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ECOSYSTEMS

Cross–Scale Interactions and Changing Pattern–Process Relationships: Consequences for System Dynamics

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ABSTRACT

Cross–scale interactions refer to processes at one spatial or temporal scale interacting with processes at another scale to result in nonlinear dynamics with thresholds. These interactions change the pattern–process relationships across scales such that fine-scale processes can influence a broad spatial extent or a long time period, or broad-scale drivers can interact with fine-scale processes to determine system dynamics. Cross–scale interactions are increasing recognized as having important influences on ecosystem processes, yet they pose formidable challenges for understanding and forecasting ecosystem dynamics. In this introduction to the special feature, ''Cross–scale interactions and pattern–process relationships'', we provide a synthetic framework for understanding the causes and consequences of cross–scale interactions. Our framework focuses on the importance of transfer processes and spatial heterogeneity at intermediate scales in linking fine- and broad-scale patterns and processes. Transfer processes and spatial heterogeneity can either amplify or attenuate system response to broad-scale drivers. Providing a framework to explain cross–scale interactions is an important step in improving our understanding and ability to predict the impacts of propagating events and to ameliorate these impacts through proactive measures.

Key words: ecological surprises; landscape ecology; propagating events; spatial heterogeneity; transfer processes.

INTRODUCTION

Cross–scale interactions are increasingly recognized as important features of ecological systems that challenge our ability to understand and forecast dynamics (Holling 1992; Levin 1992; Thompson and others 2001). Cross–scale interactions (CSI) refer to processes at one spatial or temporal scale interacting with processes at another scale that often result in nonlinear dynamics with thresholds (Carpenter and Turner 2000; Gunderson and Holling 2002; Peters and others 2004a). These interactions generate emergent behavior that cannot be predicted based on observations at single or multiple, independent scales (Michener and others 2001). Cross–scale interactions can be important both for extrapolating information about fine-scale processes to broad-scales or for down-scaling the effects of broad-scale drivers on fine-scale patterns (Ludwig and others 2000; Diffenbaugh and others 2005). The relative importance of fine- or broad-scale pattern–process relationships can vary through time, and compete as the dominant factors

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controlling system dynamics (for example, Rodó and others 2002; King and others 2004; Yao and others 2006).

Although CSI are recognized as important, a critical challenge in ecology is *how* fine-scale pattern–process relationships are connected to broader patterns and drivers to result in ecosystem change (Thompson and others 2001; Turner 2005). In addition, the Millennium Ecosystem Assessment indicated that CSI are an urgent research priority for ecologists (Carpenter and others 2006). Our goal is to provide a framework for explaining how domains of scale are connected to generate nonlinear dynamics. We focus on transport processes and spatial heterogeneity at intermediate scales as the key to linking fine- and broad-scale processes. We start this special feature with a description of the framework and its development from existing bodies of theory. The following papers in the special feature provide support for the framework from a diverse array of ecosystem types and observer perspectives. The CSI concept provides a powerful tool for improving our understanding of ecosystem dynamics and their often surprising and far-reaching consequences.

Related Frameworks

Most frameworks for nonlinear ecosystem behavior are hierarchical such that a small number of structuring processes control ecosystem dynamics; each process operates at its own temporal and spatial scale (Allen and Starr 1982; O'Neill and others 1986). Finer scales provide the mechanistic understanding for behavior at a particular scale, and broader scales provide the constraints or boundaries on that behavior. Functional relationships between pattern and process are consistent within each domain of scale such that linear extrapolation is possible within a domain (Wiens 1989). Thresholds occur when pattern–process relationships change rapidly with a small or large change in a pattern or environmental driver (Groffman and others 2006; Bestelmeyer 2006), although both external stochastic events and internal dynamics can drive systems across thresholds (Scheffer and others 2001). Crossing a threshold can result in a regime shift where there is a change in the direction of the system and the creation of an alternative stable state (Allen and Breshears 1998; Davenport and others 1998; Walker and Meyers 2004).

