PERSPECTIVES

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Disturbance and landscape dynamics in a changing world[1]

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Abstract. Disturbance regimes are changing rapidly, and the consequences of such changes for ecosystems and linked social-ecological systems will be profound. This paper synthesizes current understanding of disturbance with an emphasis on fundamental contributions to contemporary landscape and ecosystem ecology, then identifies future research priorities. Studies of disturbance led to insights about heterogeneity, scale, and thresholds in space and time and catalyzed new paradigms in ecology. Because they create vegetation patterns, disturbances also establish spatial patterns of many ecosystem processes on the landscape. Drivers of global change will produce new spatial patterns, altered disturbance regimes, novel trajectories of change, and surprises. Future disturbances will continue to provide valuable opportunities for studying pattern–process interactions. Changing disturbance regimes will produce acute changes in ecosystems and ecosystem services over the short (years to decades) and long term (centuries and beyond). Future research should address questions related to (1) disturbances as catalysts of rapid ecological change, (2) interactions among disturbances, (3) relationships between disturbance and

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society, especially the intersection of land use and disturbance, and (4) feedbacks from disturbance to other global drivers. Ecologists should make a renewed and concerted effort to understand and anticipate the causes and consequences of changing disturbance regimes.

Key words: disturbance regime; ecosystem ecology; fire; global change; landscape ecology; MacArthur Address; Pinus contorta; *scale; spatial heterogeneity; succession; Yellowstone National Park.*

Introduction

Climate, biotic communities, human population size, and land-use and land-cover patterns are all changing rapidly on Earth and receiving well-justified attention from scientists and policy makers. Numerous reports (e.g., Lubchenco et al. 1991, National Research Council 2001) have highlighted grand challenges that include understanding the consequences of and feedbacks to these important drivers. For example, the Millennium Ecosystem Assessment (2005) emphasized the consequences of habitat change, climate change, invasive species, over-exploitation of resources, and increased nutrient availability. However, disturbance regimes are also changing rapidly, and despite their profound effects on ecosystems and landscapes, disturbances generally do not receive comparable attention. Studies of disturbance can provide unique insights into ecological patterns and processes. In addition, disturbances will interact with other key drivers of global change and strongly affect ecological systems and humanity. I suggest that ecologists should make a renewed and concerted effort to understand and anticipate the effects of changing disturbance regimes.

Disturbance is a key component of ecological systems, affecting terrestrial, aquatic, and marine ecosystems across a wide range of scales. *Disturbance* has been defined variously, but I follow the general definition offered by White and Pickett (1985): "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment." Disturbances alter system state and the trajectory of an ecosystem, and thus they are key drivers of spatial and temporal heterogeneity. Disturbances happen over relatively short intervals of time; hurricanes or windstorms occur over hours to days, fires burn for hours to months, and volcanoes erupt over periods of days or weeks. In origin, disturbances may be abiotic (e.g., hurricanes, tornadoes, or volcanic eruptions), biotic (e.g., the spread of a nonnative pest or pathogen), or some combination of the two (e.g., fires require abiotic conditions suitable for ignition and burning as well as a source of adequate fuel, which is biotic). Many disturbances have a strong climate forcing, but the relative importance of different drivers varies among systems and can even vary through time in the same system. In contrast to a disturbance event, a *disturbance regime* refers to the spatial and temporal dynamics of disturbances over a longer time period. It includes characteristics such as spatial distribution of disturbances; disturbance frequency, return interval, and rotation period; and disturbance size, intensity, and severity (Table 1).

Many disturbance regimes are currently in a phase of rapid change. In the western United States, for example, the frequency of large fires has increased significantly in recent decades in association with warming temperatures, earlier snowmelt and lengthening fire seasons (Westerling et al. 2006). Risk of large fires is also increasing in other areas of the world (Bowman et al. 2009, Girardin et al. 2009), including even tundra on the North Slope of Alaska (Qui 2009). Seven of the 10 most damaging hurricanes to have affected the United States since 1949 occurred in 2004 and 2005 (Changnon 2009). Infestations of bark beetles (Dendroctonae) in western North America have been more severe and extensive than in the past, affecting higher elevations and latitudes than previously observed and leading to novel insect–host combinations (Raffa et al. 2008). Land-use intensification and climate change are increasing landsliding in mountainous regions (Restrepo et al. 2009). Globally, the Millennium Ecosystem Assessment (2005) reported an increase in the frequency of wildfires and floods during the 20th century in Europe, Asia, Africa, the Americas, and Oceania. As disturbance regimes change in concert with other global drivers, it is imperative that ecologists understand and anticipate these changes.

Because disturbances can threaten human life and property, often with deleterious effects on the built environment, the consequences of disturbance for human wellbeing can be staggering. For example, the effects of the 2004 and 2009 tsunamis in Indonesia and recent earthquakes in China and elsewhere on local communities were devastating. The economic costs of disturbance are also substantial and increasing. Annual expenditures by U.S. federal agencies on fire suppression exceeded $1 billion several times during this decade (Gebert et al. 2008). Property insurance losses because of hurricanes in the United States between 1991 and 2006 were $49.3 billion (Changnon 2009). Society has spent considerable effort attempting to mitigate negative consequences of disturbances. Ironically, some attempts to mitigate disturbance effects may unintentionally increase the vulnerability of human communities to disturbance, particularly when controlling frequent, less severe events increases the risk of infrequent, more severe events. For example, levees and floodwalls constructed in many catchments to minimize flooding may actually increase flood magnitude and frequency (Poff 2002). Similarly, historic fire suppression in some forests (e.g., ponderosa pine) characterized by frequent, low-severity fires produced unnaturally high fuel loadings that increased the risk of high-severity fires (Covington and Moore 1994, Allen et al. 2002). By enhancing understanding of the causes and consequences disturbances, ecologists can help resource managers and policy makers improve human safety and wellbeing.

Profound changes in disturbance regimes are likely to occur within our lifetimes, and the consequences of such changes for ecosystems and linked social-ecological systems will not be trivial. However, effects are difficult to predict, and many important questions remain to be answered. How will recovery patterns in the future differ from those of the past? How will multiple disturbances interact? Will ecosystems change qualitatively following disturbance, and what conditions are likely to trigger such shifts? What locations will be most vulnerable, and how can hazards to life and property be reduced? What consequences of disturbance are ultimately beneficial to society? My goal in this paper is to synthesize current understanding of disturbance with an emphasis on fundamental contributions to contemporary landscape and ecosystem ecology. I provide an historical perspective then highlight six key conceptual contributions that have emerged from more recent studies of disturbance. Finally, I identify opportunities and priorities for future study.

