

Perspectives on Global Change Theory

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Human influences on ecological drivers are increasingly recognized as dominant processes across a range of spatial and temporal scales. Regional to global-scale changes in drivers and important resources, such as atmospheric carbon dioxide concentrations, climate, and nitrogen deposition, are known to alter biotic structure, ecosystem function, and biogeochemical processes with feedbacks to human activities and the atmosphere (Petit et al. 1999; Grimm et al. 2000; Fenn et al. 2003; IPCC 2007). Human activities also directly affect ecosystems at finer scales through urbanization, species movement and extinction, and changes in land use that, in aggregate, have global impacts as human populations continue to increase and migrate (Alig et al. 2004; Theobald 2005; Grimm et al. 2008b). Although large volumes of data on global change drivers and ecological responses to them have been synthesized (e.g., Heinz Center 2002; Millennium Ecosystem Assessment 2005; Canadell et al. 2007; IPCC 2007), a coherent body of ecological theory focused on global change is lacking (Peters et al. 2008).

The U.S. Global Change Research Act of 1990 defined global change as: “Changes in the global environment—including alterations in climate, land productivity, oceans or other water resources, atmospheric chemistry, and ecological systems—that may alter the capacity of the Earth to sustain life.” It is now clear that direct and indirect human actions are responsible for most of the more dramatic change occurring today and forecast for the future (Vitousek et al. 1997b). Global change is an aggregate of different forces that op-

erate across all scales; many of these forces will be discussed in this chapter. In contrast, drivers historically studied by ecologists were assumed to occur locally and were ecosystem-specific, such as fire in forests and floods in streams. For contemporary ecological systems, a framework is needed to integrate across scales and to better understand the effects of multiple interacting drivers on ecosystem dynamics. For example, elevated concentrations of carbon dioxide (CO₂) and other greenhouse gases in the atmosphere are increasing temperatures globally whereas precipitation regimes are changing locally; ecosystem responses to these multiple, interacting drivers are often unknown (IPCC 2007). Existing ecological theories can be brought to bear on global change issues, but these theories need to be adapted and modified such that the key and sometimes unique aspects of global change drivers and responses to them are explicitly considered.

Ecosystem responses to global change drivers are often measured experimentally across a range of scales. The term “scale” generally implies a certain level of perceived detail (Miller 1978) that can be quantified using two key components: grain (the finest level of spatial and temporal resolution of a pattern) and extent (the spatial and temporal span of a phenomenon or study; Turner et al. 1989). Here we focus on a hierarchy of characteristic scales defined as the spatial and temporal scale on which ecological phenomena principally operate and can be most appropriately studied (Wu 2007). We discuss characteristic spatial scales defined primarily by spatial extent and recognize the correspondence between spatial and temporal scales (Urban et al. 1987). For example, fine scales of individuals or portions thereof (e.g., leaves) operate at small spatial (centimeters to meters) and short temporal (seconds to days) scales compared with plots or patches that contain groups of individuals, populations, or communities operating at intermediate spatial (tens of meters to ha) and temporal scales (days to years) (e.g., Shaw et al. 2002; Magill et al. 2004; Morgan et al. 2007; Siemann et al. 2007). Broad spatial scales include ecosystems at landscape scales, and biomes or geographic distributions of species at regional, continental, and global scales where pattern dynamics occur over long timescales (decades to centuries).

Fine-scale patterns of individual dynamics can be extrapolated to broader spatial extents using spatial patterns of responses combined with flows of materials (nutrients, water, propagules) and phenological responses (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Changes in regional- to global-scale patterns in vegetation structure and productivity can also be estimated directly using simulation models or remotely sensed images (Defries et al. 2000; Sitch et al. 2008). In most cases, these studies have been conducted at one scale or, in some cases, at multiple independent scales (e.g., Peterson

et al. 2003). Less attention has been devoted to how patterns and processes interact across scales to generate emergent behavior (e.g., Peters et al. 2004; Allen 2007). The propagation of fine-scale dynamics to larger scales of pattern often can not be predicted using linear extrapolation as a method for upscaling. Similarly, the overwhelming effect of broad-scale drivers on fine-scale dynamics can not be understood by simply downscaling effects of these drivers (Peters et al. 2007). Alternative approaches are needed that account for cross-scale interactions (Peters et al. 2009). Because global changes in drivers and responses are inherently cross-scale and are connected spatially (Peters et al. 2008), theories of global change must account for these interactions.

There are many well-known examples of how fine-scale processes can propagate to influence large spatial extents, and how broad-scale drivers can overwhelm fine-scale variation in pattern. For example, land use practices in central Asia, including overgrazing by livestock and cultivation of marginal lands, are interacting with effects of drought to result in high plant mortality and increased soil erosion at the scale of individually managed fields (e.g., 1–10 ha). Because most farmers and ranchers are following the same practices, these field-scale dynamics often aggregate nonlinearly with thresholds to the landscape and regional scales to generate large dust storms, the frequency of which has increased from 1 in 31 years to 1 per year starting in 1990 (Liu and Diamond 2005). As these dust storms continue to expand in spatial extent, they can travel intercontinentally to influence air quality in North America (<http://svs.gsfc.nasa.gov/goto?2957>), and can overwhelm natural determinants of local air quality (Jaffe et al. 2003).

In this chapter, we outline the characteristics of a theory of global change that draws upon a range of existing theories, including those from foraging (Sih chapter 4) and niche theory (Chase chapter 5), population biology (Hastings Chapter 6), succession theory (Pickett et al. Chapter 9), ecosystem ecology (Burke and Lauenroth Chapter 11), and environmental (Fox et al. Chapter 13) and biogeographic (Colwell Chapter 14) theory, as well as landscape ecology (Turner et al. 2001) and other disciplines such as Earth system sciences. We develop the basis for this theory and provide supporting evidence for its utility. We also provide an example where misleading results are likely to be obtained if the underlying concepts for such a theory are not accounted for, and we discuss new research directions based on this theory.

