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## A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change

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**Abstract.** In contrast to pulses in resource availability following disturbance events, many of the most pressing global changes, such as elevated atmospheric carbon dioxide concentrations and nitrogen deposition, lead to chronic and often cumulative alterations in available resources. Therefore, predicting ecological responses to these chronic resource alterations will require the modification of existing disturbance-based frameworks. Here, we present a conceptual framework for assessing the nature and pace of ecological change under chronic resource alterations. The “hierarchical-response framework” (HRF) links well-documented, ecological mechanisms of change to provide a theoretical basis for testing hypotheses to explain the dynamics and differential sensitivity of ecosystems to chronic resource alterations. The HRF is based on a temporal hierarchy of mechanisms and responses beginning with individual (physiological/metabolic) responses, followed by species reordering within communities, and finally species loss and immigration. Each mechanism is hypothesized to differ in the magnitude and rate of its effects on ecosystem structure and function, with this variation depending on ecosystem attributes, such as longevity of dominant species, rates of biogeochemical cycling, levels of biodiversity, and trophic complexity. Overall, the HRF predicts nonlinear changes in ecosystem dynamics, with the expectation that interactions with natural disturbances and other global-change drivers will further alter the nature and pace of change. The HRF is explicitly comparative to better understand differential sensitivities of ecosystems, and it can be used to guide the design of coordinated, cross-site experiments to enable more robust forecasts of contemporary and future ecosystem dynamics.

**Key words:** *ecological change; ecosystem structure and function; global-change drivers; hierarchical-response framework; pulse-perturbations.*

### INTRODUCTION

Ecologists have long recognized that ecological systems are dynamic, particularly those driven by local-scale human impacts (e.g., agriculture; Worster 1994). However, few would dispute that the primary drivers of contemporary ecological dynamics have been altered dramatically in the past 50 years as a consequence of rapid human population growth and expanding human activities (Fig. 1; Vitousek et al. 1997). These global-change drivers (GCDs) impact virtually all ecosystems, and human pressures on ecological systems

are expected to increase over at least the next century (MEA 2005). There also is increasing recognition that the ways in which ecosystems are being altered today and in the future have no historic analog (Williams et al. 2007). Indeed, alternate ecosystem states, regimes shifts, and irreversible change are becoming increasingly accepted consequences of global environmental change (Scheffer et al. 2001).

The novelty of contemporary ecological drivers suggests that our past understanding of dynamics based to a large degree on natural disturbance regimes may be inadequate for forecasting future ecosystem change (Groffman et al. 2006). A key characteristic of GCDs is that they tend to be chronic (or press) perturbations rather than the relatively discrete pulses that characterize natural disturbance regimes. Although disturbances

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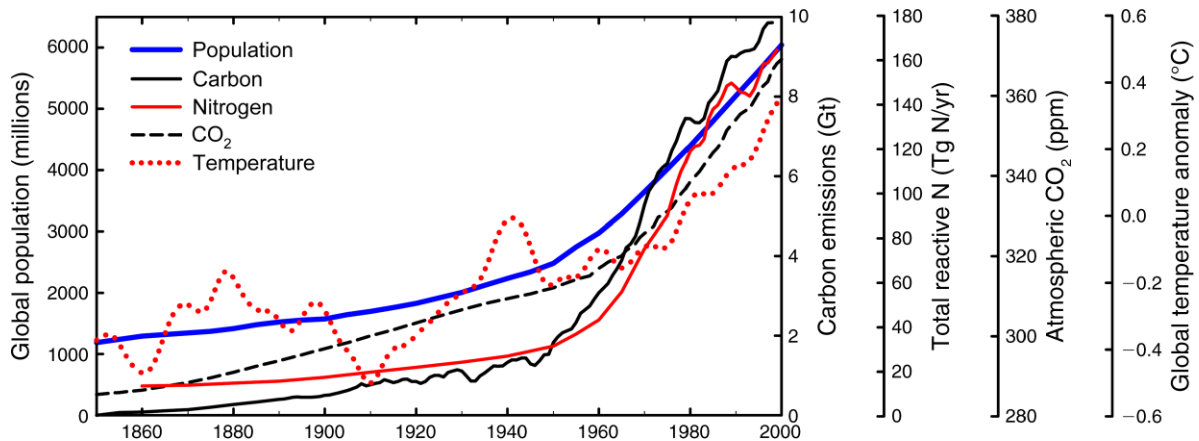


FIG. 1. Long-term trends in the global human population, CO<sub>2</sub> emissions, reactive N produced by humans, CO<sub>2</sub> concentration of the atmosphere, and the global temperature anomaly. Note the directional and cumulative increase in these metrics of global human impacts over the past 50 years. Population data are from the U.S. Census Bureau (<http://www.census.gov/>); energy consumption, from the U.S. Department of Energy Information Administration (<http://www.eia.doe.gov/>); total reactive N from Galloway et al. (2003); atmospheric CO<sub>2</sub> concentrations from the Carbon Dioxide Information Analysis Center (CIDAC; <http://cdiac.esd.ornl.gov/>); and global average temperature anomaly data (Brohan et al. 2006) from the Met Office Hadley Centre for Climate Change (<http://www.hadobs.metoffice.com/>).