A Brief Look to the Past

Understanding why and how ecological communities change over time has long been a theme within ecology (e.g., Cooper 1913, Watt 1924, 1947, Odum 1969). Although implicit in early studies, disturbance as a focal topic for ecological study was not prevalent until the late 1970s. In McIntosh's (1985) comprehensive history of ecology, *disturbance* was indexed only twice—the first related to the distinction between primary and secondary succession and the balance of nature implicit in the Clementsian view of a stable climax community; and the second related to Odum's (1969) proposed trends associated with ecosystem development and the Hubbard Brook studies of ecosystem response to disturbance. The *shifting mosaic steady state,* referring to "an array of irregular patches composed of vegetation at different ages," is an important disturbance-related concept that emerged from the studies at Hubbard Brook (Bormann and Likens 1979) as well as studies in the intertidal zone (e.g., Paine and Levin 1981). Individual patches could be in different stages of succession and change over time, but the landscape proportions of successional stages would remain constant. Thus, the shifting mosaic steady state recognized that dynamics occurring at one scale could produce a steady state at a different scale.

It was not until the late 1970s and early 1980s that disturbance as a key process structuring ecological systems across many scales emerged as a major research focus (Reiners and Lang 1979, White 1979, Mooney and Godron 1983, Sousa 1984). Disturbance received increasing attention as a driver of community structure (e.g., Levin and Paine 1974, Connell 1978, Paine and Levin 1981). Among the key factors structuring ecological communities, Levin (1976) included phase differences associated with different stages of recovery from local disturbances along with local uniqueness and differential movements of organisms. An extensive literature on population-level consequences of disturbance subsequently developed and has provided many theoretical and empirical contributions (e.g., Sousa 1984, DeAngelis and Waterhouse 1987, Ives 1995), but it is beyond my scope to cover this fully.

Table 1. Definitions of components of a disturbance regime, adapted from White and Pickett (1985) and Turner et al. (1998).

Term	Definition
Frequency	Mean or median number of events occurring at an average point per time period, or decimal fraction of events per year; often used for probability of disturbance when expressed as the decimal fraction of events per year.
Return interval	Mean or median time between disturbances; the inverse of frequency; variance may also be important, as this influences predictability.
Rotation period	Mean time needed to disturb an area equivalent to some study area, which must be explicitly defined.
Size	Area disturbed, which can be expressed as mean area per event, area per time period, or percentage of some study area per time period.
Intensity	Physical energy of the event per area per time (e.g., heat released per area per time period for fire, or wind speed for storms); characteristic of the disturbance rather than the ecological effect.
Severity	Effect of the disturbance event on the organism, community, or ecosystem; closely related to intensity, because more intense disturbances generally are more severe.
Residuals	Organisms or propagules that survive a disturbance event; also referred to as biotic legacies. Residuals are measure of severity, and thus (at least within one disturbance) an index of intensity.

Pickett and White's (1985) book, *Natural Disturbance and Patch Dynamics*, ushered in a period of concerted attention to natural disturbances in a wide range of systems and emphasized spatial heterogeneity in ecosystems. This heightened interest in disturbance coincided with the emergence of landscape ecology in North America, as ecologists began to study in earnest the causes and consequences of spatial heterogeneity (Risser et al. 1984, Turner 1989, 2005). In contrast to the densely settled landscapes of Europe, the landscapes of North America contained extensive natural and semi-natural areas in which disturbance dynamics were conspicuous. Disturbance was increasingly recognized as intrinsic to ecological communities and a fundamental driver of spatial and temporal heterogeneity.

A series of large natural disturbances during the 1980s and early 1990s focused public attention and scientific research on their causes and consequences. These included the eruption of Mount St. Helens in 1980; the Yellowstone fires of 1988; Hurricane Hugo (category 5),

Box 1. Six New Insights from Disturbance Studies

Disturbance and landscape dynamics

1) *Disturbance and landscape heterogeneity*.—Even very large disturbances do not homogenize the landscape; rather, they create spatial heterogeneity, often at multiple scales.
2) *Landscape equilibrium and scale*.—Landscape equilibrium is scale-dependent and is but one of a suite of dynamics that systems may exhibit.
3) *When space matters*.—The conditions under which spatial heterogeneity matters often can be identified.

Disturbance and ecosystem processes

4) *The functional mosaic*.—Post-disturbance heterogeneity establishes a functional spatial mosaic of process rates and feedbacks.
5) *Long-term legacies*.—Long-term spatial legacies of disturbance can persist for decades to centuries.
6) *Nutrient loss and retention*.—Not all ecosystems are "leaky" after disturbance.

which affected Puerto Rico and South Carolina in 1989; and the 1993 floods on the Mississippi River. In addition, human-induced disturbances such as the Exxon Valdez oil spill in 1989 in Prince William Sound, Alaska, garnered attention, as did the extent and pattern of harvesting of old-growth forests (e.g., Spies et al. 1994). Subsequent large disturbances have continued to attract media attention, and interest in understanding disturbance dynamics and anticipating what may happen in the future continues to grow.

Yellowstone National Park and the Fires of 1988

Because of my familiarity with the system, examples based on studies of the 1988 Yellowstone Fires will be used throughout this paper. Established in 1872 as the world's first national park, Yellowstone National Park (YNP) encompasses approximately 9000 km^2 in Wyoming, USA. Approximately 80% of YNP is dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Louden) forest, although subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) may be locally abundant in older stands at higher elevations or on moister sites. The climate is characterized by cold, snowy winters and dry, mild summers (Dirks and Martner 1982). Stand-replacing fires have occurred in Yellowstone with a return interval of 100–300 years throughout the Holocene (Romme and Despain 1989, Millspaugh et al. 2000, 2004, Schoennagel et al. 2003). Fire suppression was instituted in YNP in 1886 but was not consistently effective before 1945 (Schullery 1989). In response to growing recognition of the ecological importance of fire, a natural fire program was initiated in YNP in 1972 in which lightning-caused fires were permitted to burn in remote areas without interference under prescribed conditions. Of >200 such fires observed in the park between 1972 and 1988, 83% went out by themselves before burning >0.5 ha, and in the largest fire year prior to 1988 (in 1981), a total of 3300 ha were burned in 28 natural fires (Renkin and Despain 1992).

