Disturbance Dynamics and Ecological Response: The Contribution of Long-Term Ecological Research

MONICA G. TURNER, SCOTT L. COLLINS, ARIEL E. LUGO, JOHN J. MAGNUSON, T. SCOTT RUPP, AND FREDERICK J. SWANSON

Long-term ecological research is particularly valuable for understanding disturbance dynamics over long time periods and placing those dynamics in a regional context. We highlighted three case studies from Long Term Ecological Research (LTER) Network sites that have contributed to understanding the causes and consequences of disturbance in ecological systems. The LTER Network significantly enhances the ability to study disturbance by (a) encompassing ecosystems subject to a wide range of disturbances, (b) providing a long-term baseline against which to detect change and measure ecosystem responses to disturbance, (c) permitting observation of slow or infrequent events, (d) facilitating the use of multiple research approaches, (e) providing a focus for modeling disturbance dynamics, and (f) contributing to land and resource management. Long-term research is crucial to understanding past, present, and future disturbance dynamics, and the LTER Network is poised to make continuing contributions to the understanding of disturbance.

Keywords: scale, heterogeneity, biotic, invasion, hurricane, fire

The important role of disturbances in shaping landscapes and influencing ecosystems is now well recognized in ecology. Fires, storms, floods, pest outbreaks, species invasions, and resource extraction, to name but a few types of disturbance, affect many ecosystems over a range of spatial and temporal scales. Disturbance is defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment" (White and Pickett 1985); it may be natural or anthropogenic in origin. This general but flexible definition requires that the spatial and temporal scales of the system and disturbance be specified. Disturbances span a broad range of sizes and frequencies and can be characterized by their extent, spatial distribution, frequency or return interval, predictability, and magnitude, including both intensity and severity (White and Pickett 1985).

Increased understanding of disturbance has contributed to several important conceptual developments in ecology. Acceptance of the nonequilibrial state of many ecosystems means recognizing that ecological systems are often in some state of recovery from prior disturbance (Wu and Loucks 1995). Spatial heterogeneity is recognized as a central structuring force in ecosystems; because disturbances both create and respond to spatial heterogeneity, much understanding of ecological mosaics has resulted from research in disturbance-prone ecosystems. Recognition of scale-dependent dynamics, and of the importance of understanding the regional context of disturbance regimes as they influence the structure and function of local ecosystems, has also been enhanced by our understanding of natural and human-induced disturbances. The importance of natural disturbance regimes in determining the historic range of variability in ecosystems (e.g., Landres et al. 1999) and making ecologically informed management decisions has been catalyzed by our improved understanding of disturbance. The influence of human sociopolitical structures on landscape structure has been elucidated in part by studies of disturbance dynamics on lands under different ownerships or management (e.g., Spies et al. 1994). Disturbance continues to have a central role in ecological studies.

Monica G. Turner (e-mail: mgt@mhub.zoology.wisc.edu) is a professor in the Department of Zoology, Birge Hall, University of Wisconsin, Madison, WI 53706. Scott L. Collins is an adjunct professor of biology at Kansas State University, Manhattan, KS 66506, and at the University of Maryland, College Park, MD 20742. Ariel L. Lugo is director of the International Institute of Tropical Forestry, USDA Forest Service, Rio Piedras, Puerto Rico 00928-5000. John J. Magnuson is professor emeritus at the Center for Limnology, University of Wisconsin, Madison, WI 53706. T. Scott Rupp is an assistant professor in the Forest Sciences Department at the University of Alaska, Fairbanks, AK 99775. Frederick J. Swanson is a research geologist at the USDA Forest Service, Pacific Northwest Research Stations, Forestry Sciences Lab, Corvallis, OR 97331.

Studying disturbance is challenging. Disturbances are unpredictable and usually unplanned; they vary across a wide range of spatial and temporal scales; they may leave persistent legacies; and there may be interactions between multiple disturbances. Ecosystem responses to disturbance are similarly complex. The Long Term Ecological Research (LTER) Network offers an excellent setting for studying such episodic events in ecosystems (Hobbie et al. 2003). The sustained, multidecade, multisite character of the LTER program permits gradual, thoughtful development of complementary lines of inquiry on the problem of understanding ecological consequences of disturbance processes. The duration and nature of this program increase the prospects for observing effects of a major, infrequent disturbance where predisturbance conditions are well known and the infrastructure to support postdisturbance measurements is largely in place.

Research at LTER sites has contributed substantively to our improved understanding of the causes and consequences of disturbance in ecological systems at a variety of spatial and temporal scales. In this article, we first highlight three case studies from LTER sites that have contributed to understanding disturbances and their ecological effects. These examples are not exhaustive, but rather illustrate a range of disturbance types and scales in an array of different ecosystems. We then discuss the unique ways in which the LTER Network contributes to studies of disturbance. Finally, we conclude by discussing the opportunities for future research within or in collaboration with the LTER Network on causes and consequences of disturbance.