will continue to be important drivers of ecosystem dynamics, pulsed disturbances will occur within a pervasive backdrop of chronic GCDs. Thus, a more comprehensive understanding of how GCDs will impact ecosystem dynamics is needed. Below we argue that responses ranging from the organismal level to those involving community reordering or arrival of novel species into an ecosystem underlie how ecosystem dynamics will be impacted by chronic GCDs. However, it is the relative importance of each and the time scales of response for the different organizational levels that will determine the comparative sensitivities of ecosystems to GCDs. For example, studies have examined ecological responses to chronic N deposition (Stevens et al. 2004), climate change (Parmesan 2006), and elevated atmospheric CO<sub>2</sub> (Klironomos et al. 2005) across multiple levels of organization, but the three major levels of response—individual, community reordering and immigration or loss of species—are rarely assessed comparatively, either within or among ecosystems, despite the fact that all are components of dynamics (Shaver et al. 2000). We suggest that integration of these three levels of response into a single, comprehensive framework is critical for increasing our predictive understanding of the nature and pace of ecosystem change and for generating testable hypotheses concerning how and why ecosystems may differ in their sensitivity to chronic GCDs.

Although humans are impacting ecosystems in a variety of ways, we focus our discussion on the GCDs depicted in Fig. 1. We chose these GCDs because a key consequence of each is the *chronic alteration, either directly or indirectly, of resources in ecosystems*. Our objectives are to: (1) contrast how chronic GCDs resulting from human activities differ from natural

disturbance regimes, (2) present a mechanistic framework by which ecosystems are expected to change with chronic GCDs, (3) provide potential mechanisms for differential ecosystem response, (4) consider interactions between chronic GCDs and other anthropogenic changes, and (5) compare our framework to other frameworks of ecosystem change. We conclude with future research directions that may facilitate our understanding of the ways in which ecological systems are likely to differ in their responses to GCDs.

#### DISTURBANCE, GLOBAL CHANGE, AND RESOURCE ALTERATIONS

Natural disturbances are widespread, integral, and even required for the persistence of many ecosystems (Pickett et al. 1989). Moreover, disturbance history may be viewed alongside climatic and edaphic variables in its importance for understanding extant ecological dynamics (White and Jentsch 2001). Although natural disturbances alter ecosystems in innumerable ways, a common feature is that they generally are discrete in time (e.g., fire, floods, hurricanes), with their frequency of occurrence typically limited to a single or few events within and/or among years (or within/among generations of the dominant biota; Fig. 2A). Even natural disturbances that extend across multiple years (e.g., droughts, pest outbreaks) are relatively discrete with respect to their frequency of occurrence over time. By definition, natural disturbances tend to directly impact the biota of ecosystems (Pickett and White 1985). It is this disruption of biotic structure and associated biogeochemical processes, often driven by alterations in community structure, that leads to a pulse in available resources, (Fig. 2B; e.g., Bormann and Likens 1979).

One important consequence of human activities has been the disruption of natural disturbance regimes on a global scale (Dale et al. 2001). In many cases, disturbances have become more frequent and/or intense over time (e.g., fire and floods), while in other cases, disturbance frequency and intensity have decreased (e.g., fire suppression and hydrologic regulation). These human-caused alterations of disturbance regimes can impact resources in different ways (Fig. 2A). With more frequent and intense disturbances, the frequency of resource pulses that occur between years can increase, such as with fire, drought, flood, or El Niño events (e.g., Huntington 2006, Westerling et al. 2006). Alternatively, resource pulses can increase within a year or generation but not vary between years, such as with an increase in extreme weather events intra-annually as predicted with climate change (IPCC 2007). A reduction in disturbance events with fire suppression or hydrologic regulation (Malamud et al. 2005, Poff et al. 2007) would result in fewer pulses in resources, both within and between years.

All of the scenarios described above represent relatively long-term shifts in the frequency and intensity of resource pulses compared with natural disturbance regimes (Fig. 2A). However, at the extreme of human-caused changes in resources are chronic (or “ramped” press, sensu Lake [2000]) resource alterations. These alterations are fundamentally different from post-disturbance pulses in that they are generally continuous, and are often directional and cumulative. Chronic alterations are the product of some of the most well-known and widespread global-change drivers (GCDs), such as increases in N deposition and atmospheric- $\text{CO}_2$  concentrations, as well as altered precipitation regimes (IPCC 2007). In addition, resources can be altered indirectly as a consequence of climate warming and/or elevated  $\text{CO}_2$  that can cause chronic alterations in water balance and the biogeochemical cycling of key nutrients (Field et al. 1992, Shaver et al. 2000).