During the summer of 1988, severe fires burned in YNP under conditions of extreme drought and high winds (Christensen et al. 1989, Renkin and Despain 1992), surprising scientists and managers and focusing attention worldwide on wildfire. Many ecologists claimed then that past fire suppression was responsible for the size and severity of the fires, but evidence does not support this claim (Turner et al. 2003). In forests with a natural crown-fire regime, including boreal and subalpine forests, fires are driven by climate rather than variation in fuel (Bessie and Johnson 1995, Schoennagel et al. 2004, Littell et al. 2009). The 1988 fires were large, affecting ~36% of the park and challenging ecologists to address this scale effectively (Knight and Wallace 1989). However, the fires clearly were not an ecological catastrophe, and Yellowstone has proven to be remarkably resilient to these large, severe fires (Turner et al. 2003, Schoennagel et al. 2008).

What Has Been Learned from Studies of Disturbance?

Progress in landscape and ecosystem ecology has benefitted from ecological studies of disturbances. I highlight six key conceptual contributions focusing on disturbance and landscape heterogeneity, landscape equilibrium and scale, when space matters, the functional mosaic, long-term legacies, and nutrient loss and retention (Box 1). There have also been advances in population and community ecology from studies of disturbance (e.g., Bunnell 1995, Hunter 1999), with particular emphasis on changes in habitat quantity, quality and configuration. These topics are important but beyond the scope of this paper.

Disturbance and landscape dynamics

Studies of disturbance were instrumental in the development of landscape ecology in North America, providing solid empirical footing to concepts that were

FIG. 1. Aerial view in October 1988 of the landscape mosaic produced by the Yellowstone fires (photo credit: M. G. Turner).

initially abstract. Because disturbances both respond to and create landscape heterogeneity, disturbance was identified early on as ideally suited for landscape studies (Risser et al. 1984) and was the theme of the first annual U.S. landscape ecology symposium held in January 1986 in Athens, Georgia (Turner 1987). Disturbances created conspicuous spatial patterns that could be studied rigorously, and they often did so at scales well beyond those amenable to controlled experiment. Increased availability of spatial data, development of geographic information systems (GIS), and enhanced computing capability also contributed to progress. Studies of disturbance led to substantial improvements in understanding heterogeneity, scale and thresholds in space and in time and catalyzed new paradigms in ecology.

Disturbance and landscape heterogeneity.—Although small "patch" or "gap" disturbances were recognized as sources of spatial heterogeneity (Pickett and White 1985), the occurrence of large "catastrophic" disturbances raised the specter of extensive areas being homogenized and even destroyed. There were numerous claims that Yellowstone had been ruined by the 1988 fires, and the burned forests were sometimes referred to "moonscapes." However, the now-iconic aerial view of the burned landscape revealed otherwise (Fig. 1). The fires had created a complex spatial mosaic of patches that varied in size, shape, and severity (Turner et al. 1994). Intensive studies of the postfire landscape demonstrated that the fires had indeed increased the heterogeneity of the Yellowstone landscape (Turner et al. 1994). Although the burned areas were large, the complex configuration resulted in nearly 75% of the burned area being <200 m from an unburned forest edge (Turner et al. 1994). Furthermore, there was variability in fire severity throughout the landscape.

Studies initiated following other disturbances in different ecosystems also found that large disturbances created significant spatial heterogeneity (Turner et al. 1997*a*, Foster et al. 1998, Parsons et al. 2005, Whited et al. 2007, Kupfer et al. 2008). Spatial variation in disturbance severity is now appreciated more fully, along with recognition that biotic residuals (i.e., surviving roots and rhizomes, as well as soil and canopy seedbanks) are often abundant even within very large disturbances. Disturbances typically create spatial heterogeneity in ecological systems: even very severe natural disturbances typically do not homogenize the landscape. Because land use and management can fundamentally alter spatial heterogeneity (e.g., by homogenizing at some scales and introducing new pattern at other scales), emulating natural disturbances has been proposed as an effective strategy in land management, especially of forests (e.g., Attiwill 1994, DeLong and Tanner 1996).

Landscape equilibrium and scale.—Studies of disturbance challenged existing equilibrium theory in ecology. The past inability to incorporate heterogeneity and multiple scales into concepts of stability contributed, in part, to the failure of the classical equilibrium paradigm in ecology (Wu and Loucks 1995). Romme's (1982) study of historical fire in the Yellowstone landscape was among the earliest to test the shifting mosaic steady-state concept in a new region. Through detailed dendrochronological study, Romme (1982) found no evidence of an equilibrium mosaic either in a single watershed or subsequently across a 129 600-ha portion of the Yellowstone landscape (Romme and Despain 1989). Rather, the proportion of the landscape occupied by different successional stages fluctuated widely over time. Empirical studies of other landscapes also found marked fluctuations in landscape composition (e.g., Baker 1989), particularly when disturbances were large and infrequent (Turner et al. 1993, Moritz 1997). Theoretical studies indicated that equilibrium was but one of several possible outcomes (Turner et al. 1993). The steady-state mosaic was found to apply only in some cases; landscape equilibrium was scale dependent (Turner et al. 1993). Thus, studies of disturbance ultimately contributed to a major shift from an expectation of steady state to a paradigm that recognized dynamic equilibria as well as nonequilibrial systems (Turner et al. 1993, Wu and Loucks 1995, Perry 2002).

Studies of scale dependence in landscape equilibrium and nonequilibrium also contributed to the growing understanding of scale in ecology (Levin 1992), and they continue to further this understanding (e.g., van Nes and Scheffer 2005). Characterizing disturbance regimes in complex landscapes is a key component of the *historical range of variability* (HRV; Landres et al. 1999, Keane et al. 2009), which assumes that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems, and that past conditions provide context for managing ecological systems today. Understanding the history of a landscape helps determine whether particular events fall within or outside the expected variability in the system. Management may also attempt to emulate natural disturbance regimes (Attiwill 1994, Long 2009). More recently, studies of disturbances have also informed understanding of nonlinear dynamics, thresholds and cross-scale interactions in ecology (Peters et al. 2004, 2007, Allen 2007).

When does space matter?—The question of when spatial heterogeneity matters for ecological processes lies at the heart of landscape ecology (Turner 1989, 2005, Strayer 2003). Studies of the 1988 Yellowstone fires allowed this question to be addressed in two ways: (1) did the fires respond to landscape patterns, and (2) did the post-fire landscape pattern influence succession? Analyses of fire spread patterns demonstrated that fires that burned early in the season did respond to landscape patterns (Turner et al. 1994), burning more readily through older forests with abundant and well-connected fuels and being constrained by natural fire breaks and young forest. However, the later fires that accounted for most of the area burned showed little, if any, response to landscape pattern (Turner et al. 1994). These fires burned readily through forests of all successional stages and were not stopped even by large features such as the Grand Canyon of the Yellowstone. The later fires burned under extreme, persistent drought and high winds (Renkin and Despain 1992).