Under some conditions, thresholds may be recognized when changes in the rate of fine-scale processes within a defined area propagate to produce broad-scale responses (Gunderson and Holling 2002; Redman and Kinzig 2003). In these cases, fine-scale processes interact with processes at broader scales to determine system dynamics. A series of cascading thresholds can be recognized such that crossing one pattern–process threshold induces the crossing of additional thresholds as processes interact (Kinzig and others 2006). For example, a series of thresholds defined by increases in the rate of fire spread occur in wildfire as the dominant processes and scales change over time (Peters and others 2004a). Wildfires are often initiated with a single lightning strike that ignites a tree or patch of herbaceous vegetation. Initially, the rate and extent of fire spread is related to individual tree properties, such as the density and spatial arrangement of green versus brown leaves or needles. Fire spread to another tree within a patch of trees depends on fuel characteristics of the patch interacting with individual tree properties. Some trees will ignite easily whereas other trees with similar characteristics may not burn or will burn slowly because of low connectivity with adjacent trees. As the fire continues to spread, additional patches of trees will ignite depending on interactions among fuel load characteristics connecting patches, fuel load within the patch, and individual tree properties. The dominant process changes through time from the scale of individual trees to within-patch variation to among-patch connectivity. For very large fires, land–atmosphere interactions can become operative to create fire-generated weather that results in a rapid increase in the rate of fire spread. At this point in time, broad-scale processes drive system dynamics by overwhelming processes at tree and patch scales. Thus, wildfire behavior can only be explained by considering interactions among pattern–process relationships occurring at each spatial and temporal scale.

Recent theories and ideas about system behavior have used hierarchy theory as a basis for describing interactions among processes at different scales. Such theories include complex systems (Milne 1998; Allen and Holling 2002), self-organization (Rietkerk and others 2004), panarchy (Gunderson and Holling 2002), and resilience (Holling 1992; Walker and others 2006). CSI are an integral part of all of these ideas. However, these frameworks do not explain *how* patterns and processes at different scales interact to create nonlinear dynamics. Because CSI-driven dynamics are believed to occur in a variety of systems, including lotic invertebrate communities in freshwater streams (Palmer and others 1996), lakes (Stoffels and others 2005), mouse populations in forests (Tallmon and others

2003), soil microbial communities (Smithwick and others 2005), coral reef fish recruitment in the ocean (Cowen and others 2006), human diseases (Rodó and others 2002), and grass–shrub interactions in deserts (Peters and others 2006), it is critical that ecologists find ways to measure CSI. We hope that the ideas presented in this and the following set of papers facilitate this endeavor.

FRAMEWORK FOR CROSS–SCALE INTERACTIONS AND CHANGING PATTERN–PROCESS RELATIONSHIPS

We hypothesize that intermediate-scale properties of transfer processes and spatial heterogeneity determine how pattern–process relationships interact from fine to broad scales (Figure 1). Although we recognize that a continuum of scales exists and our framework is sufficiently general to accommodate additional scales, we focus on three domains of scale: ''fine'' at the scale of individual plants and animals, ''intermediate'' at the scale of groups of individuals of the same or different species, and ''broad'' refers to large spatial extents such as landscapes, regions, and the globe. Fine-scale pattern–process relationships include both biotic (for example, recruitment, competition, mortality) and abiotic processes (for example, sediment loss, soil water dynamics) that influence the distribution and abundance of individuals. Intermediate-scale pattern–process relationships refer to the spatial patterns of groups of individuals (for example, patches or populations) that both influence and are structured by transfer vectors (for example, wind, water, fire, dispersing animals) that move materials and effects horizontally and vertically (for example, propagules, nutrients, disturbances). Broad-scale pattern–process relationships include atmospheric circulation processes that influence pattern from landscapes to regions and continents. Environmental drivers, such as climate, disturbance, and human activities, influence pattern–process relationships at each domain of scale.