Collectively, natural and altered disturbance regimes and human-caused global changes represent a suite of impacts on resources that can be conceptualized within a *pulse-press* continuum of resource alterations (Fig. 2A; Ives and Carpenter 2007). By recognizing that resource alterations are generated along a continuum from discrete resource pulses to chronic (press) resource alterations, our understanding of the drivers of contemporary ecological dynamics will be more complete. For example, natural disturbances, such as fire or insect outbreaks, result in *biotically mediated* pulses in resources. These resource alterations can in turn feed back on subsequent biotic responses either directly through fluctuations in population densities or indirectly via species interactions (Ives 1995). However, the primary cause of post-disturbance resource alterations is not a change in resource inputs, but rather a change in the biota (Fig. 2B). Chronic resource alterations contrast with post-disturbance resource pulses in three

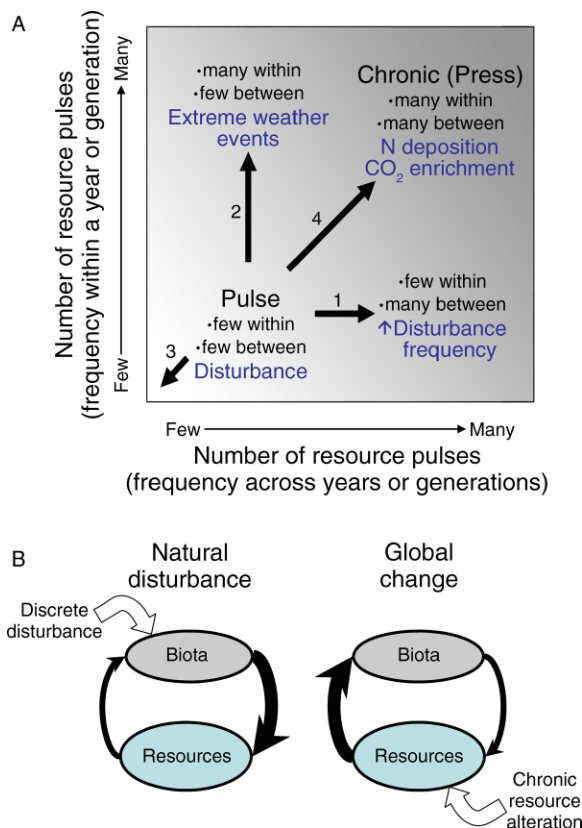


FIG. 2. (A) Four scenarios of how anthropogenic changes (alterations in disturbance regimes, global changes) are altering the frequency of resource pulses occurring within and between years (or generations of organisms) when compared to natural disturbance regimes. Most natural disturbance regimes result in pulses in resources that are discrete (i.e., occurring few times within and between years). However, anthropogenic changes are altering the ways in which resource pulses occur in ecosystems either directly or indirectly (depicted by arrows) by (1) increasing the frequency of resource pulses across years, such as with more frequent fire or other disturbances; (2) increasing the frequency of resources pulses within years, such as with more extreme weather events; (3) decreasing the frequency of resource pulses both within and between years, such as when disturbance regimes are attenuated or eliminated altogether; and (4) increasing the frequency of resource pulses both within and between years, with the most extreme changes represented by chronic, directional, and cumulative resource alterations that result directly (increased N deposition and  $\text{CO}_2$  levels, altered precipitation regimes) or indirectly (warming impacting soil water balance) from human-caused global changes. (B) Comparison of the way in which resources and biota feed back on each other in ecosystems subjected to natural disturbance (left) vs. those human-caused global changes that result in chronic resource alterations (right). The key difference between these two scenarios is that local-scale changes in biota drive resource alterations with natural disturbance. In contrast, global changes, such as elevated atmospheric  $\text{CO}_2$ , climate change, and nitrogen deposition, are external to the ecosystem and result in chronic (press) alterations in resources that directly impact the biota and drive ecosystem responses.

important ways: (1) they are not generated *directly* by changes in the biota, species composition, or community structure, although they may lead to such changes, (2) biotic feedback is minimal on future resource levels because the drivers of altered resource levels are operating at a much larger scale (for example, changes in local community structure do not feed back on global increases in atmospheric-N deposition), and (3) resource alterations do not diminish over time but instead resources may continue to increase, as with rising atmospheric CO<sub>2</sub> concentrations or may accumulate within ecosystems (e.g., N saturation). Biotic feedbacks to local resource levels will still occur with GCDs, and ecosystem properties can feed back to affect climate (Field et al. 2007). However, with global change, the overwhelming determinant of local-scale resource levels is often external to the ecosystem as opposed to internal via local natural disturbance. These key distinctions challenge our ability to predict contemporary or future ecosystem dynamics based on our understanding of the effects of natural disturbances.

Although the scenarios depicted in Fig. 2A represent novel modes of resource alterations relative to natural disturbance regimes, chronic alterations in particular may pose the greatest risk of pushing ecological systems along novel trajectories of change. Explicit consideration of the consequences of these chronic, cumulative, and directional resource alterations as key agents of ecological change is critical for addressing many of the environmental challenges facing ecologists and society today (NRC 2001). For these reasons, we focus the remainder of our discussion on *chronic* resource alterations associated with GCDs. We present a conceptual framework that is based on what we view as three key processes underlying ecological responses to these alterations, and discuss how chronic resource alterations may interact with other global-change factors.