Collectively, the patterns of burning in YNP indicated that landscape pattern may be important under some, but not all, environmental conditions. Landscape pattern was unimportant for fire spread when burning conditions were severe (Turner and Romme 1994). More generally, disturbances appear to respond to landscape heterogeneity when the disturbance is of moderate intensity and has a distinct directional orientation or locational specificity such that some locations (e.g., ridgetops, edges) are more vulnerable than others (Boose et al. 1994, Kramer et al. 2001, Turner 2005). There is no predictable effect of landscape pattern or position when the disturbance has no directionality, such as the smaller gap-forming downbursts in the upper Midwestern United States (Frelich and Lorimer 1991), or when disturbance intensity is extremely high (Moritz 1997).

The postfire YNP landscape mosaic allowed the effects of spatial pattern on succession to be evaluated. Plant reestablishment following the 1988 fires was surprisingly rapid, but spatial variability in burn severity and patch size affected early succession (Turner et al. 1997*b*, 1999). For example, vascular plant species richness was greater in patches that were small and less severely burned; the effects of patch size persisted through at least 2000, although the effects of burn severity had diminished (Turner et al. 1997*b*, 2003). The most striking variation in postfire vegetation was in the density of postfire lodgepole pine regeneration (Fig. 2), which ranged from 0 to >500 000 stems/ha primarily in response to two contingent factors: (1) the proportion of lodgepole pine trees in the prefire stand that bore serotinous cones, and (2) the local severity of the fire (Turner et al. 1997*b*, 1999). Regeneration was more abundant in locations with higher pre-fire serotiny and in or near areas of less-severe, stand-replacing fire in which needles and cones were not completely consumed (Anderson and Romme 1991, Turner et al. 1997*b*). Thus, the spatial pattern of burn severity had a significant imprint on postfire forest structure.

Comparative analyses of succession following different disturbances have suggested more generally that the size, shape, and configuration of disturbed habitat influences successional trajectories. Succession is more variable and less predictable when biotic residuals are few (i.e., in areas of high disturbance severity), when disturbed patches are large (and thus dispersal is required for re-colonization), and when the interval between disturbances is short relative to the lifespan of the dominant organisms (Turner et al. 1998, Frelich and Reich 1999).

Summary: disturbance and landscape dynamics.—In sum, several general ecological insights have emerged from studies of natural disturbance (Box 1). First, even very large disturbances do not homogenize the landscape; rather, disturbances more typically create heterogeneity in space and time. This variability may be informative in its own right (Fraterrigo and Rusak 2008) and functionally significant. Second, equilibrium is a scale-dependent concept, and equilibrium is but one of a suite of dynamics that can be observed in ecological systems. And third, the conditions under which spatial pattern matters for ecological responses often *can* be identified, although determining when spatial heterogeneity can and cannot be ignored remains challenging.

Ecosystem processes

Because they create vegetation patterns, disturbances can also establish the spatial patterns of many ecosystem processes on the landscape. The shifting mosaic steady state (Bormann and Likens 1979) recognized this explicitly, and Odum's (1969) strategy of ecosystem development helped set the stage for hypothesized functional dynamics with time since disturbance. However, although the basic causes of heterogeneity in ecosystem processes have been recognized for a long time (Jenny 1941) and temporal dynamics were well studied (Chapin et al. 2002), integration of the spatial perspective of landscape ecology with the process focus of ecosystem ecology lagged (Lovett et al. 2005, Turner 2005). Ecology does not have a spatially explicit theory of ecosystem function (Strayer et al. 2003, Turner and Chapin 2005), and spatial empirical studies of ecosystem process rates are challenging. Studies of disturbance have helped to bridge this gap.

The functional mosaic.—Ecosystem processes following disturbance have been well studied with respect to functional changes associated with succession. For example, changes in carbon pools and fluxes during forest succession are well known (Fig. 3a; Chapin et al. 2002), and the mechanisms underpinning these changes have been described and debated (e.g., Ryan et al. 1997, Gower 2003). Because nitrogen (N) often limits net primary production, the effects of disturbance on N cycling also have received widespread attention (Chapin et al. 2002). However, spatial heterogeneity in pools and fluxes *within* a given successional stage has received scant attention, as research focused on temporal change often sought to minimize the "noise" resulting from spatial variation.

The enormous variation in density of lodgepole pine regeneration after the 1988 fires suggested that ecosystem process rates might be strongly affected by these differences in forest structure. An obvious question was whether the landscape mosaic of postfire tree density affected carbon pools and fluxes within the burned area. Field studies were combined with aerial photo analysis, and results revealed that the postfire patterns of tree density produced a landscape mosaic of process rates within the burned areas (Turner et al. 2004). Ten years after the fires, aboveground net primary production ranged from 0.04 to 15.12 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$ and increased with tree density (Turner et al. 2004). This positive relationship was still strong in 2005, although there was an indication of declining ANPP in stands of highest tree density (Fig. 4a; Turner et al. 2009). We have suggested that different trajectories of biomass accumulation are initiated in stands of varying tree density (Kashian et al. 2006). The mosaic of tree density also