Domain, propositions, and mechanisms

The domain of a theory of global change is the causes and consequences of ecological properties of systems when the natural and human-induced driv-

ers interact across a spatial and temporal hierarchy of characteristic scales. As a theory of global change develops, there are four key propositions that need to be considered—two occur under current conditions with natural variation in drivers, and two are unique to systems experiencing global change (Table 12.1). These four propositions provide the context from which we derive our perspective on global change theory.

Our propositions follow from the eight fundamental principles of a theory of ecology, as proposed by Scheiner and Willig (2008; Chapter 1). In addition, spatial and temporal interactions of patterns and processes, originally articulated by (Watt 1947), are a fundamental concept in our developing theory. Our perspective integrates a number of theories operating at specific scales with theories that link scales. We also incorporate ideas from other disciplines (physical sciences, human systems) to address connectivity by water, wind, and humans. We believe that any global change theory needs to be organized by spatial scales that correspond to scales through time.

Propositions under current conditions

In our developing theory, pattern-process relationships interact across a hierarchy of scales (proposition 1) to result in spatial heterogeneity and connectivity among spatial units to be the critical system properties governing dynamics (proposition 2, Table 12.1). Our first proposition is derived from hierarchy theory (Allen and Starr 1982) and a framework for interactions across scales (Peters et al. 2004; 2007). Our second proposition combines a framework developed for heterogeneous arid landscapes (Peters et al. 2006) with an emerging connectivity framework designed to relate fine-scale dynamics with broad-scale drivers (Peters et al. 2008).

Proposition 1. Interactions across scales. Our first proposition is that there is natural variation in environmental drivers and system responses that form a hierarchy of interacting spatial and temporal scales (Fig. 12.1a). This proposition expands on general principles from hierarchy theory, where 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 et al. 1986). Finer scales provide the mechanistic understanding for behavior at a particular scale, and broader scales provide the constraints or boundaries on that behavior. Other chapters in this book describe these fine-scale mechanisms more completely (Holt Chapter 7; Burke and Lauenroth Chapter 11) or describe the relationships among scales, such as the use of patches to explain landscape-scale dynamics in metapopulation theory (Hastings Chapter 6) and succession theory (Pickett et al. Chapter 9), and develop scaling relationships (Leibold Chapter 8)

Table 12.1 The domain and four propositions associated with a developing theory of global change. Propositions 1 and 2 occur under current conditions with natural variation in drivers. Propositions 3 and 4 are unique to systems experiencing global change.

Domain

Causes and consequences of ecological properties of systems when the natural and human-induced drivers interact across a spatial and temporal hierarchy of scales.

Propositions

1. Pattern-process relationships interact across a hierarchy of scales.
 2. Intermediate-scale properties associated with connectivity and spatial heterogeneity determine how pattern-process relationships interact from fine to broad scales. More specifically:
 - a. Global-scale patterns emerge from a hierarchy of interacting processes that propagate responses from fine to broad scales (i.e., plants to landscapes and regions). Fine-scale patterns often cannot be understood without knowledge of broader-scale processes.
 - b. Dynamics at any location on the globe are affected to varying degrees by transfer processes that connect adjacent as well as distant locations.
 - c. Transfer processes (wind, water, biota) connect locations via the movement of organisms, materials, disturbance, and information. The loss of historic transfer processes can result in disconnected locations. Conversely, an increase in magnitude and frequency of transfer processes can increase connectivity among previously isolated locations.
 - d. Spatial heterogeneity determines how drivers and transfer processes interact and feedback on one another across scales.
 - e. The relative importance of fine- or broad-scale pattern-process relationships can vary through time, and alternate as the dominant factors controlling system dynamics.
 3. Human activities associated with disturbance and modifications of resources are ultimately the dominant drivers of global change.
 4. Global change drivers are of unprecedented magnitude.
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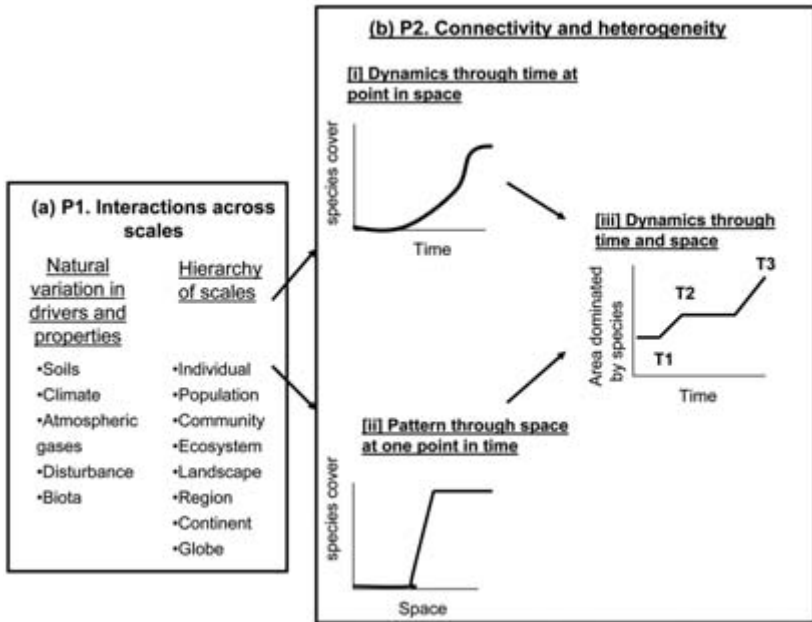


Figure 12.1. Two propositions upon which a global change theory is based are occurring under current conditions: natural variation in system properties (drivers and responses) and connectivity among spatial units that link dynamics through time and across space. Connectivity is represented by the slope of each line segment between each pair of thresholds (T1-T2, T2-T3). Species cover is used as an example; other response variables are possible.

