How do ecologists measure resilience?

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RESILIENCE AND STABILITY OF ECOLOGICAL SYSTEMS

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INTRODUCTION

Individuals die, populations disappear, and species become extinct. That is one view of the world. But another view of the world concentrates not so much on presence or absence as upon the numbers of organisms and the degree of constancy of their numbers. These are two very different ways of viewing the behavior of systems and the usefulness of the view depends very much on the properties of the system concerned. If we are examining a particular device designed by the engineer to perform specific tasks under a rather narrow range of predictable external conditions, we are likely to be more concerned with consistent nonvariable performance in which slight departures from the performance goal are immediately counteracted. A quantitative view of the behavior of the system is, therefore, essential. With attention focused on achieving constancy, the critical events seem to be the amplitude and frequency of oscillations. But if we are dealing with a system profoundly affected by changes external to it, and continually confronted by the unexpected, the constancy of its behavior becomes less important than the persistence of the relationships. Attention shifts, therefore, to the qualitative and to questions of existence or not.

Our traditions of analysis in theoretical and empirical ecology have been largely inherited from developments in classical physics and its applied variants. Inevitably, there has been a tendency to emphasize the quantitative rather than the qualitative, for it is important in this tradition to know not just that a quantity is larger than another quantity, but precisely how much larger. It is similarly important, if a quantity fluctuates, to know its amplitude and period of fluctuation. But this orientation may simply reflect an analytic approach developed in one area because it was useful and then transferred to another where it may not be.

Our traditional view of natural systems, therefore, might well be less a meaningful reality than a perceptual convenience. There can in some years be more owls and fewer mice and in others, the reverse. Fish populations wax and wane as a natural condition, and insect populations can range over extremes that only logarithmic

ELTON1 noted the dangers of human simplification of the natural environment if ecosystems become less stable as they become more simple. The consequence may be increasingly unstable populations leading to extinction, further simplification and even more instability. That there might be a single relationship between such gross variables as stability and complexity is intriguing theoretically, in a field where generalizations are scarce. The evidence on this topic is controversial. Early theoretical studies were logically simplistic, if appealing, in suggesting that complex systems were more stable. Later theoretical studies were more sophisticated and suggested exactly the opposite. Field studies are, superficially, ambiguous and contradictory. If we are to resolve some of this controversy by pointing to several different definitions of stability, of complexity and of various potential variables of interest. Several score permutations of these definitions are possible and different ones will yield different results. The earlier theoretical treatments and field studies typically address different combinations from those of later studies; in the few cases where they treat the same combination, there is often good agreement. Most combinations, however, have not been explored and few have been studied extensively by both theorecticians and field workers.

Early studies2-4 argued that increased complexity enhanced ecosystem stability. This seemed so certain that the idea became a central feature of ecology texts. Walla5 makes one of his core principles of ecology: "... the accumulation of biological diversity ... promotes population stability." Later studies2,6 typically came to the opposite conclusion. To see why early confidence was misplaced is easy with hindsight. The first of Elton's six arguments was a theoretical one: simple population models are characteristically more stable than those more complex models were expected to fluctuate less. A second theoretical argument, that of MacArthur2, was that the more pathways for energy to reach a consumer, the less severe would be the failure of any one pathway. Perhaps because it represents conventional wisdom (don't put all your eggs in one basket), the argument was not given a formal mathematical treatment. The conflict between this argument and the diametrically opposite one from later studies is one I shall try to resolve.

One of Elton's lines of evidence involved the increased chance of pest outbreaks in agricultural systems, and the absence of pesticide outbreaks in tropical (but not temperate) forests and the prevalence of population cycles in the Arctic and, finally, the ease with which species can invade small, remote (and hence species-poor) oceanic islands. Elton's data were few: the absence of pest outbreaks in the tropics was based on casual conversation with three tropical foresters2. Furthermore, man's impacts on agricultural systems are many and varied: simplification may not be the only, or even the main cause of their instability.

Simply, the early theoretical arguments and field studies were heterogeneous and incomplete. Yet this heterogeneity only points to the fact that there are many questions to be answered in the discussion of stability—complexity relationships. No single question has logical supremacy.

Definitions

Table 1 lists definitions I shall use to build an array of complexity—stability questions. This set of definitions is not exhaustive2-5; I have included those definitions that have been most studied or which promise to be amenable to both theoretical and field studies. One can create 'complexity—stability' questions by taking combinations of measures of complexity, stability, and variables of interest. Looking at all the possible combinations suggests some features that should be discussed before answers are sought. With the definitions Table 1, I will probably not observe it except in transition to a new equilibrium. Rather special dynamics are required to permit

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Fig. 1. An illustration of the diametrically opposite effects of increasing complexity on two different measures of stability. Results are from model systems where the single herbivore is removed from a system of very closely interacting plants. As the number of competitive interactions between plants increases (abscissa), the system is more likely to lose plant species (upper graph) but change biomasses lower (lower graph) when the herbivore is removed. In the lower graph, the rates of biomasses plotted is the total biomass of plants without herbivory/total biomass of plants with herbivory. Numbers indicate number of plant species in the system.
Ecological Resilience
The ability to absorb disturbance and still maintain the same relationships between populations or state variables (Holling 1973)

Engineering Resilience
The time taken for recovery after a disturbance (Pimm 1984)
Measuring the Inertia and Resilience of Ecosystems

Walter E. Westman

The resilience of natural ecosystems is a property of keen interest to both theoretical and applied ecologists. Resilience, in this context, refers to the degree, manner, and pace of restoration of initial structure and function in an ecosystem after disturbance. It is an important ecological characteristic, reflecting ultimately the nature and complexity of homostatic processes in an ecosystem.