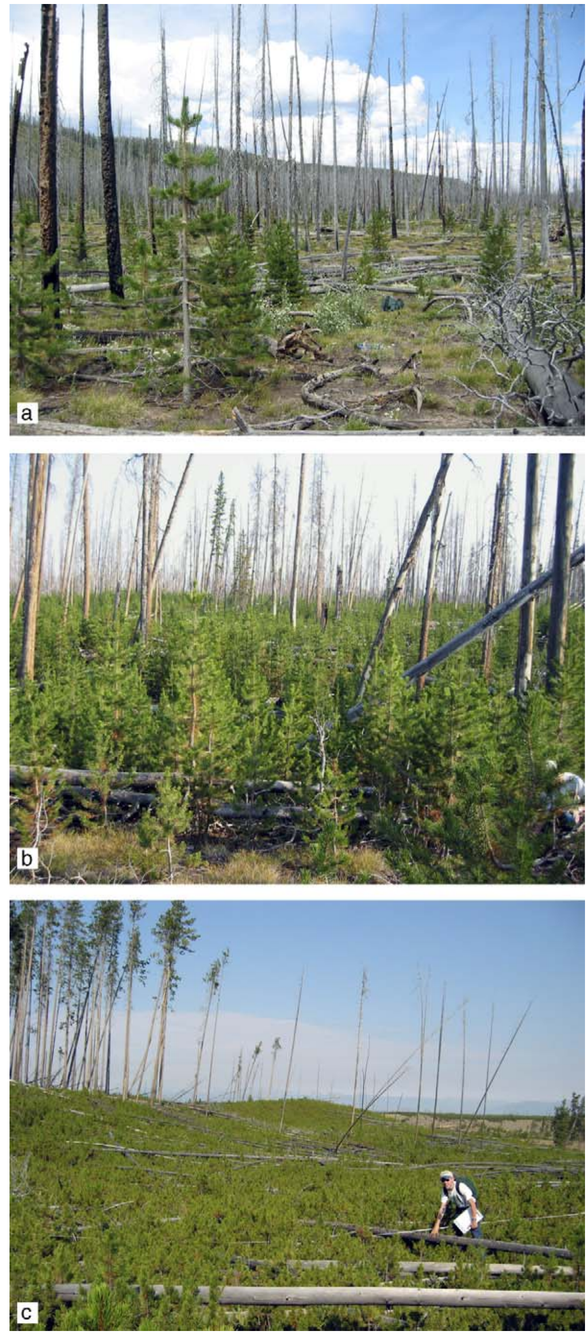

Fig. 2. Photos taken in summer 2003 illustrate the wide variation in density of lodgepole pine regeneration following the 1988 Yellowstone fires. Tree densities shown here are (a) 566 trees/ha, (b) 51 300 trees/ha, and (c) 454 000 trees/ha, with tall trees that survived the fire in background on left (photo credits: M. G. Turner).

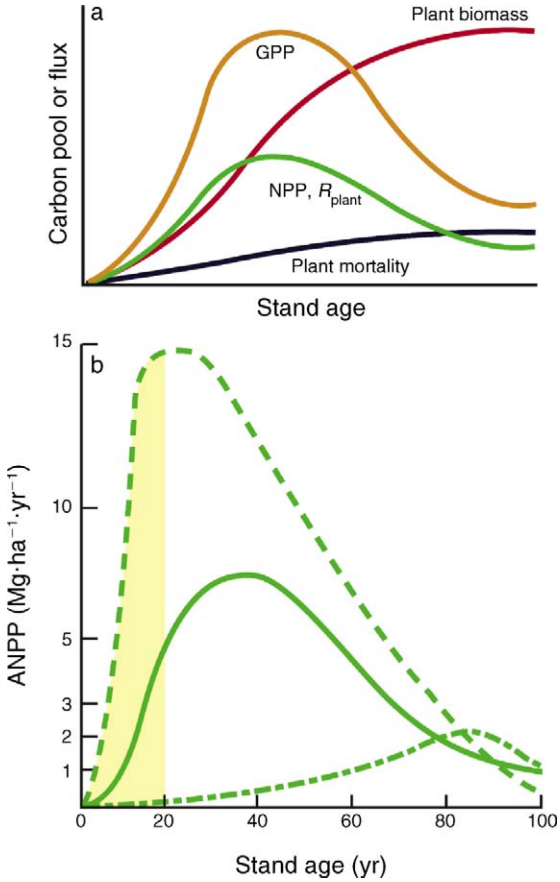

FIG. 3. (a) Schematic of how carbon pools and fluxes change, on average, during forest succession. Key to abbreviations: the GPP, gross primary production; NPP, net primary production; R_{plant}, carbon flux associated with plant respiration. The figure is adapted from Chapin et al. (2002). (b) Schematic of the range of pathways for aboveground net primary production (ANPP) in lodgepole pine stands that regenerated at different densities after the 1988 Yellowstone fires. The shaded area indicates values measured through 2005 (Turner et al. 2009); dashed lines indicate hypothesized future trajectories of biomass accumulation, adapted from Kashian et al. (2006).

produced a landscape mosaic of foliar nitrogen (N) concentrations and pool sizes (Fig. 4b; Turner et al. 2009). Thus, in contrast to the predictable change in the mean over time (Fig. 3a), our studies revealed multiple trajectories of biomass accumulation over time (Fig. 3b). Because they are determined by initial patterns of postfire lodgepole pine regeneration, these pathways are ultimately caused by contingencies that include prefire stand attributes (primarily serotiny) and the spatial pattern of disturbance severity. The range of this spatial variation may be of comparable magnitude to the temporal variation in the mean over successional time (Fig. 3b).

Long-term legacies.—If disturbances impose new patterns of ecosystem structure and function, how long do these patterns persist? Disturbance studies have underscored the importance of historical events in explaining contemporary ecosystems and shown that legacies may persist for decades to centuries (Foster et al. 1999). Using a postfire chronosequence in YNP, Kashian et al. (2005*a*, *b*) found that spatial variability among stands of the same age diminished over time, but effects of the initial disturbance-imposed pattern on tree densities and growth rates were detectable for nearly two centuries following fire. Smithwick et al. (2005*b*) also detected measurable legacies of historic fire on soils in a subset of the YNP chronosequence stand for decades after fire. Studies by DeLuca and colleagues have demonstrated the persistent legacy of fire on nitrification rates in western ponderosa pine (*Pinus ponderosa*) forests (DeLuca et al. 2006). Charcoal is incorporated into the soil and appears to adsorb organic compounds that influence nitrification, and postfire charcoal in the soil may enhance nitrogen availability for decades. Thus, the "ghost of disturbance past" may have long-lasting effects in contemporary ecosystems.

Nutrient loss and retention.—The consequences of disturbance for nutrient loss and retention have been the subject of a large body of ecological research. Many