#### THE HIERARCHICAL-RESPONSE FRAMEWORK

Our knowledge of the basis for differential sensitivity of ecosystems to chronic resource alterations is limited compared to that for natural disturbances and pulsed perturbations. We define “sensitivity” here as including both the rate and magnitude of change in the structural and functional attributes of ecosystems. Many studies of chronic resource alterations have been done in a single system and over relatively short time scales (e.g., <5–10 years; Carpenter et al. 2001, Elser et al. 2007). Often such experiments use discrete changes in resource addition rather than gradual increases (Klironomos et al. 2005), and few have assessed differences among ecosystems in directly comparable ways. Below we draw upon the pulse-press literature to provide a basis for developing a synthetic conceptual framework of ecosystem response to chronic resource alterations. Our focus is on comparative responses and differences in sensitivity among ecosystems, as well as explicitly linking a suite of

proposed mechanisms with those ecosystem attributes that may underlie variation in response to global-change drivers (GCDs).

Theoretical and empirical studies suggest that predicting the consequences of chronic resource alterations depends on both the direct effects of changing environmental conditions on the biota, and the indirect effects of interactions among species within the community. The former approach is exemplified by numerous global-change studies focused on individual (physiological/metabolic) responses to elevated CO<sub>2</sub>, N addition, warming, and precipitation manipulations. In addition to individual effects, interspecific interactions also can determine the response of population densities to changing resource conditions (e.g., Schmitz 1997). Predicting how altered resource availability will interact with other drivers of change, such as invasive species, is further complicated by an incomplete understanding of how the different spatial and temporal scales of ecosystem response are interconnected (Peters et al. 2004).

To provide a common basis for comparing ecosystem sensitivity to chronic resource alterations, we propose the *hierarchical-response framework* (HRF). This conceptual framework includes what we and others posit are the important mechanisms that operate at disparate spatial scales but that underlie ecological change over time (Fig. 3; Shaver et al. 2000, Neilson et al. 2005). The HRF focuses primarily on processes through time by depicting the positive or negative trajectories of change in ecosystem function and structure (e.g., biodiversity, productivity, energy balance) in response to continued input and potential accumulation of resources. The HRF links well-established and temporally and spatially distinct ecological processes—*individual (physiological/metabolic)*, *species reordering (within ecosystem)*, and *species loss and immigration (between ecosystem)*—and builds on existing ecological theory focused on physiological/metabolic responses (Field et al. 1992), interspecific competition (Tilman 1982), and local–regional processes (Ricklefs 1987).

In the HRF, the initial response to chronic resource alterations occurs at the individual level (e.g., physiological or metabolic processes, mortality). These responses occur rapidly and range from biochemical to the leaf or organ level. For example, with chronically high N deposition, physiological responses (e.g., increased photosynthetic rates in plants) often result in an initial, rapid increase in net primary productivity (Fig. 3A). Similarly, elevated CO<sub>2</sub> concentrations have been shown to directly alter plant physiology as well as indirectly improve plant water relations (Morgan et al. 2004). Numerous resource manipulation studies have demonstrated that physiological responses drive short-term ecosystem dynamics (Reich et al. 2006). However, the extent to which these individual-level responses can affect ecosystem change will be constrained by the genotypic diversity and traits of the extant biota, the



degree of local-scale adaptation, particularly in the dominant species (Whitham et al. 2006), and whether mortality occurs. The progressive limitation of other resources may also constrain response trajectories (Luo et al. 2004). Importantly, these individual responses not only represent the “fast” responses (seconds to months) of the ecosystem, but also can potentially underlie responses at the population and community levels, as well as evolutionary responses (Lambers et al. 1998, Jump et al. 2008).

As resources accumulate and/or resource alterations continue over time, gradual-to-rapid changes in species abundance may occur as the physiological limits of some species are exceeded (Fig. 3B). Mortality and/or altered competitive interactions will occur in some cases in such a way that certain species are favored over others. These changes in species abundance may occur at intermediate time scales (months to decades) and underlie changes in biodiversity and stability. An example can be found in experiments at Cedar Creek, Minnesota, USA, where chronic N addition led to a decline in species richness and a reordering of species abundance rankings over a 5–8 year period (Collins et al. 2008b). Thus, chronic resource alterations (increases or decreases) can eventually lead to species reordering and altered ecosystem functioning.

Ecosystems may vary in the rates at which species reordering within communities occurs. Potential constraints on species reordering include (1) functional trait diversity within the extant biota (e.g., Hulot et al. 2000); (2) the strength and direction of interactions among species (Ives 1995); (3) recruitment processes other than dispersal, e.g., seed production and germination, seedling establishment; (4) the rate of population turnover within the community (Klug et al. 2000); and (5) the extent of resource limitation and rate of biogeochemical cycling of a system (DeAngelis 1992). As a result, the time lag between change dominated by individual-level responses and that driven by species reordering will vary among ecosystems, with the most striking shifts in community structure occurring when there are rapid, nonlinear changes in population densities (Slavik et al. 2004).