The concept of pattern-process interactions provides a general mechanism for dynamics within scales that lead to shifts in “scale domains” (*sensu* Wiens 1989). 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 (Bestelmeyer 2006; Groffman et al. 2006); both external stochastic events and internal dynamics can drive systems across thresholds (Scheffer et al. 2001).

Interactions among local and broader-scale processes can be important to patterns of distribution, abundance, and diversity (Ricklefs 1987; Levin 1992; Carpenter and Turner 2000). These cross-scale interactions generate emergent behavior that cannot be predicted based on observations at single or multiple independent scales. For example, human activities at local scales can drive land change dynamics at regional scales (Luck et al. 2001; Dietz et al. 2007). Cross-scale interactions can also be important to metapopulation dynamics

(Hastings Chapter 6) in that demographic and dispersal processes interacting with habitat heterogeneity can drive these dynamics across scales (Schooley and Branch 2007). A number of theories have used hierarchy theory as a basis for describing cross-scale interactions, including theories of complex systems (Milne 1998), self-organization (Rietkerk et al. 2004), panarchy (Gunderson and Holling 2002), and resilience (Holling 1992). Recently, a framework was developed to explain how patterns and processes at different scales interact to create nonlinear dynamics with thresholds (Peters et al. 2004; 2007). This framework focuses on the importance of connectivity and spatial heterogeneity in determining how pattern-process relationships interact across scales and forms the basis for our proposition 2.

Proposition 2. Connectivity and spatial heterogeneity. Our second proposition is that intermediate-scale properties associated with connectivity and spatial heterogeneity determine how pattern-process relationships interact from fine to broad scales (Fig. 12.1b). Within a domain of scale (i.e., fine, intermediate, or broad), patterns and processes reinforce one another and are relatively stable. However, changes in drivers or disturbance can modify these pattern-process relationships in two ways. (1) Fine-scale patterns can result in positive feedbacks where new processes and feedbacks become important as the spatial extent increases. This change in dominant process is manifested as nonlinear threshold changes in pattern and process rates. The nonlinear propagation of fire through time is one example where connectivity in fuel load shifts from individual tree morphology to within-patch distribution of overstory and understory plants to among-patch variability in topography and species distributions as the spatial extent of a fire expands (Allen 2007). (2) Broad-scale drivers can overwhelm fine-scale processes, such as regional drought that produces widespread erosion and minimizes the importance of local process such as competition to ecosystem dynamics. At the scale of landscapes, dispersal of invasive species can overwhelm local environmental variation in vegetation, soils, and grazing pressure to drive invasion dynamics (Peters et al. 2006).

Spatial heterogeneity and connectivity are interrelated: it is the combination of trends through time and patterns across space that lead to measures of connectivity. For example, expansion of an invasive species across a landscape can follow a nonlinear pattern where cover of the invasive increases through time for any given point within a spatial extent (Fig. 12.1b[i]). At any given point in time, invasive species cover is heterogeneously distributed across the spatial extent in a number of different ways, from uniformly high or low or with a gradient or ecotonal spatial structure (Fig. 12.1b[ii]). Combining trends through time with patterns in space leads to nonlinear changes in area dominated by the invasive species as a percentage of the spatial extent through

time (Fig. 12.1b[iii]). There are three thresholds in the system that are points in time where the slope of the line changes discontinuously as the dominant process changes (T1, T2, T3). A species that initially invades a landscape will first spread within a patch such that local recruitment of seeds and competition among plants are the dominant processes. As more seeds are produced and more plants succeed within a patch, a threshold is crossed where dispersal to other patches becomes increasingly important to landscape-scale pattern. The slope of each line segment (e.g., % invasive cover/ha/y) between each pair of thresholds (T1–T2; T2–T3) is a measure of the connectivity of plants of the invasive species across the landscape. The importance of spatial context is illustrated by the adjacency of each point to other points such that points closer to the area dominated by the invasive species are more likely to be invaded than points at greater distances.

Our connectivity proposition is itself based on the following related propositions (Table 12.1) developed from Peters et al. (2007). (1) Global-scale patterns emerge from a hierarchy of interacting processes that propagate responses from fine to broad scales (i.e., plants to landscapes and regions). Fine-scale patterns often cannot be understood without knowledge of broader-scale processes. (2) Dynamics at any location on the globe are affected to varying degrees by transfer processes that connect adjacent as well as distant locations. (3) Transfer processes (wind, water, biota) connect locations via the movement of organisms, materials, disturbance, and information. The loss of historic transfer processes can result in disconnected locations. Conversely, an increase in magnitude and frequency of transfer processes can increase connectivity among previously isolated locations. (4) Spatial heterogeneity determines how drivers and transfer processes interact and feed back on one another across scales. (5) The relative importance of fine- or broad-scale pattern-process relationships can vary through time, and alternate as the dominant factors controlling system dynamics.

We illustrate changes in cover through time and across space as estimates of connectivity and a description of the mechanisms producing these changes using a landscape change scenario from the northern Chihuahuan Desert in southern New Mexico, USA (Peters et al. 2004). A combination of field survey-based maps (1915, 1928/29), black-and-white aerial photos (1948), and pan-sharpened QuickBird satellite images (2003) were georegistered for a 942 ha pasture at the USDA ARS LTER site north of Las Cruces, NM (32°30'N, 106°48'W) (Fig. 12.2a). Three classes of vegetation were digitized manually, and ARCGIS was used to obtain the area occupied by each of three classes through time: shrubs, grasses, and the ecotone between them.