LTER contributions to understanding disturbance

The LTER Network encompasses ecosystems that experience a wide array of disturbances across a range of spatial and temporal scales. Many studies of disturbance at LTER sites have taken advantage of natural events and studied them from an experimental perspective using varied methods. Understanding has often been enhanced by the existence of predisturbance data, and some events have been detected because of the regular long-term measurements made in the systems. White and Jentsch (2001) recently implored ecologists to seek generality in studies of disturbance. They emphasized the need for choosing a focus of interest and level of resolution for study; for establishing the spatial and temporal frame of reference; for documenting disturbance duration, intensity, and magnitude; and for determining patterns of disturbance regimes. The LTER program is uniquely positioned to address these needs and contribute to our general understanding of disturbance dynamics. Here we illustrate the contributions of long-term research to general understanding of disturbance by highlighting examples from three LTER sites: a temperate lake ecosystem that experienced invasion of exotic species, a tropical forest affected by a hurricane, and a temperate grassland influenced by fire.

Long-term research can detect, monitor, and understand unanticipated events. Long-term measurement of ecosystem and community structure makes possible the detection and analysis of infrequent events that produce long-term ecological changes. For example, the introduction of an exotic species or a new but systemic stressor like acid rain may lead to fundamental and persistent, rather than episodic, changes in system structure and function. The disturbance and its initial effects may be subtle, local, and difficult to detect, yet its long-term influence may be profound and extensive (Hrabik and Magnuson 1999, Lodge et al. 2000).

The LTER program provides a framework designed to detect, understand, and generalize from infrequent and unexpected events using site-based research. Long-term research at the North Temperate Lakes LTER site in northern Wisconsin detected the initial invasion of the exotic rainbow smelt *(Osmerus mordax)* in Crystal and Sparkling Lakes and the early colonization of the exotic rusty crayfish *(Orconectes rusticus)* in Trout Lake (figure 1). The LTER program allowed observation and analysis of the time course of changes in ecosystem structure and function following these two invasions. Embodied in these studies of changing biodiversity were fundamental ecological questions about disturbance; dispersal; ecosystem transformation, resistance, and resilience; and the restoration of ecosystem structure and function.

Smelt were not found in Crystal and Sparkling Lakes, and the rusty crayfish had just colonized the littoral zone of Trout Lake, when the North Temperate Lakes LTER site was established in 1981 (Hrabik et al. 1998, Lodge et al. 1986). Introducing species was not part of designed research; rather, research took advantage of the unanticipated arrival of new species in the LTER lakes. Research at the North Temperate Lakes LTER site documented the arrival, dispersal, and effects of the exotics; the mechanisms by which the biotic community was transformed; and the density thresholds for response.

The invasions profoundly altered the LTER lake ecosystems. After the rainbow smelt invaded Sparkling Lake in 1982, the previously abundant cisco *(Coregonus artedii)* no longer successfully reproduced (McLain 1991, Hrabik et al. 1998). Cisco continued to produce viable eggs, but virtually none of the young-of-year cisco survived their first summer of life. Only one large cisco was observed by 1998. In Crystal Lake, yellow perch *(Perca flavescens)* declined in abundance and body condition (an index of growth rate) following invasion of smelt in 1985 (Hrabik et al. 1998). The young-of-year perch grew more slowly, and decreasing numbers survived their first summer. No young of year have been caught in late summer during recent years, and the adult population numbers only a few. In Trout Lake, rusty crayfish were first observed in 1979 near a popular boat landing (Lodge et al. 1986). The crayfish dispersed slowly along the inshore waters of the lake, and 18 years later in 1997 occupied the littoral zone of the entire lake (Wilson 2001). As the crayfish dispersed, more than 80% of the aquatic macrophyte species disappeared at sample sites, two resident species of crayfish *(O. virilus* and *O. propinquus)* nearly disappeared, and some fishes and benthic invertebrate groups declined in abundance (Wilson 2001).

Figure 1. Studies of the invasion of rusty crayfish and rainbow smelt in the North Temperate Lakes LTER site documented profound changes in lake ecosystems. Photographs: John Magnuson.

Mechanisms of community change varied greatly among lakes, depending on differences in the initial biotic community and in the invading species. In Sparkling Lake, predation by smelt on young-of-year cisco was the mechanism of change (McLain 1991, Hrabik et al. 1998). Predation was so intense that survival of young cisco declined essentially to zero. In oligotrophic Crystal Lake, intense competition for food between smelt and perch was the agent of change. In Trout Lake, the dispersing rusty crayfish eliminated their preferred foods (macrophytes, fish eggs, and many benthic invertebrates) while maintaining high population densities by using alternate prey (Wilson 2001). Declines in the native crayfish species resulted from complex mechanisms including competition, predation, differences in abilities to evade predation, and reproductive interference or hybridization (Lodge et al. 2000).