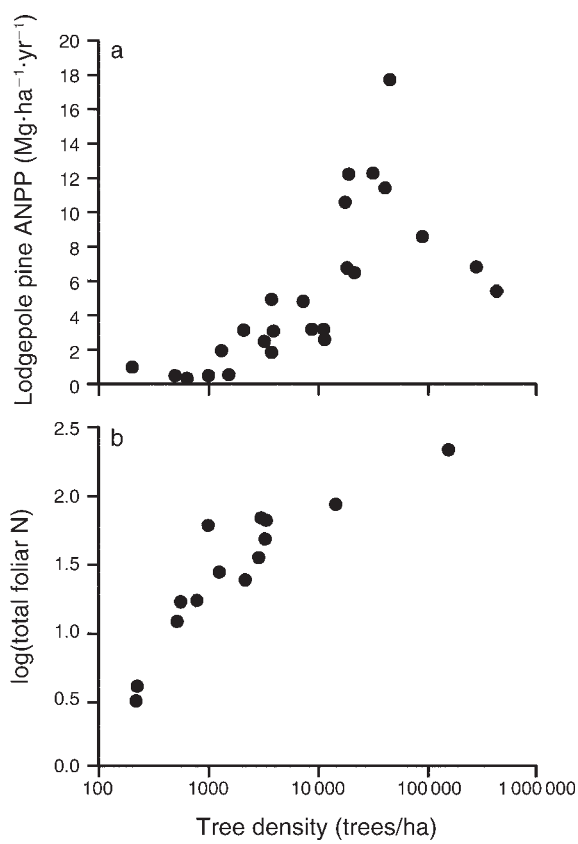

FIG. 4. Variation in (a) aboveground net primary production and (b) total pool of foliar N in 17-yr-old postfire lodgepole pine stands that established following the 1988 fires in Yellowstone National Park. The figure is adapted from Turner et al. (2009).

studies have demonstrated elevated rates of nutrient availability after disturbance as well as substantial nutrient loss through leaching and transport. Conventional wisdom appears to view nutrient loss following disturbance as a general phenomenon, despite recognition of a wider range of potential responses (e.g., Vitousek and Melillo 1979, Vitousek et al. 1979, Boerner 1982).

Expectations about the consequences of disturbance for nutrient loss and retention have been shaped by the elegant experimental studies conducted at Hubbard Brook and presented in many general biology and ecology texts. Bormann and Likens (1979) found substantial losses of nitrate following clearcutting in a steep watershed characterized by relatively fertile soils and deciduous forest. Stream nitrate concentrations spiked well above levels considered safe for human consumption, and nitrate remained elevated for several years. The experimental treatment included not only clearcutting, but also prolonged herbicide application that prevented any vegetative regrowth, including graminoids, forbs, and shrubs. The original papers are very clear about the treatments, but these consequences are often described as owing solely to clearcutting (and by extension, are often anticipated after other disturbances that kill trees).

Nitrogen dynamics associated with surface and prescribed fires have been well studied (e.g., Wan et al. 2001), but few studies had addressed N following natural stand-replacing fire (Smithwick et al. 2005*a*). Some N is lost when biomass is consumed by fire, but whether additional N is lost or retained following fire varies. In YNP, our studies have suggested that early postfire lodgepole pine forests conserve rather than lose N. In laboratory incubations, consumption of ammonium exceeded gross production, and in the field, net N immobilization was observed in year-long in situ incubations (Turner et al. 2007). During the initial postfire years, N uptake by understory vegetation is also important (Metzger et al. 2006). As succession proceeds, the rapidly growing lodgepole pines become a strong sink for N (Turner et al. 2009), and the landscape mosaic of postfire tree density produces a landscape mosaic of foliar N pools. Inorganic N availability as indexed using resin bags decreased with increasing tree productivity (Turner et al. 2009), suggesting that the trees are accessing inorganic N effectively. Chronosequence studies have shown that ecosystem N stocks also recovered fairly quickly, within 40–70 years after the fire (Smithwick et al. 2009). Collectively, these observations are consistent with recent suggestions of a shift from a microbial to a vegetative N sink as succession proceeds (Chapman et al. 2005). The role of fire as a vegetation manager may be more important than its role as a nutrient mineralizer (Hart et al. 2005).

Thus, studies of disturbance provide evidence that nutrients may be conserved following some major disturbances (e.g., Vitousek and Matson 1985, Martin and Harr 1989, Yermakov and Rothstein 2006, Turner et al. 2007). Perhaps the early work at Hubbard Brook represents the endpoint of high nutrient loss along a continuum of possible responses to disturbance. The observed high losses occurred under conditions of high nutrient availability, complete removal of vegetation (including the understory), steep topography, and shallow soils. Consequences of disturbances for nutrient cycling may differ substantially among ecosystems and with disturbance type and severity, and mechanisms of retention may be very important, especially in nutrient-limited systems (Vitousek and Reiners 1975, Turner et al. 2007).

Summary: disturbance and ecosystem processes.—In sum, new insights about ecosystem processes have resulted from studies of disturbance (Box 1). First, post-disturbance heterogeneity can establish a mosaic of process rates and feedbacks; thus, spatial heterogeneity in ecosystem processes even in the same age class should not be neglected. Second, the spatial legacies of disturbance for ecosystem structure and function can persist for decades to centuries. Thus, the past may be important in explaining the present, and contemporary disturbances may set the stage for ecological dynamics well into the future. And finally, not all ecosystems are leaky after disturbance, and a wider range of potential biogeochemical responses to disturbances, including nutrient retention, may not be uncommon.

A LOOK TO THE FUTURE

Looking toward the decades ahead, disturbance regimes will likely move into uncharted territory. Global climate change will alter disturbance regimes because many disturbances have a significant climate forcing. Although ecologists have recognized this consequence of global warming for a long while (e.g., Graham et al. 1990), there is an urgent need for more comprehensive evaluation of scenarios of future disturbance regimes. Biotic invasions, change in species assemblages, and expansion and intensification of land use will also influence disturbance dynamics. What will happen when disturbance regimes change? How should society respond? What combinations of factors will cause surprises and qualitative shifts in ecosystems? The past may not predict the future, yet the lessons learned over the past few decades will become increasingly important as we anticipate responses of ecological systems to change.

Disturbances will continue to provide valuable opportunities for gaining insights about pattern–process interactions. From landscape and ecosystem studies, it is clear that even large, severe natural disturbances are not ecological catastrophes in many systems. However, an ecosystem may not be resilient to a novel disturbance or disturbance regime, and qualitative changes may ensue. For example, whitebark pine forests throughout the northern Rocky Mountains are currently being attacked by white pine blister rust (*Cronartium ribicola*), a

Box 2. Priorities for Future Research

Disturbance as a catalyst

- Where, when, and how will disturbance catalyze abrupt rapid and significant change in ecological communities and accelerate change in response to slow drivers?
- What are the implications of such rapid changes for ecosystem processes?

Interacting disturbances

- Where, when, and how will interacting disturbances produce synergistic effects?
- When does a disturbance amplify or attenuate the effects of another, or alter its probability of occurrence?
- What are the effects of disturbance frequency and sequence?

Disturbances and society

- Where, when, and how will disturbances interact with patterns of land use and land cover?
- How should society respond to changing disturbance regimes?
- How can the vulnerability of populations and infrastructure—and the potential for catastrophe—be reduced?