In this landscape-scale example, most points on the landscape convert from

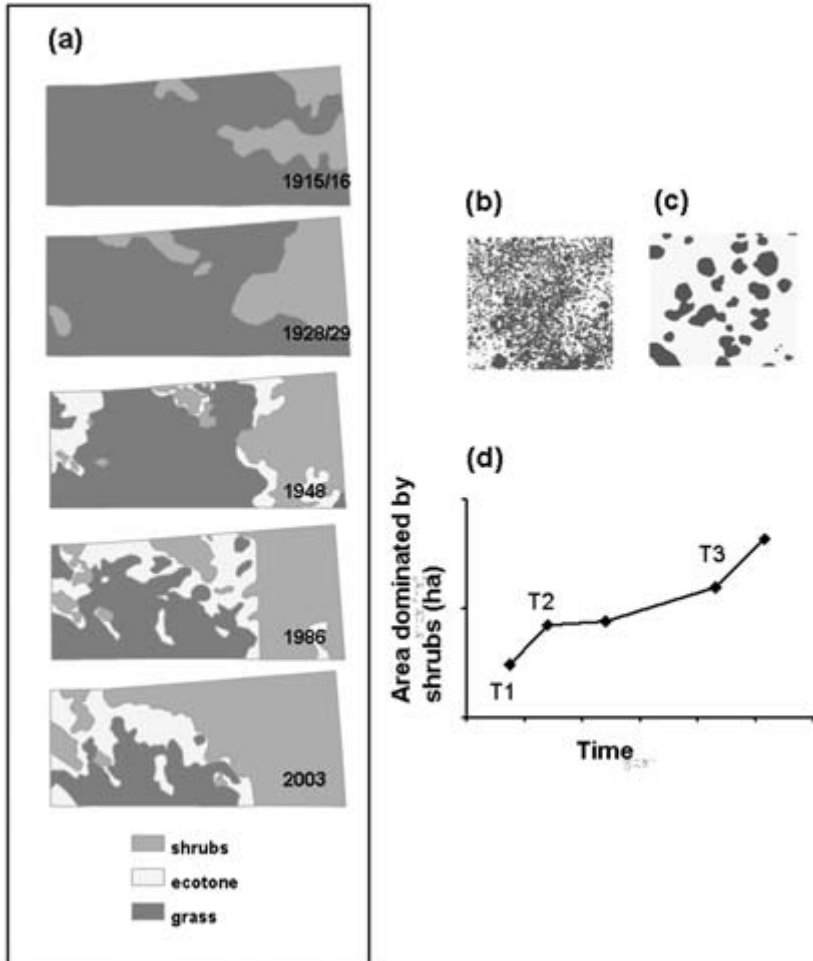


Figure 12.2 An example of a measure of connectivity in shrubs in the northern Chihuahuan Desert. Area covered by one of three vegetation types: shrubs, grasses, and the ecotone between them, was calculated for four dates using vegetation types and aerial photos on the left, and displayed through time in the graph for shrubs only. Three points in time and space were found where the rate of change in area increased nonlinearly to indicate a threshold (T1, T2, T3). The slope of each line segment between thresholds is a measure of the connectivity of shrubs over that time period. Insets show homogeneous plant cover [green in (b)] when the area is dominated by grasses. Under shrub dominance, patches of shrubs [green in (c)] are disconnected by bare interspaces that allow erosion by wind and water. Adapted from Peters et al. (2004).

grass-dominated (Fig. 12.2b) to shrub-dominated cover (Fig. 12.2c) through time. At any point in time, in general, the pattern across the landscape changes from grass-dominated in the west-southwest (left side of panels in Fig. 12.2a) to shrub-dominated in the east (right side of panels in Fig. 12.2a). Aggregating this information to the entire landscape results in a nonlinear increase in area dominated by shrubs through time (Fig. 12.2d). Three thresholds occur that are likely associated with a change in the dominant process driving dynamics across the landscape, from interspecific competition between individual plants in the early stages (prior to T1) to connections between shrubs by fine-scale water redistribution and long-distance seed dispersal (T1–T2). Recruitment and seed dispersal (T2–T3) create connections among shrub patches as infilling occurs, although at a slower rate than the previous years. At later stages (T3→), the density and spatial arrangement of shrub patches result in low connectivity among isolated shrubs. In contrast, bare soil interspaces become highly connected by wind erosion to result in deposition of soil and nutrients under shrub canopies. These positive feedbacks to shrub persistence promote the development of dune fields that further limit success of grasses (Peters et al. 2004).

Additional propositions under global change

There are two additional propositions that are unique to and characterize phenomena considered under global change (Table 12.1), and these in particular present unique challenges to existing theories (Fig. 12.3b).

Proposition 3. Human drivers of global change. The third proposition is that human activities associated with disturbance and modifications of resources are ultimately the dominant drivers of global change (P3: Fig. 12.3b top panel). The consequences of this proposition are that the dynamics and characteristics of key drivers previously recognized as governed by natural earth systems processes and feedbacks, such as atmospheric CO₂ and other greenhouse gases, climate, and nitrogen deposition, are now determined to a large extent by human activities. These activities are a product of cultural, economic, and social systems (Pickett et al. 2001b).

