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Craig R. Allen
University of Nebraska - Lincoln, callen3@unl.edu

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Commentary

Ecosystems and Immune Systems: Hierarchical Response Provides Resilience against Invasions

Craig R. Allen
Clemson University

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INTRODUCTION

Janssen (2001) provides the stimulus for thoughtful comparison and consideration of the ranges of responses exhibited by immune systems and ecological systems in the face of perturbations such as biological invasions. It may indeed be informative to consider the similarities of the responses to invasions exhibited by immune systems and ecological systems. Clearly, both types of systems share a general organizational structure with all other complex hierarchical systems. Their organization provides these systems with resilience. However, when describing the response of ecological-economic systems to invasions, Janssen emphasizes the human-economic response. I would like to expand on his comparison by focusing on how resilience is maintained in complex systems under the threat of invasion.

The response of the immune system, i.e., the distributed system of immune cells that respond without central control, is only one part of a complex hierarchical system (the human body), and this response occurs at different levels in that hierarchy. Within a range of scale, there is a diversity of response types at the cellular level of individual immune system components, where different types of cells respond to slightly different insults in slightly different ways at slightly different speeds. This diversity of response within a scale occurs in ecosystems as well, where different types of immune cells are analogous to different species in ecological systems. Within a range of scale, some species compete with invaders for food or space, and others may prey upon them. Competition, predation, and other species interactions and functions occur in numerous forms across species. This diversity of response and function provides a robust check to a variety of invasions. Janssen's example of the I LOVE YOU virus shows how diversity—in this case, a diversity of e-mail software programs—prevented a global failure of computers and thus the Internet system. Those of us not using Microsoft Outlook as an e-mail program provided firewalls that stopped the spread of the virus. This within-scale response is complemented by a cross-scale response when an invasion "scales up."

In immune systems as in ecosystems, when a pathogen or perturbation exceeds the level of control inherent in the diverse response at one scale, controls at broader scales are activated (Peterson et al. 1998). For example, when spruce budworm (*Choristoneura fumiferana*) outbreaks first occur in boreal forests, initially only "small-scale" birds such as warblers consume budworms. However, when budworms begin to proliferate, other small birds start to consume them (a within-scale diverse response). As budworm densities increase and budworms aggregate, larger birds, such as vireos and thrushes, begin to prey upon them. As the outbreak progresses further and entire stands of trees are involved, the largest birds, such as Corvids, prey upon them; budworms now represent an aggregated large-scale perturbation. In combination, a diversity of function within size classes of birds and a redundancy of function across scales (size classes) provide strong and highly resilient control of budworm populations (Holling 1988, Peterson et al. 1998).

Slower and broader responses to invasions of the human body by pathogens also occur. Fever is a whole-system response that follows the failure of a very localized response. The slowest response is the change in gene frequency that occurs across generations and results from natural selection. This "redundancy across scales" complements the diversity of response within a single scale. In an example derived from the immune system, a localized infection (incipient invasion) first engenders a local response from a few immune cells. If that response is unsuccessful, a broader response occurs, and the immune system begins to manufacture more immune cells. As a pathogen invasion progresses, other systems become involved, and shivering may begin. A whole-system response in humans will involve systematic responses such as shivering, and may include behavioral changes. Ecosystems respond in a similar way, although without the emergent property of behavior. This nested hierarchy adds resilience to the response of complex ecological and human systems to the great range of insults that can be broadly classified as invasions.

EFFECTS OF INVASIONS ON RESILIENCE

In ecological systems, invasions may occur in a range of broad classes related to scale. They may be restricted to within a single range of scale (over limited body size classes), leading to a decrease in resilience due to the loss of one scale of response to further insults (assuming that functions are not replaced). They may occur at scale breaks, where there may be heightened variability even in unperturbed systems, which may or may not lead to a loss of resilience (Allen et al. 1999). They may replace lost species (or obsolete technologies) as well as their functions, for example, digital phones replacing analog phones, cars replacing horses, or coyotes replacing red wolves (note that a true replacement is never really possible). Invaders may also take the place of recently extinct or extirpated species without replacing their original functions, which also leads to a loss of resilience. Examples include fire ants replacing many native ants but no longer carrying out their ecological function of seed dispersal (Zettler et al. 2001), or malls replacing community general stores without restoring lost social functions. It is not entirely clear that invasion of the human system by pathogens can occur at more than one scale, although the response by immune systems is multiscaled when needed.

Humans and the ecosystems they inhabit are intricately linked. Both ecological and economic diversity drive resilience in human-ecological systems. If human-ecological systems share a long history of co-adaptation, they appear to self-organize to achieve a state of dynamic stability that reflects the limitations of the landscape (Berkes and Folke 1998). Invasions by nonindigenous species or technologies can alter that trajectory.