Feedbacks

- Where, when, and how will disturbances feedback to global cycles?
- What changes are offsetting, and what changes result in positive feedback?

nonnative pathogen, and the mountain pine beetle (*Dendroctonus ponderosae*), a native bark beetle. Beetle distributions were limited previously by cold temperatures at the high elevations occupied by whitebark pine, and the tree species is a naïve host that lacks beetle defense mechanisms. Mortality of whitebark pine is now substantial and widespread, and other conifers are likely to replace whitebark pine (Schrag et al. 2008). Cascading effects on grizzly bears (*Ursos arctos horribilis*) are anticipated because whitebark pine seeds are an important food source for the bears. Understanding the effects of novel disturbances or disturbance regimes and how these are translated through ecosystems is a critical research need. In the remainder of this section, I identify four areas of high priority for future research (Box 2).

Disturbance as a catalyst

In the presence of gradually changing drivers, disturbances are fast variables that trigger rapid and significant change in ecological communities. Inertia in ecological communities may mask impending state change because long-lived organisms (e.g., trees) may make the system appear unresponsive to environmental changes even though the regeneration niche may be shifting (e.g., Johnstone et al. 2010, Landhäusser et al. 2010; although Van Mantgem et al. 2009 have detected increased tree mortality rates in undisturbed western forests). Following a disturbance, community composition can shift abruptly to species that are better suited to current conditions (e.g., Dunwiddie 1986, Cwynar 1987). Such dynamics are already being observed today. In the Yukon, Canada, lodgepole pine is extending its range northward following fire, colonizing burned sites previously dominated by spruce (Johnstone and Chapin 2003). In Alaska, white spruce (*Picea glauca*) is replacing black spruce (*Picea mariana*) following fire and permafrost decline (Wirth et al. 2008). In the southern boreal forest of North America, severe windthrow and fire are resulting in rapid shifts in dominant tree species (Frelich and Reich 2009). Disturbance may accelerate changes in species composition or even biome boundaries (Frelich and Reich 2009), and potentially hasten transitions to "no-analogue communities" (Williams and Jackson 2007). Such changes will have enormous implications for the quantity, quality and distribution of habitat and likely influence the biogeography of many species. If large-scale changes in biotic communities occur after disturbances, there will also be significant consequences for many ecosystem processes. Understanding the interaction between fast and slow variables is very important for anticipating future ecosystems in the face of global warming.

Interacting disturbances

Different disturbances can and will interact with each other, and despite the rapid increase in understanding of the consequences of individual disturbances, their interactions are poorly understood. Prior disturbance can exert a strong effect on ecosystem response to a subsequent disturbance (e.g., Paine et al. 1998, Davies et al. 2009). Recent experimental studies have indicated that sequences of extreme events may produce synergistic vegetation responses, and furthermore that the sequence itself (e.g., the order of flood and drought) matters (Miao et al. 2009). However, there remains a paucity of empirical information about whether and when a disturbance will amplify or attenuate the effects of another, or change the probability of its occurrence. For example, there is substantial interest in how the extensive outbreaks of bark beetles may affect future wildfire in western North America (e.g., Bebi et al. 2003, Jenkins et al. 2008, Derose and Long 2009). Conventional wisdom assumes that the risk of fire is elevated in beetle-killed forests, yet empirical data are few (Simard et al. 2008). Our recent studies in lodgepole pine forests of Greater Yellowstone indicate that bark beetle infestation reduces canopy bulk density substantially and reduces the projected risk of active crown fire (Simard 2010; M. Simard, W. H. Romme, J. M. Griffin, and M. G. Turner, *unpublished manuscript*).

Changes in disturbance frequency alone may also lead to surprising disturbance interactions. Successive disturbances that occur in relatively short time (i.e., compound disturbances) may have synergistic effects (Paine et al. 1998). Whether increased disturbance frequency produces a qualitative change in the state of an ecosystem will depend in part on the state of the system when it is disturbed. The "double whammy" will be pronounced if the system has not yet recovered from the first disturbance when affected by the second. For example, the cumulative effects of repeated hurricanes could qualitatively change vegetation characteristics and C balance (Busing et al. 2009). Sequential fires in the same location could convert a forest to non-forest if the interval between the fires was less than the time required for the trees to be reproductive. Future climate projections now suggest that fire regimes may change even more dramatically than many scientists had previously imagined (Littell et al. 2009). In the Yellowstone region, projections from the current GCMs suggest that weather conditions like 1988 will represent the *average* rather than the extreme year (A. M. Westerling, *unpublished data*); the increased fire frequencies that would accompany such a change could dramatically alter the YNP landscape.

Increased disturbance frequencies will be especially important for C cycling. In Canadian boreal forests, variation in landscape carbon balance have been driven largely by increased fire frequency, rather than by direct ecophysiological effects of climate (Bond-Lamberty et al. 2007). Projections for effects of disturbance and climate change in black spruce forests of central Canada found that only an increase in disturbance frequency (four forest fires during a 150-yr simulation) caused net ecosystem production to become negative (Chertov et al. 2009). Rapid, irreversible state changes can occur when multiple environmental changes reduce the resilience of long-established disturbance–recovery regimes (Chapin et al. 2004, Frelich and Reich 2009). This is conspicuous in western United States shrublands in which invasion by nonnative cheatgrass (*Bromus tectorum*) is associated with substantial increases in fire frequency (D'Antonio and Vitousek 1992) and major changes in terrestrial carbon storage (Bradley et al. 2006). Understanding interactions among multiple drivers, including disturbances, remains a key general challenge in contemporary ecology (Darling and Cote 2008).

Disturbances and society

The relationship between humans and disturbance is complex. Because humans have altered disturbance regimes both purposefully (e.g., fire suppression, flood control) and inadvertently (e.g., land-use practices), understanding disturbance dynamics can be an important part of understanding the behavior of linked social–ecological systems (Chapin et al. 2004, 2006, 2008). On the one hand, disturbances such as flooding and fire have been recognized for millennia as events that can renew ecosystems. Native Americans used fire to enhance production of forage and improve habitat, and floodplains have long been recognized as fertile sites for crops. On the other hand, floods, fires, and storms can all destroy life and property. Fire suppression and flood control are perhaps the best examples of society's attempts to control disturbance, but inadvertent effects are also common. For example, increased population density is associated with more fire ignitions in many parts of the world (Achard et al. 2008, Calef et al. 2008). In the tropics, forest fragmentation exacerbates the severity of wind disturbance and may elevate the risk of fire (Laurance and Curran 2008).