When combined with the widespread direct impacts of human actions on biological and ecological systems, this proposition means that many of the primary forces of change in ecology, as well as responses, interactions, and consequences of change, operate either partially or completely independent of evolutionary mechanisms, such as natural selection, that historically have been considered essential for understanding the ultimate basis of and context for ecological dynamics (Vitousek et al. 1997b; Palmer et al. 2004). For example,

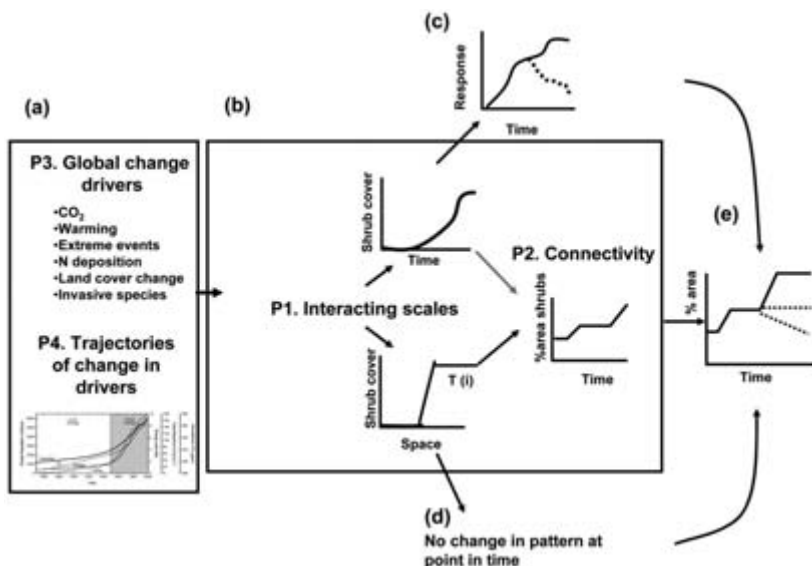


Figure 12.3 Our emerging theory of global change includes the two propositions under current conditions—variation in system properties (P1) and connectivity (P2)—combined with global change drivers (P3) that are experiencing changing trajectories through time (P4). The result is that connections among spatial units are increasing in both magnitude and frequency of occurrence primarily as a result of changes to trajectories through time rather than substantive changes in pattern.

plant communities that exist in urban ecosystems do not necessarily reflect adaptations to the local environment—instead the environment is often altered to permit the species to coexist. Thus, the spatial patterns of individuals, their population dynamics, and overall productivity are largely a function of human activities and preference driven by socioeconomic factors (Grimm et al. 2008a). Other examples include agricultural fields, water bodies devoted to aquaculture, planted “improved” pastures, and forest plantations in which the dominant species and their traits are no longer a product of evolutionary and ecological interactions, but instead are largely influenced by a human value system. Less obvious, but no less pervasive, is the attempted management and restoration (decidedly human activities) of natural areas to match environments and to achieve ecological states that may no longer exist (Hobbs et al. 2006), thus requiring significant resource inputs and human intervention (Seastedt et al. 2008).

Proposition 4. Change in trajectories of global change drivers. Our fourth proposition is that global change drivers are of historically unprecedented

magnitude. As a consequence, they are leading to trajectories of ecosystem responses that differ radically from those observed in the past (Fig. 12.3b bottom panel). Increasing concentrations of atmospheric CO₂ and other greenhouse gases are primarily related to human activities, in particular fossil fuel emissions and land use change driven mainly by tropical deforestation (IPCC 2007). Atmospheric CO₂ concentrations have increased ca.100 ppm since 1750, and are currently higher than at any time in at least the past 650,000 years (Siegenthaler et al. 2005). These changes in atmospheric chemistry result in global temperature increases and regional increases or decreases in precipitation that often interact with changes in land cover to feed back to local weather (Pielke et al. 2002). Human activities also result in increases in nitrogen deposition in the form of nitrate from the combustion of fossil fuels and from ammonium, a by-product of animal metabolism and fertilization (Vitousek et al. 1997a; Fenn et al. 2003).

Recent studies predict that some future climates will have no historic analogs, and some extant climates may disappear (Fox 2007; Williams et al. 2007a). These novel climates would likely result in new species associations (Hobbs et al. 2006), and the disappearance of climates could result in species extinctions (Overpeck et al. 1991). These “no analog” communities may result in ecological surprises with unknown responses to future climates (Williams and Jackson 2007). Additional global change drivers will likely interact with novel climates to result in even more surprising dynamics (Hobbs et al. 2006). One likely result of novel climates interacting with changes in other global drivers is that ecosystems will be pushed past critical thresholds to result in irreversible ecosystem state changes. These state changes or regime shifts are increasingly recognized as important consequences of global change (Scheffer et al. 2001; Folke et al. 2004). Critical thresholds are often crossed either during or following a state change such that a return to the original state is difficult or seemingly impossible (Bestelmeyer 2006).

Combining these four propositions enables new predictions to be made about the effects of changing global drivers on ecosystem responses across scales. Because global change drivers have altered trajectories through time compared to historic dynamics, ecological responses through time at any point in space may have complex dynamics that may either continue to increase or even decrease (Fig. 12.3c). For example, shrub cover in Fig. 12.2 could continue to expand across arid and semiarid landscapes under conditions of increasing CO₂ concentrations and higher winter precipitation that favors shrub growth over grasses (Morgan et al. 2007). Alternatively, shrub cover could decrease if climatic changes favor grasses and increase fire frequencies (Briggs et al. 2005). Because the processes associated with shrub expansion (recruitment, competi-

tion, mortality) are not expected to change under global change, the general spatial pattern at any point in time is not expected to change (Fig. 12.3d). Thus, one prediction is that changes in the temporal characteristics of global change drivers will impact arid landscapes more than changes in the spatial pattern of these drivers. The combination of altered temporal dynamics and no changes in spatial patterns can generate system responses with either increases, decreases, or no changes in responses through time and space with thresholds that indicate changes in level of connectivity (Fig. 12.3e). In addition, changes in spatial pattern may result via unexpected interactions in drivers and responses, such as the emergence of extreme climatic events, pest outbreaks, and altered disturbance regimes (Running 2008), that would result in even more complex or surprising behavior.