In our framework, within a domain of scale (that is, fine, intermediate or broad), patterns and processes can reinforce one another and be relatively stable (Figure 1A). Changes in external drivers or disturbances can alter pattern–process relationships in two ways. *First*, altered patterns at fine scales can result in positive feedbacks that change patterns to the point that new processes and feedbacks are induced. This shift is manifested in nonlinear, threshold change in pattern and process rates. For example, in arid systems, disturbance to grass patches via heavy livestock grazing can reduce the competitive ability of grasses and allow shrub colonization. After a certain density of shrubs is reached in an area and vectors of propagule transport (for example, livestock, small animals) are available to spread shrubs to nearby grasslands, shrub colonization and grass loss can become under the control of dispersal processes rather than competition. Shrub expansion rates can increase dramatically (Peters and others 2006). As shrub colonization and grazing diminish grass cover over large areas, broadscale wind erosion may govern subsequent losses of grasses and increases in shrub dominance. These broad-scale feedbacks ''down scale'' to overwhelm fine-scale processes in remnant grasslands. Once erosion is an important landscape-scale process, neither competition nor dispersal effects have significant effects on grass cover. *Second*, direct environmental effects on pattern–process relationships at broad scales can similarly overwhelm fine-scale processes. For example, regional, long-term drought can produce widespread erosion and minimize the importance of local grass cover or shrub dispersal to patterns in grasses and shrubs.

Under the conditions that intermediate-scale transfer processes and spatial heterogeneity are not important, then linear extrapolation can be used to aggregate information from fine to broad scales (Strayer and others 2003; Peters and others 2004b; Turner and Chapin 2005). Alternatively, if transfer processes are negligible yet spatial heterogeneity is important, then an area can be stratified to obtain homogeneous, independent cells where linear extrapolation can also be used to aggregate within each cell. Aggregation to the entire spatial extent is typically accomplished using weighted averaging or similar techniques.

However, when connections among spatially heterogeneous areas via transfer processes are important, then a spatially-explicit approach is needed that accounts for the rate, magnitude, and direction of materials being transported (Strayer and others 2003; Peters and others 2004b; Turner and Chapin 2005). Under these conditions, examination of patterns and processes at a single scale or even multiple scales is insufficient. Studies are needed that include pattern–process relationships interacting across a range of appropriate scales. For example, recent studies show that the cross–scale relationships between cholera and the change in frequency and intensity of ENSO events since 1976 can only be determined using nonlinear statistical techniques that include data collected at appropri-