Janssen's example of an ecological-economic response to invasions, i.e., the response to the invasion of fire ants (*Solenopsis invicta*) in the southeastern United States, describes a purely human-economic response. Concurrent to this response, a purely ecological response occurs as well. Ideally, the two would work in tandem, although often the human-economic response is at odds with the ecological response. The large-scale human-economic response to fire ant invasion was to fit World War II bombers with the equipment necessary to broadcast Mirex bait and drop it on more than 56×10^6 ha of the southeastern United States between 1962 and the cancellation of its registration by the US EPA in 1978 (Williams et al. 2001). In addition to reducing fire ant populations, this response must also have reduced the populations of many of the native ants that serve as competitors to fire ants, and may have hastened the invasion by fire ants and increased the severity of its impact. In contrast, the ecological response to fire ant invasion is characterized by changes in the foraging patterns of native ants, shifts in guild and functional group structure, and alterations in predatory and competitive relationships. A truly robust response would engage both ecological and human-economic systems in a complementary, rather than competitive, manner.

RESILIENCE-EMBRACING RESPONSES TO INVASIONS

Janssen states that resilience is influenced by how systems are managed. This is true, but ecological resilience depends on how systems are self-organized as well as how little they are managed! In this context, I define management as any action that reduces the variability within a variable or suite of variables. Resilience is highest when the full range of variability is allowed, and when a system is allowed to evolve according to its own trajectory. Thus, management should help a system develop along its natural trajectory.

When does the management or immune response fail? When is system resilience exceeded? These responses fail when the invader is too novel, too fast, or too abundant. They fail when the system has invested too much in the wrong defense or is not diverse enough, or when the response is not consistent with the system trajectory, i.e., when the response is against the inherent "path dependency" of the system (Makse et al. 1995). They also fail when invasions occur after the system has already been threatened by previous invaders; in this case, the system is not necessarily any less resilient, but simply too overwhelmed to respond. Long-term solutions to biological invasions do not involve human management, especially by chemical means, although clearly it may be necessary to resort to this occasionally. In general, this "pathological" approach (Meffe and Holling 1996) of rigidly controlling variability not only is bound to have a disastrous impact in the future, but also encompasses only short-term institutional memory and prevents the evolution of memory in ecological systems. Human beings and human institutions are not only agents of control in ecological-economic systems. They are also components of the ecological system itself, namely, its self-organizing biotic and abiotic processes and the communities and species therein, which develop emergent properties such as resilience and invasion resistance even in the absence of humans and their institutions.

Computer scientists are exploring responses to virtual viruses in which viruses similar in form to known computer viruses are recognized and filtered. A filtering approach to invasions is needed, and several institutions have developed such an approach. However, with biological invasions of the macro kind, the most useful approach is "guilty until proven innocent" (Ruesink et al. 1995). Guilty if similar surely works, but seemingly harmless, nonindigenous species may not be recognized as harmful until they are well established and some other perturbation makes apparent the loss of resilience they have caused.

Janssen's premise is that ecosystems share many features with immune systems. He explicitly considers human-ecological linked systems, but then describes mostly the human response to invasions. Although many urban-social-economic systems seem to have coevolved with the ecosystems within which they are embedded, modern human institutions too often exert such strong controls over the processes that produce ecological structure (for example, hydrology and fire) that we fail the linked system model. In "modern" societies, the human-economic system often dramatically overshadows, alters, and squelches ecological pattern and process, so that renewal of ecological systems based on natural processes cannot occur. If the ecological-economic system that results contains little that is truly ecological, it will probably be brittle (Light et al. 1995) and prone to invasion and collapse.

It is useful to consider the similarities of response exhibited by immune systems and ecological systems to invasions. Clearly, both immune systems and ecological systems share a general organization with all complex hierarchical systems. They both are diverse, with components (species or immune cell types) operating individually, they are characterized by localized interactions among their components, and they carry out some form of selection (Levin 1998). This type of organization provides these systems with resilience. Additionally, when the level of resilience in either of these systems is exceeded, a nonlinear response occurs. This response also highlights the differences between immune systems and ecological systems. Ecosystems much more easily integrate new components without radical reorganization. In humans, the incorporation of new species of "friendly" bacteria is a rare event. Indeed, it would be unfortunate if human systems did integrate new components in a strictly Gleasonian fashion (Gleason 1926). Furthermore, when resilience is exceeded in ecosystems, a new state of ecological organization is expected to develop rapidly. If resilience is exceeded in immune systems, the only apparent alternative for the human system is death.

Is this comparison and analogy useful for ecosystem management, which is Janssen's primary focus? Absolutely. As with the human body, we must be wary of too much remedial intervention in the face of invasions. Overmedicating trivial illnesses leads to hardier pathogens and weakened populations of "friendly" bacteria, leaving the body more vulnerable to progressively worse infections. In ecosystems, too much intervention can have an analogous effect.

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Address of Correspondent:
Craig R. Allen
USGS-BRD
South Carolina Cooperative Fish and Wildlife Research Unit
G27 Lehotsky Hall
Clemson University
Clemson, South Carolina, USA 29634
Phone: (864) 656-4461
Fax: (864) 656-1034
allencr@clemson.edu

Online at http://www.ecologyandsociety.org/vol5/iss1/art15/