A framework for global change

The four propositions combine to form a conceptual framework that has connectivity as its foundation (Fig. 12.4; modified from Peters et al. 2008). At the global scale, a hierarchy of interacting scales governs dynamics. Dynamics at any one location on the globe depend on both local patterns and processes at that location, and the movement of materials via transfer processes from other locations. All places on Earth are connected through a globally mixed atmosphere and regionally through a variety of biotic and abiotic mechanisms, such as human transport of propagules, toxins, and diseases as well as propagation of disturbances and changes in land use as influenced by global economics. Thus, changes in one location can have dramatic influences on both adjacent and nonadjacent areas, either at finer or broader scales. Transfer processes associated with the movement of air, water, animals, and humans provide these connections, both within and across scales (Fig. 12.2).

Disruptions in connectivity are also becoming increasingly important, often in different parts of a system that are increasing in connectivity. For example, land use practices over the past several centuries have increased the density of corn and soybean fields in the Midwestern U.S. to result in a highly connected mosaic of agricultural fields. In contrast, the plowing of tallgrass prairie for agricultural fields has resulted in disconnected remnant prairie locations throughout the region. As a result, movement of agricultural pests and disease among fields is facilitated, but the movement of plants and animals between fragmented remnant prairies is difficult because of the large distances between fragments.

Transfer processes and spatial heterogeneity can either amplify or attenuate system response to broad-scale drivers. Amplification occurs when the rate of

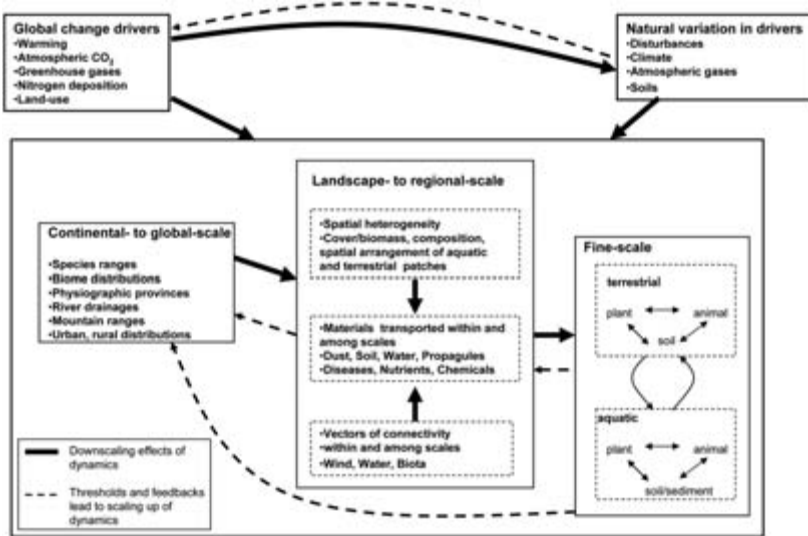


Figure 12.4 Connectivity framework. Global change drivers and natural drivers are influencing a hierarchy of scales of system properties and responses. Each scale has its characteristic patterns and processes, and scales interact to generate changing pattern-process relationships through time and across space. Downscaling occurs when broad-scale drivers overwhelm fine-scale pattern (e.g., hurricanes), and upscaling occurs when fine-scale patterns and processes propagate to influence large spatial extents (e.g., dust plumes from field-based landuse practices). Redrawn from Peters et al. (2008).

change in system properties increases. This increase can result from high spatial heterogeneity or homogeneity that promotes cascading events, such as the nonlinear spread of wildfires (Peters et al. 2004). Cascading events in which a fine-scale process propagates nonlinearly to have an extensive impact have also been documented in the climate system, in lakes, and in the invasion of perennial grasslands by woody plants (Lorenz 1964; Peters et al. 2004; 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 et al. 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). The spread of wildfires also attenuates with time and with decreases in fuel load or changes in weather conditions. In addition, broad-scale drivers, such as drought, can act to overwhelm fine-scale variation in vegetation, topography,

and soils to result in homogeneous responses over large areas (Albertson and Weaver 1942).

The relative importance of fine- or broad-scale pattern-process relationships can vary through time and compete as the dominant factors controlling system dynamics. 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 et al. 2006). Processes that connect spatial units, such as dispersal of woody plants, are important under some conditions whereas local processes, such as soil texture, dominate on other sites; in both cases, broad-scale drought can overwhelm finer-scale processes to result in similar dynamics during dry years (Yao et al. 2006).

Insights from connectivity perspective

We illustrate the importance of a connectivity-based theory of global change for addressing one specific ecological problem: the effects of hurricanes on ecological systems. We first show how our first two propositions apply to current conditions for both drivers and ecosystem responses. We then show how the two global change-specific propositions (anthropogenic origin of drivers and changes in trajectories of drivers) are needed to understand and predict the impacts of hurricanes within the context of other global change drivers in the future.

Current conditions

Drivers of hurricane activity. Although it is readily accepted that hurricanes are disturbances with major impacts on ecosystems, the drivers controlling the formation, intensity, and track of hurricanes remain poorly understood. Recent research indicates that hurricane development is affected by drivers and processes operating across a range of spatial and temporal scales (proposition 1) and that these drivers and processes interact such that spatial heterogeneity and connectivity among spatial units are important (proposition 2). Because these propositions are related, we discuss them together within the context of hurricane development.