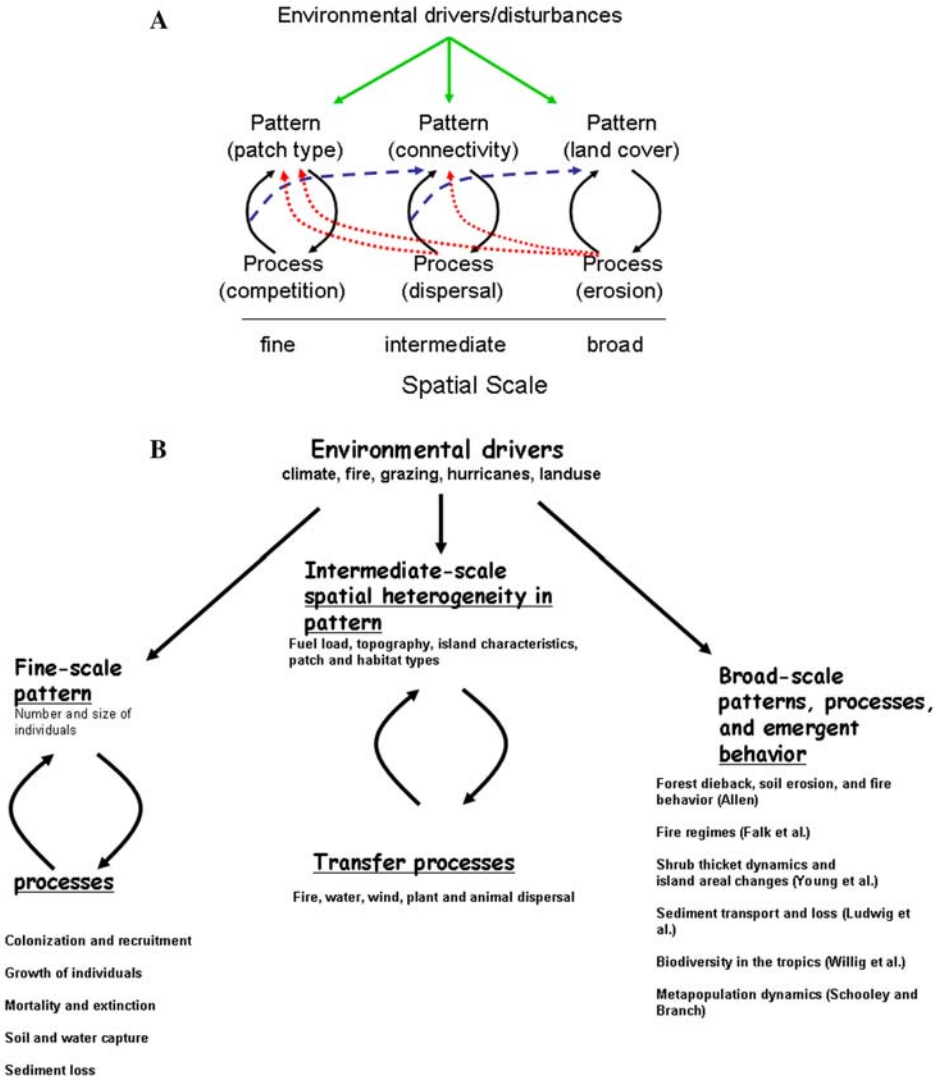

Figure 1. A Diagram representing cross–scale interactions. *Solid arrows* represent pattern–process feedbacks within three different scale domains with one example of pattern and process shown for each domain. *Green arrows* indicate the direct effects of environmental drivers or disturbances on patterns or processes at different scales (for example, patch disturbance vs. climate). *Blue arrows* indicate the point at which altered feedbacks at finer scales induce changes in feedbacks at broader scales (for example, fine-scale changes cascade to broader scales). *Red arrows* indicate when changes at broader scales overwhelm pattern–process relationships at finer scales. **B** Our framework for understanding cross–scale interactions focuses on the importance of transfer processes and spatial heterogeneity at intermediate scales providing the linkage between fine-scale processes and broad-scale pattern. Environmental drivers can influence each domain of scale. *Arrows* showing cross domain interactions are not shown. Authors of papers in this special issue are listed with their broad-scale pattern and emergent behavior.

ate scales (Rodó and others 2002). Previous studies that failed to find a relationship between global climate change and human disease transmission often included linear approaches and scale mismatches (Pascual and others 2000; Patz 2002).

Transfer processes and spatial heterogeneity can either amplify or attenuate system response to broad-scale drivers (Diffenbaugh and others 2005). Amplification occurs when the rate of change in system properties increases nonlinearly. This increase can result from high spatial heterogeneity that promotes connectivity and cascading events, such as in the wildfire example described above (Peters and others 2004a). Cascading events in which a fine-scale process propagates nonlinearly to have a large impact have also been documented in the climate system and in lakes (Lorenz 1964; Wilson and Hrabik 2006).

Attenuation occurs when the rate of change decreases through time, such as the decrease in wave amplitude as the wave form associated with a tsunami increases (Merrifield and others 2005). The result is that the greatest effects of a tsunami occur closest to the source of the seismic event, and spatial heterogeneity in land or sea features become increasingly important as distance from the seismic event increases (Fernando and McCulley 2005). Thus, small-scale variation in wave height and impact were related to coral reef heterogeneity off the coast of Sri Lanka following the tsunami of 2005 that did not occur at closer locations such as Banda Aceh (Fernando and McCulley 2005). In other cases, the relationship between transfer processes and spatial heterogeneity is more complex. For example, connectivity of larvae from coral reef fishes is more locally important and regionally more variable than previously thought based on new analyses of dispersal constraints interacting with physical oceanography (Cowen and others 2006).