From landscape and ecosystem studies, it is clear that even large, severe natural disturbances are not necessarily ecological catastrophes. However, the potential for catastrophe lies at the intersection of natural disturbance and development; interactions with land-use patterns are extremely important. The built environment is often less resilient than the natural ecosystem, and, as was so apparent in the aftermath of Hurricane Katrina, the consequences for human life and property can be devastating.

Widespread increases in population density and infrastructure in areas that are subject to natural disturbances are problematic, especially for disturbances that are of high severity and low frequency. In the United States, exurban development has expanded in many areas of the country (Brown et al. 2005) and the wildland–urban interface has increased (Radeloff et al. 2005). Population and housing density have increased in areas that burn or flood regularly, which poses substantial risk to life and property (e.g., Hammer et al. 2009). Coastal areas are critical to nearly half the world's population and subject to severe hurricanes; in the United States, 19 million people live within one km of the shoreline and 11.6 million live below 3-m elevation (Lam et al. 2009). Unfortunately, these patterns are setting the stage for future conflict between people and disturbances.

Identifying incentives to encourage development in areas of lower risk (and discourage development in areas prone to severe natural disturbance) should be of high priority in socioecological systems. Decreasing the vulnerability of disturbance-prone regions also requires understanding how the risk of extreme events may change (Stanturf et al. 2007). Changing disturbance regimes may alter the "ground rules" that governed many patterns of human settlement in the past and galvanize a community. For example, two 150-yr floods within 10 months (August 2007 and June 2008) along the Kickapoo River severely damaged Gays Mills, Wisconsin, and prompted residents to consider relocating their town to higher ground. Seven miles to the north, the town of Soldiers Grove escaped serious damage because it had moved uphill following a damaging flood in 1978. Relocation may be practical for smaller communities, but it remains problematic for areas of high population density. Actions to reduce local vulnerability, e.g., using nonflammable building materials and creating "defensible space" around homes in fire-prone areas, should also be encouraged.

There is a great need for planners and policy makers to understand the dynamics of natural disturbances and to anticipate the consequences of changing risk. Coping mechanisms may include increasing resilience in the ecological and social system, engineering to reduce vulnerability, and modifying behavior either locally or at larger scales. In some situations, restoration of a natural disturbance regime is feasible and may increase resilience in the system. For example, prescribed fire or mechanical thinning can reduce unnatural fuel buildup in southwestern ponderosa pine forests and reduce the risk of high-severity fire to which these ecosystems are not adapted (Moore et al. 1999, Roccaforte et al. 2008). Similarly, because extensive levee networks can increase rather than reduce flooding (U.S. Geological Survey 1999, Criss and Shock 2001), restoring the connections between rivers and their floodplains and increasing wetland cover could potentially increase water storage capacity and reduce flooding (Poff 2002). Altered disturbance regimes may have acute impacts on property and yield of food and fiber, and injuries or mortality could increase. Thus, the effects of changing ecological disturbance regimes on ecosystem services and human wellbeing need greater attention.

Feedbacks

Disturbance dynamics have important feedbacks to global cycles through their effects on greenhouse gas emissions and albedo, and feedbacks may be either negative (dampening) or positive (amplifying). For example, volcanic eruptions could produce negative feedbacks that result in global cooling, and rapid vegetation growth after disturbance may increase the strength of a carbon sink. However, positive feedbacks may accelerate changes that are underway. Increased fire in tropical peatlands (Van der Werf et al. 2008) and the boreal forest has increased carbon emissions (Kasischke et al. 1995, Kurz and Apps 1999, Balshi et al. 2007, 2009), which can reinforce climate warming. The mountain pine beetle outbreak in British Columbia, Canada, converted the forest from a small net C sink to a large net C source (Kurz et al. 2008*a*). The risk of future natural disturbances leads to substantial uncertainty in future carbon balance (Kurz et al. 2008*b*). However, feedbacks also extend beyond atmospheric C. Changing fire regimes may alter evapotranspiration at regional scales (Bond-Lamberty et al. 2009), and burning of boreal wetlands is increasing atmospheric mercury emissions, which may exacerbate mercury toxicity in northern food chains (Turetsky et al. 2006). The feedback of black carbon to climate warming through forcing of sea ice and glacier albedo is also receiving increased attention; deposition of black carbon produced by boreal fires may enhance summer melting by reducing albedo (Kim et al. 2005, Randerson et al. 2006). The effects of extreme climatic events and other disturbances—including consequences of multiple events—were identified as key areas of uncertainty with respect to the effects of climate change on forest biogeochemistry (Campbell et al. 2009). Feedbacks of disturbance to climate warming are complex, in part because some changes are offsetting but also because the direction of change in disturbance regimes—and hence the potential for negative and positive feedbacks—will vary spatially across the globe (Goetz et al. 2007). Determining when and how disturbances feedback to other global drivers remains a key research need (Box 2).

CONCLUSION

Disturbance is an important ecological process, and studies of disturbance have made key contributions to the development of landscape and ecosystem ecology. Notions of "catastrophe" have been challenged, mechanisms of resilience have been identified, and the role of spatial heterogeneity in ecological processes has been elucidated. Natural disturbances may leave a very long-lasting footprint that shapes ecosystem structure and function long into the future. However, disturbance regimes are changing rapidly now, and the tempo of change is accelerating. Drivers of global change will produce new spatial patterns, altered disturbance regimes, novel trajectories of change, and surprises. Spatial and temporal variation in disturbance and successional processes must be incorporated more explicitly into studies of global change, augmenting ongoing work (e.g., Jentsch et al. 2007, Hopkinson et al. 2008). Policy must also incorporate an understanding of disturbance dynamics and a long-term commitment to managing risk (Tompkins et al. 2008) while considering a range of adaptive strategies (Millar et al. 2007, Chapin et al. 2008). Extreme events must be given special consideration because their potential impacts on ecosystems and people are substantial (Katz et al. 2005, Mitchell et al. 2006, Mills 2009).

We face an uncertain future in a changing world. Changing disturbance regimes will produce acute changes in ecosystems and ecosystem services over the short term (years to decades) and long term (centuries and beyond). It is imperative that we think boldly about how best to understand and adapt to these changes. Future trends in disturbance size, frequency, and severity are difficult to predict, and changes in disturbance will vary among regions (Hassim and Walsh 2008, Vecchi et al. 2008, Dankers and Feyen 2009, Flannigan et al. 2009). Nonetheless, amidst the many pressing challenges that command attention, ecologists must increase efforts to understand and anticipate the causes and consequences of changing disturbance regimes and engage in the policy process.

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