With continued alterations in resources over time, some species are expected to go locally extinct, although this response will be moderated by phenotypic plasticity and adaptive changes (Davis and Shaw 2001). Other species may immigrate into the ecosystem introducing novel species (or genotypes) better suited to the new resource levels. Local extinction has been well documented in N-fertilization experiments in a variety of herbaceous-plant communities, and many plant and animal species have shown dramatic range expansions and contractions with climate warming along latitudinal and elevation gradients (Suding et al. 2005, Parmesan 2006). This phase is expected to result in the largest shift in ecosystem structure and function as these populations rapidly increase and disrupt competitive interactions

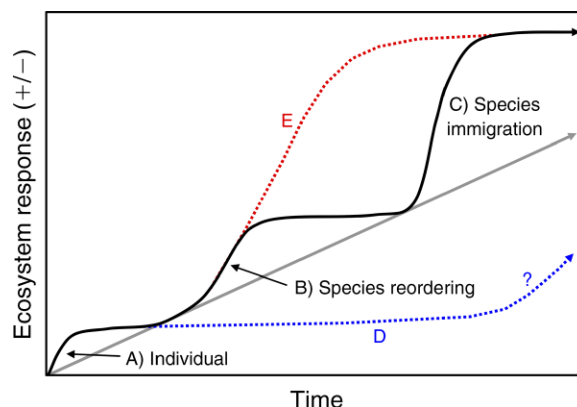


FIG. 3. The hierarchical-response framework (HRF). This conceptual framework depicts the hierarchy of mechanisms underlying ecological change (either positive or negative) as ecosystems are exposed over time to chronic (press) resource alterations (black line). Ecological change variables include, but are not limited to, biodiversity, net primary productivity, nitrogen retention, energy balance, trophic structure, and decomposition. In this framework, relatively modest ecosystem responses are initially driven by (A) relatively rapid individual-level (physiological/metabolic, mortality) responses of the biota to changing resource availability. The magnitude and extent of this response will be limited by the degree of physiological/metabolic acclimation and local-scale adaptation possible for the resident species. Large shifts in ecosystem response are expected to emerge with (B) reordering of species in the community as a result of some species being favored by changing conditions at the expense of others. This phase may require longer periods of time depending on the rate of population turnover or may be attenuated depending on the strength of internal interactions. Finally, (C) new species that are better suited for these new resource levels may immigrate into the ecosystem resulting in the largest change in ecosystem response. The lag period prior to this immigration phase will be determined partially by the regional species pool and dispersal limitation, and by the strength of internal interactions in the community. In contrast to this nonlinear series of responses, gradual linear change (gray line) in ecosystem response would occur if the magnitude and rate of change were similar for all three mechanisms (A, B, and C). The hierarchical progression of change ideally depicted by the HRF has potential exceptions. (D) Ecosystems dominated by very long-lived species with slow turnover rates, such as forests, may appear to be resistant to change as resources accumulate over time. Their primary response may be limited to physiological acclimation for decades or centuries until disturbance or a large-scale mortality event results in population/community turnover. Conversely, ecosystems that become susceptible to invasion by exotic species or pests/pathogens due to resource alterations may bypass changes driven by physiological or community reordering and (E) experience large changes in structure and function in a relatively short period of time.

(Fig. 3C; Hobbs et al. 2006). Key limitations for the species-immigration transition are the number and abundance of species in the regional pool, the distance to the source of new species, and their traits and migration rates (Ricklefs 2004, Neilson et al. 2005).

The response trajectory depicted in the HRF is sequentially determined by different ecological processes arrayed hierarchically, which facilitates focus on the most likely determinant of change through time.

However, a more likely scenario is for these mechanisms to operate in combination and concurrently. For example, individual-level responses are expected to occur together with species reordering and immigration. In addition, there are likely to be important exceptions to the response trajectory, particularly for ecosystems that are already near thresholds of change (Peters et al. 2004), such as loss of sea ice in high-latitude ecosystems (IPCC 2007). Nonetheless, depicting the key processes underlying the dynamics of ecosystem change in this way generates general predictions concerning the temporal scales over which each process will operate, the expected time lags associated with each process, and the trajectory and relative magnitude of change resulting from each process separately. These predictions include (1) when physiological/metabolic mechanisms are the primary mode of response to chronic resource alterations, ecosystem responses will be limited in magnitude; (2) when new species/genotypes successfully invade ecosystems—particularly if they are potentially dominant, have unique traits, or are pests/pathogens—ecosystem change in structure and function will be substantial; and (3) that the time course of ecosystem response to chronic resource alterations will be nonlinear and temporally variable due to the stochastic nature of species establishment and immigration and the inherent nonlinearity in population-growth dynamics. Alternatively, ecosystem change in response to chronic resource alterations could be gradual and linear (Fig. 3). There is ample empirical and theoretical evidence, however, to suggest that transitions between the three controls on ecosystem response in the HRF will more likely be nonlinear (Scheffer et al. 2001, Briske et al. 2006). Such nonlinear changes may even include relatively abrupt changes and multiple alternative ecosystem states.