Discussions of the concept of ecosystem resilience are relatively recent, and a variety of terms has been proposed for properties of resilience. The ability of a natural ecosystem to restore its structure following acute or chronic disturbance (natural or human-induced) is here termed resilience, consistent with the use of Clapham (1971). This same set of properties is subsumed under the term stability by May (1973), Holling (1973), and Omnns (1973) and termed elasticity by Cairns and Dickson (1977). Given the definition of resilience above, it would seem useful to limit “stability” to the pattern of fluctuations in a relatively un-impacted ecosystem over time, a usage consistent with the first eight properties of stability discussed by Whittaker (1975). Traditionally, fluctuations in ecosystem structure have referred to variations in population densities of component species, but in theory other measures of ecosystem structure or function (e.g., biomass, net primary production, nutrient stocks, species richness) could be used. Since different properties of ecosystem structure and function will not necessarily vary at parallel rates, however, the ecosystem parameters chosen for study will have a crucial influence on the degree of stability or resilience observed.

A property of ecosystems distinct from those discussed above is the ability of a system to resist displacement in structure or function when subjected to a disturbing force. This property is referred to as “inertia” by Omnns (1973) and Cairns and Dickson (1977). Omnns (1973) considered inertia a type of stability; Holling (1973) termed the same property “resilience.” It is perhaps least confusing to retain “inertia” as a property separate from those exhibited by an ecosystem in a relatively unimpacted state (stability properties) and those exhibited by a disturbed ecosystem (resilience properties).

Notions of inertia and resilience in ecosystems are of considerable interest to applied ecologists, environmental managers, and planners. Those involved in planning development projects often wish to know which of a variety of potential sites might recover most quickly after disturbance from adjacent development or might resist change from the proposed impact most. This question arises, for example, in planning the route of a pipeline or transmission line through wilderness. Similarly, planners seek to predict which sites for surface mining will pose the least difficulties in subsequent rehabilitation efforts, or which route for oil tanker traffic will minimize risk of exposure of spilled oil to those marine ecosystems with the least ability to recover.

In the United States, the National Environmental Policy Act of 1969 focused planners’ attention on the issue of ecosystem resilience by requiring each environmental impact statement to describe any “irreversible and irrevocable commitments of resources” (Sec. 102(C)(vi)) involved in the proposed action. The ability of planners to assess the irreversibility of damages sustained by a natural ecosystem has been hampered to date by lack of precise definitions and measures of the characteristics of ecosystem resilience.

**Characteristics of Inertia and Resilience**

In Table 1, I suggest five characteristics of the inertia and resilience of a system. The first three of these have been discussed by Omnns (1973) in the context of properties of stability. The table provides examples of applications of these terms to the inertia and resilience of a simple object (a metal coil) and of a complex homostatic system (an ecosystem).

Inertia refers to the resistance to disturbance of an object or system, whereas the remaining four terms are properties of resilience, which refer to ways in which the disturbed system recovers. Elasticity refers to the time involved in restoration; amplitude to the degree of brittleness of the system; hysteresis to the degree to which the pattern of recovery is not simply a reversal of the pattern of initial alteration; and malleability to the ease with which the system can become permanently altered.

At first glance it might seem desirable to develop a uniform set of indices of the characteristics of resilience applicable to all natural ecosystems. In practice, however, the most appropriate measures are likely to differ with the goals of investigation, the nature of the impact, and the biome under investigation. This observation does not preclude the possibility of using identical measures of each property of resilience for a range of ecosystems being subjected to the same kind of impact. I examine below how a variety of...
Which definition do ecologists use when testing for resilience to disturbance?

Do ecologists measure resilience as they have defined it?
Engineering Resilience
The time (t) taken for recovery (r) after a disturbance

Ecological Resilience
The ability to absorb disturbance and still maintain the same relationships between state variables (r)

Westman's Resilience
The degree (d), manner, and pace (t) of recovery (r) of ecosystem structure and function after disturbance
How do ecologists define and measure resilience?

Review of papers (1973–2012) citing:

- Holling (1973)
- Pimm (1984)
- Westman (1978)
- Connell and Sousa (1983)
- Ives and Carpenter (2007)

experiment* OR compar* OR observ*
959 papers identified

226 experimental studies

317 observational studies

96 measured ecosystem response to disturbance

96 measured ecosystem response to disturbance

189 papers tested resilience to disturbance
Findings?

Brace yourself for some bar graphs...
Does measurement match definition?

- **Ecol**: 50% No, 10% Yes
- **Eng**: 60% No, 5% Yes
- **Ecol+Eng**: 10% No, 5% Yes
- **Westman**: 50% No, 10% Yes
Tests of resilience: What do ecologists measure?
Which definition do ecologists use when testing for resilience to disturbance?

Cite Holling & sometimes quote definitions consistent with ecological & engineering resilience

Do ecologists measure resilience as they have defined it?

No, except those citing Westman

How do ecologists measure resilience? Poorly!
Experimental test of resilience to heat disturbance
Meta-analysis of resilience to disturbance

Gunning for resilience Rottnest Island December 2013
How does recovery differ among ecosystems?

Kelp forest, soil community, coral reef, tropical forest, temperate forest, grasslands, bryophyte communities, estuarine fish
Fire, grazing, drought, hurricane, earthquake, bleaching, anoxia, storm surge, heat stress
Thanks!

Etienne Laliberte Raphael Didham
Mats Dynesius Brandon Bestelmeyer
James Glimour Loretta Battaglia
Natasha Banning Jodi Price John Dwyer
Takehiro Sasaki Andrew Denham
Charles Price Mandy Trueman Eric Seabloom
Peter Bellingham Alistair Becker
Brian Starzomski Lauren Hallett Jane Catford

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