holland J. 1995. *Hidden order: how adaptation builds complexity*. Reading (MA): Addison-Wesley.
- Holling CS. 1973. Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23.
- Holling CS. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. *Mem Entomol Soc Can* 146:21–32.
- Holling CS. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol Monogr* 62:447–502.
- Holling CS. 2001. Understanding the complexity of economic, ecological, and social systems. *Ecosystems* 4:390–405.
- Hostetler M. 1999. Scale, birds, and human decisions: a potential for integrative research in urban ecosystems. *Landscape Urban Plan* 45:15–9.
- Korcelli P. 1977. *An approach to the analysis of functional urban regions: a case study of Poland*. International Institute for Applied Systems Analysis, Laxenburg, Austria. Report No. RM-77-52.
- Krummel JR, Gardner RH, Sugihara G, O'Neill RV, Coleman PR. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321–4.
- Manly BF. 1996. Are there clumps in body-size distributions. *Ecology* 77:81–6.
- Papageorgiou GJ. 1980. On sudden urban growth. *Environ Plan A* 12:1035–50.
- Peterson GD, Allen CR, Holling CS. 1998. Ecological resilience, biodiversity and scale. *Ecosystems* 1:6–18.
- Restrepo C, Renjifo LM, Marples P. 1997. Frugivorous birds in fragmented neotropical montane forests: landscape pattern

- and body mass distribution. In: Laurance WF, Bierregaard RO, Moritz C, Eds. *Tropical forest remnants: ecology, management and conservation of fragmented communities*. USA: University of Chicago Press. p 171–89.
- Summers R, Heston A. 1991. The penn world table (mark 5): an expanded set of international comparisons, 1950–1988. *Q J Econ* 106:327–68.
- Walker B, Kinzig A, Langridge J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2:95–113.
- West GB, Brown JH, Enquist BJ. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276:122–6.