It is almost a certainty that ecosystems will differ in the relative importance that each process plays in determining the overall nature and pace of change, the time scales over which each operates, and their interactions (e.g., additive, synergistic). Variation in rates of change and durations of lag periods between transitions will determine what is perceived as the relative sensitivities of ecosystems to change. The challenge is to identify the determinants of differences in sensitivity. We propose that at least two major factors will determine such differential sensitivity: (1) the magnitude and types of resource alterations (e.g., N deposition vs. climate variability), and (2) ecosystem attributes, such as levels of biodiversity and resource pool sizes. Although knowledge of both is critical to understanding how and why ecosystems differ in their responses to chronic resource alterations, below we focus primarily on those ecosystem attributes thought to be important in determining differential sensitivity. We also provide hypotheses concerning how each may contribute to variation in response among ecosystems.

#### MECHANISMS FOR DIFFERENTIAL ECOSYSTEM RESPONSE

We have an incomplete understanding of what determines the sensitivity of different ecosystems, community types, or trophic levels to any single chronic resource alteration, and know even less about effects of multiple types of resource alterations. Response trajectories vary depending on the type and amount of resources. Our most comprehensive understanding of responses to resource alterations comes from decades of studies at the physiological or organismal level. Reviews and meta-analyses have provided insight into the magnitude of responses and constraints for a large number of species and resources, as well as the attributes of species that determine initial changes in ecosystem function (i.e., Curtis 1996). In contrast, less is known of the attributes of species and ecosystems that determine the nature and pace of community change, such as species turnover, with chronic resource alteration, despite recognition of the importance of immigration in particular for understanding responses to global change (Shaver et al. 2000, Neilson et al. 2005). We can pose general hypotheses and make predictions that identify mechanisms expected to be important in generating differential ecosystem sensitivity to chronic resource alterations. We focus mainly on community-level mechanisms since species reordering and the introduction of new species are community processes. These mechanisms are not meant to be exhaustive or exclusive, but rather are provided as examples of the types of attributes that may have value for predicting how ecosystems may differ in their magnitude and rate of response.

#### *Dominance*

Demographic turnover of species within an ecosystem will determine how rapidly species reordering may occur (Thuiller et al. 2008). However, it is the extent to which a particular species impacts ecological processes that will determine the relative magnitude of the effects of species replacement and loss on ecosystem response (Huston 1997). It is well known that for most ecosystems the dominant species mediate most ecological processes (Whittaker 1965). The *dominance hypothesis* is based on the idea that dominant species control the majority of the resources (including space) and/or have disproportionate impacts on species interactions. Thus, when chronic resource change favors new dominant species, it is the rate at which the extant species can be replaced and the traits of these new species that will determine the overall response of the ecosystem, as well as its new structure and function. This hypothesis predicts, for example, that ecosystems dominated by long-lived species with slow demographic turnover will be relatively slow to respond to resource alterations (Fig. 3D), particularly if critical thresholds of resource availability are not crossed (Chapin et al. 2004). In contrast, ecosystems dominated by short-lived species should respond more rapidly (Morris et al. 2008). It also



PLATE 1. View of the long-term Rainfall Manipulation Plots (RaMPs) experiment at the Konza Prairie Biological Station in northeast Kansas, USA. This experiment is designed to assess the independent and interactive effects of two projected global change factors—more extreme rainfall regimes and warming—in native, mesic grassland. In the foreground is an unsheltered control plot with an infrared lamp. These lamps elevate temperatures year-round by  $\sim 2^{\circ}\text{C}$ . In the background is a rainfall manipulation shelter where rainfall events are captured, stored, and reapplied to the plot underneath either immediately (control treatment) or as a more extreme pattern that increases the size of events, reduces their number, and lengthens the period of time between events without changing annual rainfall amount. Photo credit: A. K. Knapp.

predicts that if resource alterations lead to disease outbreaks or pest species targeting the dominant species, ecosystem structure/function may be affected rapidly and substantially. One corollary prediction of this hypothesis is that in those ecosystems in which the dominant species do not control the majority of resources or species abundances are relatively even, rates of response to environmental change may be more gradual, reflecting the composite attributes, or complementarity, of multiple species (Gamfeldt et al. 2008).

#### *Biogeochemistry*

Ecosystems can differ dramatically in the sizes of key carbon and nutrient pools, as well as rates of biogeochemical transformations and turnover. The *biogeochemical hypothesis* predicts that pool sizes and transformation/turnover rates will determine the rate and magnitude of ecosystem response to chronic resource alterations. For example, all else being equal, ecosystems with high nutrient availability would be expected to respond minimally to chronic and directional changes in nutrients, except when chronic inputs push these systems across thresholds (e.g., N saturation; Aber et al. 1998). In contrast, systems with limited nutrient availability would be expected to respond rapidly to alterations in nutrient inputs (DeAngelis 1992). Interactions among resources can be particularly

important. For example, water limited systems may only respond to chronic nutrient additions during periods of above average moisture availability (Collins et al. 2008a).