Physical processes interacting within and among scales predominate in the development of hurricanes (Goldenberg et al. 2001); these processes are directly or indirectly affected by global change drivers. Hurricanes that affect North America most often start as small thunderstorms in the Western Sahel region of Africa and increase in spatial extent and intensity as they propagate

westward across the Atlantic Ocean (Dunn 1940; Landsea 1993). Both local factors, such as sea surface temperatures within the region of hurricane development, and broad-scale factors, such as the El Niño-Southern Oscillation (ENSO) in the tropical Pacific and continental precipitation in West Africa determine whether or not an African thunderstorm develops into a hurricane (Gray 1990; Glantz et al. 1991; Landsea and Gray 1992; Saunders et al. 2000; Donnelly and Woodruff 2007).

Ecological responses to hurricanes. Hurricanes impact ecosystems across a range of spatial and temporal scales that influence ecosystem responses. Spatial pattern of damage resulting from hurricanes is scale-dependent: at the scale of individual trees and small stands, tree age and height, species composition, stand structure, and soil conditions influence amount and type of damage (Foster and Boose 1992; Ostertag et al. 2005). At broader scales, spatial variability in vegetation, land use, environmental conditions, and disturbance history are important as well as landscape- and watershed-scale factors that connect spatial units, such as wind speed and direction, precipitation intensity, and topographic gradients (Boose et al. 2001; Sherman et al. 2001). Recent studies suggest that ecosystem properties, such as stand age and condition, forest type, and aspect, and landscape-scale measures of connectivity, including distance to nearest perennial stream, are more important predictors of forest damage patterns than broad-scale drivers of wind speed and duration (Kupfer et al. 2008).

Ecosystem responses following hurricanes are also scale-dependent (reviewed in Everham and Brokaw 1996; Lugo 2008), and can include interactions across scales as a result of changes in connectivity among spatial units (Willig et al. 2007). For example, landscape reconfiguration and disruption of dispersal among patches by hurricanes can interact with local demographics of species to influence patterns in biodiversity across scales (Willig et al. 2007).

Global change conditions

Drivers of hurricanes, although incompletely understood, are being influenced by anthropogenic sources of variation (proposition 3), and the trajectories of these drivers are changing (proposition 4). We focus on both local and broad-scale drivers that are likely to change.

Local drivers. Sea surface temperatures (SSTs) have increased nonlinearly over the 20th century in the Atlantic Ocean (Trenberth 2005). This trend has been attributed to global warming and human activities (IPCC 2007). In addition, the amount of total column water vapor over the global oceans has increased 1.3% per decade (Trenberth 2005). Both higher SSTs and increased

water vapor tend to increase energy available for atmospheric convection and thunderstorm production that can lead to hurricane development. There is general agreement that human-induced environmental changes occurring in hurricane regions can increase hurricane intensity and rainfall (Goldenberg et al. 2001; Emanuel 2005; Webster et al. 2005). There is less agreement on predicted effects of global warming on hurricane frequency with unclear evidence that frequencies are changing beyond the range of historic variation (Henderson-Sellers et al. 1998; Goldenberg et al. 2001).

Broad-scale drivers. Over the past 5000 years, the frequency of intense hurricane landfalls on centennial to millennial timescales was likely related to variations in ENSO and the strength of the West African monsoon (Donnelly and Woodruff 2007). Thus, reliable forecasts of remote conditions will be needed for predicting the occurrence and intensity of hurricanes in North America (Pielke and Landsea 1999). In addition, nonlinearities in the climate system that lead to threshold dynamics may make predictions based on historic trends difficult and unreliable (Rial et al. 2004).

For ENSO, a 155-year reconstruction from the tropical Pacific shows a gradual transition in the early 20th century and an abrupt shift in 1976 to new periodicities that reflected changes in the regional climate towards warmer and wetter conditions (Urban et al. 2000). The dramatic shift in 1976 coincided with a global shift in temperatures attributed to anthropogenic global warming (Graham 1995; Mann et al. 1998). Thus, global warming could further alter the frequency of ENSO cycles. However, additional factors need to be considered, such as sharp decreases in sea surface temperatures in the Atlantic Ocean interacting with dust-induced feedback processes that can moderate hurricane intensity (Lau and Kim 2007).

Factors that influence future rainfall in the Western Sahel will undoubtedly affect the number, duration, and intensity of hurricanes in North America (Webster et al. 2005). Climate projections for this region are unclear: one model predicts severe drying in the latter part of the 21st century while another predicts wet conditions throughout this time period, and a third model predicts modest drying (Cook and Vizy 2006). Clearly, better climate predictions and an understanding of the relationship between rainfall and wave formation are needed before rainfall on the continent of Africa can be used to predict hurricanes in the North Atlantic.

New insights to ecological systems

Atmospheric scientists have known since at least the 1960s that hurricanes connect the African and North American continents (Gray 1968). However,

the complex cross-scale interactions determining hurricane development, intensity, and movement track have only recently been recognized and better appreciated as critical elements of a connected Earth system. A sense of urgency in understanding and prediction now predominates in the literature, in particular as our global environment continues to change and as hurricane damage increases with population density and wealth along U.S. coastlines (Pielke and Landsea 1999).