EXAMPLES OF CSI

Although each paper in this special feature has a unique broad-scale pattern and emergent behavior to be understood and predicted, similar fine-scale processes and environmental drivers are often studied, and a small set of transfer processes and spatial heterogeneity characteristics are required to explain these dynamics (Figure 1B). This generality suggests great promise in applying our framework to many other systems and questions where pattern–process relationships may change with spatial and temporal scale.

Using our common framework provides new insights into dynamics for a variety of systems, ranging from fire behavior and vegetation response in temperate forests (Allen 2007; Falk and others 2007) to gastropod biodiversity in tropical forests (Willig and others 2007), sediment movement from rangelands (Ludwig and others, unpublished data) muskrat metapopulation dynamics in freshwater marshes (Schooley and Branch 2007), and shrub thickets and barrier island dynamics (Young and others 2007). For example, new insights to fire behavior and forest dieback were found by considering interactions among fire spread, water flow, and insect pest dispersal with spatial heterogeneity in fuel loads, bare soil patches, and insect food resources; drought and livestock grazing act to modulate these interactions (Allen 2007). Falk and others (2007) were able to explain the spatial and temporal distribution of fires only after connectivity in fuel loads as affected by landforms and climate were explicitly considered.

In a coastal system, the apparent paradox between expanding shrub thicket areas and decreasing island areas was explained by understanding the role of variability in ocean currents and sediment transport (Young and others 2007). Sediment movement from upland rangelands to downslope areas also required information about the connectivity of patches by water (Ludwig and others, unpublished data).

Animal dynamics an also be understood within a CSI framework. Variability in the biodiversity of gastropods in tropical forests was hypothesized to be explained by local demographics interacting with dispersal among forest patches created by hurricanes (Willig and others 2007). Predicting metapopulation dynamics of muskrats in freshwater marshes requires an understanding of spatial heterogeneity of habitat quality and patch connectivity (Schooley and Branch 2007).

IMPROVING UNDERSTANDING AND PREDICTIONS

Relating phenomenon across scales remains a critical problem in ecology (Levin 1992). Because CSIs often result in nonlinear or unexpected behavior that make understanding and prediction difficult, it is critical to identify the conditions or systems that are susceptible to these interactions. Approaches that have been used previously include measuring responses at multiple scales simultaneously and then testing for significant effects of variables at each scale (for example, Smithwick and others 2005; Stoffels and others 2005). Experimental manipulations can be used to examine processes at fine and intermediate scales, and to isolate and measure impacts of broad-scale drivers under controlled conditions (for example, Palmer and others 1996; King and others 2004). Stratified-cluster experimental designs show promise as efficient methods for considering multiple scales in spatial variables, and to account a priori for distance as related to transport processes in the design (Fortin and others 1989; King and others 2004).

Quantitative approaches also show promise in identifying key processes related to CSI. Statistical analyses based on non-stationarity (Rodo and others 2002) and nonlinear time series analysis (Pascual and others 2000) are useful for identifying key processes at different scales. Spatial analyses that combine traditional data layers for fine- and broad-scale patterns with data layers that use surrogates for transfer processes at intermediate scales (for example, seed dispersal) can isolate individual processes and combinations of processes that influence dynamics in both space and time (for example, Yao and others 2006). Simulation models that use fine-scale models to inform a broader-scale model can be used to examine the relative importance of processes and drivers at different scales, and their interactions, to system dynamics (Moorcroft and others 2001; Urban 2005). Coupled biological–physical models that include population processes and connectivity among populations as well as broad-scale drivers have been used to show the conditions when connectivity is important, and to identify the locations that are more susceptible or resilient to management decisions (Cowen and others 2006).

We hope this Special Feature will help catalyze development of new concepts and approaches for dealing effectively with the challenges of CSI posed by the rapid and multi-scale changes occurring on Earth.

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