#### *Biodiversity*

Levels of biodiversity (genetic, functional traits, and species) within an ecosystem will undoubtedly be important in influencing its sensitivity to change. The *biodiversity hypothesis* posits that the number and traits of species will constrain the extent to which species reordering and immigration will occur, and the nature and pace of the resultant response (Suding et al. 2008). For example, depending on the level of functional complementarity among species, the replacement of a dominant species by one that is less common in the community could result in either no change or large changes in ecosystem structure and function depending on the ability of the species to compensate for the reduced abundance or loss of the dominant species (Smith and Knapp 2003, Gamfeldt et al. 2008). Similarly, invading species may have large impacts on ecosystem processes or may have little or no impact depending on the degree of dominance, functional complementarity, and subsequent impacts on species interactions (e.g., Vitousek and Walker 1989). The level of diversity and traits of species within the extant



community also can determine establishment success of new immigrants under changing conditions (Fridley et al. 2007). Moreover, genetic diversity will play an important role in selection and in the acclimation or adaptive responses of species (Jump and Penuelas 2005). Acclimation and adaptive change, potentially facilitated by high genetic diversity, could constrain the extent to which ecosystem attributes, such as biodiversity, change by allowing species to maintain their abundance and avoid extinction under the continually changing conditions associated with altered resource availability (but see de Mazancourt et al. [2008]).

#### *Trophic interactions*

When considering multiple trophic levels, asynchrony in interacting species responses (pollinators, predators, pathogens) will likely result either directly or indirectly from chronic resource alterations (Carpenter et al. 2001, Parmesan 2006). The *trophic hypothesis* predicts that this trophic mismatch in response will create complex and transitory dynamics in ecosystems, as well as impact the ways in which chronic alterations propagate across trophic levels. As an example, long-lived trees are likely to respond primarily physiologically for an extended period of time based on slow population-turnover rates, whereas canopy insects or pathogens are likely to transition more rapidly from metabolic responses to community reordering or compositional change given the relatively rapid turnover times and mobility of these taxa. If the more-rapid responses of key pathogens, such as pine bark beetles, increase mortality of the dominant tree species (Raffa et al. 2008), community reordering and species turnover may be accelerated relative to rates predicted by the dominance hypothesis. For an aquatic ecosystem, the opposite might be expected; the producer community may transition quickly from physiological response to community reordering as a result of rapid turnover rates of phytoplankton, whereas the vertebrate consumers may remain in the metabolic response phase longer given their relatively slower population-turnover times. Understanding asynchrony in trophic responses to climate change has recently been recognized as a critical need in global-change research (Visser and Both 2005).

#### INTERACTIONS WITH OTHER GLOBAL-CHANGE DRIVERS (GCDs)

The HRF (hierarchical-response framework) focuses on chronic resource alterations and their consequent impacts on ecosystem dynamics, but these drivers will not occur in isolation. Rather, interactions with natural disturbance regimes and other GCDs will influence rates and trajectories of ecosystem response. There are a number of examples of rapid ecosystem shifts being triggered by pulsed disturbances or stochastic events occurring within the backdrop of gradual environmental change (Scheffer et al. 2001, Raffa et al. 2008). Because human activities are likely to increase the occurrence of

these pulsed and stochastic events (Fig. 2A), the likelihood of these events triggering rapid changes is expected to increase in the future, as ecosystem resilience is eroded by chronic resource alterations. For example, evidence from the southwestern United States suggests that piñon pine mortality during chronic drought (Breshears et al. 2005) was exacerbated by elevated soil nitrogen availability (M. F. Allen, *unpublished data*). Thus, atmospheric-N deposition interacted with drought to cause more rapid ecosystem change than would occur with either driver alone.

In addition to altered disturbance regimes accelerating trajectories of change, other anthropogenic pressures, such as habitat fragmentation, land-use change, overexploitation, pollution, and invasive species, also are expected to have important impacts on rates and trajectories of ecosystem response. Of these drivers, land-use change and habitat fragmentation in particular could amplify changes in species abundances (J. M. Fraterrigo, *unpublished data*) hastening species replacement. These anthropogenic impacts also are key drivers of biodiversity loss with important consequences for ecosystem functioning and stability (Sala et al. 2000). Loss of species could limit the capacity of ecosystems to respond to changing conditions, or may facilitate or hamper species turnover depending on which species are lost. In lakes, loss of top predators with overexploitation has been shown to increase asynchrony in trophic responses with chronic nutrient augmentation as a result of a trophic cascade, resulting in a dramatic and rapid shift in ecosystem state (Carpenter et al. 2001). In addition, loss of diversity at regional scales may limit the extent to which species are available to immigrate and take advantage of changing environmental conditions (Tilman et al. 1994). Finally, invasions by native or exotic species, perhaps facilitated by resource alterations (Davis et al. 2000), could result in large and rapid ecosystem change by bypassing the hierarchy of responses ideally depicted in the HRF (Fig. 3). Such rapid transitions have been observed with species invasions (e.g., Mack and D'Antonio 1998) and are expected to increase in frequency in the future.