Ecological systems will continue to be influenced by hurricanes, both in obvious and subtle ways because of connections that link spatial and temporal scales (Hopkinson et al. 2008). Ecosystems in the track of hurricanes along the coast of North America are composed of species that evolved under the current hurricane regime, and it remains to be seen how different parts of these systems and different ecosystem types will respond as hurricane activity changes in the future (Michener et al. 1997). Even ecosystems located outside the direct path of hurricanes can be affected by a change in disturbance regime: deserts in southern New Mexico received within several days ca. 43% of the annual average rainfall as a result of the remnants of Hurricane Dolly in 2008. These extreme, remote events are not included in climate change projections for these systems (Seager et al. 2007), yet an increase in hurricane activity would reverse the direction of these projections from drier to wetter. Because these deserts have undergone dramatic changes from grasslands to shrublands over the past 150 years that are at least partially related to drought cycles, an increase in rainfall may provide opportunities for some landscape locations to revert to grass dominance, a state change that is considered unlikely under current climatic conditions.

Furthermore, hurricanes are not the only disturbance with local and global drivers that impact ecological systems across scales (Dale et al. 2001). Hurricanes are often associated with other disturbance events that accentuate the effects of wind and rain: drought often follows hurricanes with its own effects on surviving organisms (Covich et al. 2006). Fire can follow hurricanes with greater impacts on birds than the hurricane itself (Lynch 1991).

Research directions

Future research should include both theory development and advances in the types of studies conducted within the realm of global change. We outlined key characteristics of a developing theory of global change based on existing knowledge. As new information is obtained that increases both the depth of knowledge on specific aspects of ecosystem responses to changing drivers and the breadth of knowledge on interrelationships among components of the

Earth System, the propositions developed here will likely need to be refined, expanded, or replaced.

A consideration of drivers and responses interacting across multiple spatial and temporal scales is needed in global change studies as well as an explicit measurement of transport processes when they are important to dynamics. Five characteristics of systems have been identified to account for multiple scales of variation (reviewed in Peters et al. 2006): (1) local processes (e.g., recruitment, competition, and mortality) interacting with microsite environmental variability (e.g., climate, soils, disturbance history), (2) historic legacies that influence the local environmental conditions, the current assemblage of species, and their ability to respond, (3) current environmental drivers, (4) future environmental drivers with local- to global-scale variability, and (5) transport processes that connect spatial units across a range of scales, from the landscape to the globe.

It is the spatial scaling of characteristics 3–5 that ecologists need to consider when studying ecological problems within the context of global change, yet this aspect has received the least amount of attention to date. A consideration of variability in drivers from remote locations, such as rainfall in West Africa that influences hurricane activity in North America, is often missing from ecological studies. Although there is increasing recognition of the importance of ENSO and other climatic cycles on local rainfall patterns, the interaction of these cycles with other drivers (e.g., elevated CO₂, nitrogen deposition) has not typically been considered, although climatic cycles are related to disturbances, such as wildfire (Kitzberger et al. 2007).

Because measurement of transport processes is typically time and labor intensive, it is important that an initial step in ecological studies be to determine where, when, and how transport processes *may be* important relative to the other drivers in order to decide if sampling is justified. An important aspect of this developing global change theory and its associated framework is that transport processes need to be considered within the context of the properties of the system and the questions to be addressed, but they do not need to be explicitly sampled for all questions.

Both direct and indirect drivers, such as disturbances, have characteristic spatial and temporal scales that need to be studied as interactive effects on ecosystems. Wildfires, floods, insect outbreaks, and other episodic events are not yet included in climate change models (Running 2008), yet they often interact across scales to result in surprising ecosystem responses (e.g., Allen 2007; Ludwig et al. 2007; Young et al. 2007).

Recently, new approaches to studying continental-scale problems under global change have been presented (e.g., Crowl et al. 2008; Grimm et al.

2008b; Hopkinson et al. 2008; Marshall et al. 2008; Williamson et al. 2008). Here we summarize three key recommendations from these papers that are relevant across scales. First, existing long-term datasets can be used to compare trends across sites. Similar patterns in data through time for sites located throughout a region or in different parts of the continent can suggest the presence of a global driver determining synchronicity in these dynamics, such as observed with wildfires and climatic cycles (Kitzberger et al. 2007). Alternatively, similar internal processes may be controlling system dynamics in different locations to overwhelm variation in drivers. A major limitation to these multisite analyses has been accessibility of comparable data. Recent efforts at synthesizing long-term data and metadata from many U.S. sites are allowing these comparisons to be conducted (e.g., <http://www.ecotrends.info>). Second, coordinated efforts are needed to explicitly examine the importance of fine- to broad-scale drivers and transport processes to ecosystem dynamics across many sites. Existing networks of sites need to be coordinated such that comparable data are collected and compared dynamically in order to identify connections among sites, and to predict effects of cascading events as they influence adjacent and noncontiguous areas, such as the impacts of wildfires on air and water quality in burned sites and at distant locations. Third, simulation models are needed to complement experiments in order to provide more complete spatial and temporal coverage of ecosystem responses to global change drivers. Process-based models will be required to forecast a future with conditions that are unprecedented in Earth's history. In contrast, an empirical extrapolation of responses based on current or past conditions will result in large uncertainty. Multidisciplinary approaches will be needed to account for the complexity of interactions across scales and levels of organization in the ecological hierarchy.

Summary

Direct and indirect drivers of ecological systems are changing nonlinearly in response to human activities. These drivers and ecological systems interact across a range of spatial and temporal scales that often result in nonintuitive ecosystem dynamics. We outline some basic propositions to frame the development of a theory of global change based on connectivity within and among adjacent and noncontiguous spatial units. This nascent theory builds on several more mature bodies of theory developed for specific scales or levels of organization, and uses the concept of cross-scale interactions based on transport processes to link several of these theories. As our knowledge of the interacting components of the Earth System expands with improvements in sensing, mea-

suring, and modeling technologies, we expect corresponding refinements to the theory that will improve its coherence and utility.

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