#### RELATIONSHIP TO OTHER FRAMEWORKS OF ECOSYSTEM CHANGE

The HRF (hierarchical-response framework) complements other frameworks that focus on dynamic regimes and ecological thresholds (e.g., Shaver et al. 2000, Beisner et al. 2003, Scheffer and Carpenter 2003, Briske et al. 2006). Points of intersection between the HRF and previous frameworks include: (1) chronic resource change as the primary driver of ecological dynamics, and (2) changes in structure and function can be driven by shifts in dominance among extant biota, either by species reordering or through species-replacement dynamics. However, the HRF expands upon these frameworks in several important ways. First, it identifies and links several key processes and mechanisms that



may lead to change over a broad range of time scales. Second, the HRF is designed to be comparative, and thus provides an organizational structure for assessing the relative sensitivities of ecosystems to change, including the processes responsible for alterations in structure and function. Third, the HRF is compatible with theory developed for the existence of alternative states. Although pulsed disturbances or stochastic events are generally invoked as triggers of ecosystem change (but see van Nes and Scheffer 2004), such events are not necessary for similar change to occur in the HRF. Rather, chronic resource alterations alone can lead to rapid ecosystem change based on the inherent nonlinearity of population growth, the lags associated with species reordering, or the immigration of new species into a novel habitat. Moreover, with chronic resource change, a reduction in resource inputs at or below previous levels will likely not be sufficient to return the ecosystem to its original condition once species reordering or immigration occurs (Clark and Tilman 2008). Thus, with both the HRF and previous frameworks, hysteresis is predicted to be an important feature of responses to chronic resource alterations.

Overall, the HRF and other frameworks predict that rapid and large changes in ecosystem structure and function will occur more frequently in the future as a consequence of global-change-driven chronic resource alterations. This change is, in part, because human activities are altering disturbance regimes in myriad ways (Fig. 2A), and the interaction of these changes within the backdrop of chronic resource alterations will further increase the rate of nonlinear changes in ecosystem structure and function. The value of the HRF is that it highlights the mechanisms underlying change and provides a structure to generate hypotheses that, when tested, will enhance our understanding of how and why ecosystems differ in their sensitivity to chronic resource alterations and press-pulse disturbance interactions.

#### FUTURE RESEARCH DIRECTIONS

With increased awareness that the nature and pace of change in ecological systems is unprecedented and that much of this change is driven by novel and chronic resource alterations, the kinds of questions asked and the research approaches employed may require reexamination as well. For example, do well-known ecological responses to pulsed or short-term press resource additions predict responses to chronic resource alterations, such as long-term and low-level atmospheric-N deposition or eutrophication? Have past resource-alteration experiments been conducted at the appropriate temporal and spatial scales to assess the full suite of potential hierarchical responses to chronic resource alterations? How does the rate of resource alteration influence the nature and pace of change in ecosystems? Further, how are different resources likely to interact with each other and other global-change drivers (GCDs)

to impact ecosystem dynamics? And finally, what are the key characteristics of ecosystems that will determine the rates and consequences of change and the potential for ecosystem recovery?

Research that focuses on the continuum between resources pulses and chronic resource alterations is needed to address these questions, as are studies of the interactions among these and other anthropogenic impacts. There are a number of past and ongoing experiments, some long term, assessing the impacts of chronic resource alterations associated with global change, such as FACE experiments (information *available online*),<sup>5</sup> N addition experiments (PDTNet, Cleland et al. 2008; LiNX, Mulholland et al. 2008), and acid rain manipulations (RAIN, Wright et al. 1994). However, with notable exceptions (e.g., RaMPs [see Plate 1], Knapp et al. 2002; JRGCE, Zavaleta et al. 2003; CLIMATE, Mikkelsen et al. 2008), few are examining interactions among multiple GCDs, and none is assessing the interactive impacts of chronic resource alterations across multiple ecosystem types. The latter will require long-term, multi-site research designed explicitly to assess the relative sensitivity of a broad range of ecosystem types to chronic resource alterations and interactions with other GCDs. Such innovative and broad-scale endeavors will allow the ecological community to build upon the vast knowledge gained from numerous single-site, single-factor studies. In addition, these experiments will be essential for generating the knowledge necessary for understanding and predicting differences in rates and trajectories of change among ecosystems and for improving global-change models. Ecologists now recognize that understanding effects of GCDs on ecosystems demands a new perspective—one in which rapid, nonlinear responses to chronic resource alterations is the norm rather than the exception. However, change in both perspective and practice is critical if we are to gain the predictive understanding necessary to cope with the unprecedented environmental conditions observed today and expected in the future.

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