These data have been used to enhance understanding of what may happen in other lakes of the region if they are colonized by these exotic species. A model of smelt dispersal among lakes in the Bear River Watershed near the Trout Lake Station (Hrabik and Magnuson 1999) suggested that suitable habitat for smelt is present only in some lakes, and only some of those lakes are connected by surface waters allowing smelt dispersal from adjacent lakes. Model simulations suggested that only 25% of the inhabitable lakes would be invaded by smelt, even after 1000 years, if invasion occurred only through connecting streams in this region with high proportions of landlocked lakes (figure 2). However, if the observed rate of invasion into isolated lakes via human transport, as people inadvertently move organisms around in their boats and bait buckets, was included in the model, then 50% of the lakes were projected to be invaded after only 200 years, 75% after 300 years, and almost all after 1000 years. This result has important implications for the long-term use of biological reserves and the significance of people in dispersal.

Invasions of island-like environments such as lakes are a unique type of disturbance. The dense populations of rainbow smelt and rusty crayfish originated from a small number of colonists, likely transported by well-intentioned or uninformed humans. After such an invasion, the resulting disturbance frequency becomes continuous or annual through reproduction of the invader, making it a continuous stress. In that sense, it is not like the more periodic disturbance of prairie fires or flood pulses of large river systems, where the disturbance is incorporated into system behavior. As a lake ecosystem loses species, return to an original state is impossible in a strict sense; the system has been transformed both structurally and functionally. For the foreseeable future, any resilience exhibited by a lake ecosystem would come from a complex process involving human management response as a part of the system behavior. Human reactions to undesirable invaders could include, and have included, the reduction or elimination of the invaders and reintroduction of some of the lost species. Such ideas are now being explored in Sparkling Lake, where experimental removal of both the rusty crayfish and the rainbow smelt will be conducted.

Long-term research has changed understanding of tropical forest dynamics. Paradigms for understanding the structure and function of tropical forests in the Luquillo LTER site, Puerto Rico, had evolved from a long tradition of research that spanned decades before the LTER program began. Hurricane Hugo, a category IV hurricane with sustained winds over 166 kilometers per hour, passed over the northeast corner of the island of Puerto Rico on 18 September 1989, one year after LTER funding began. Hurricanes are an important force influencing forest composition and structure on numerous islands and coastal regions; 15 hurricanes have passed over the island of Puerto Rico in the past 300 years (Scatena and Larsen 1991). LTER studies of the effects of Hurricane Hugo benefited tremendously from the extensive predisturbance data for the site and resulted in dramatic changes to our under-

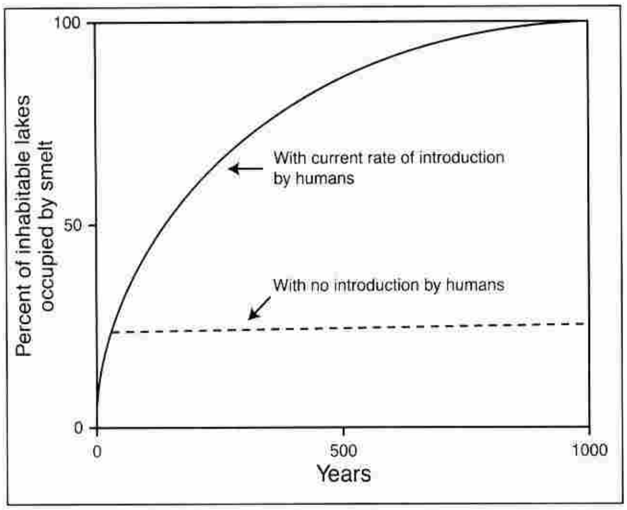

Figure 2. Simulated percentage of lakes invaded by rainbow smelt in the Bear River watershed in North Central Wisconsin under two conditions: (1) no further introduction by humans and (2) at the current rate of human introduction (modified from Hrabik and Magnuson 1999).

standing of the role of disturbance in the Luquillo Forest. For example:

- Ideas of fragility were replaced by ideas of resilience. Although Connell proposed in 1978 that rain forests were resilient, the prevailing view of these ecosystems remained one of fragility, as reflected in the book by Farnsworth and Golley (1974) entitled Fragile Ecosystems. The LTER study in Luquillo after Hurricane Hugo was the first to provide empirical evidence for tropical forest resilience (Walker et al. 1996).

- The rates of ecosystem processes were reassessed. Over a period of more than 20 years, rates of litterfall in the Luquillo Forest did not deviate significantly from about 5 megagrams per hectare per year ($Mg \bullet ha^{-1} \bullet yr^{-1}$), and aboveground biomass accumulation did not exceed 5 $Mg \bullet ha^{-1} \bullet yr^{-1}$. The estimated net aboveground primary production (NAPP) ranged from 10 to 12 $Mg \bullet ha^{-1} \bullet yr^{-1}$. These results suggested that rate processes were constant in these forests (Lugo and Scatena 1995). However, in the five years after Hurricane Hugo, Scatena and colleagues (1996) observed a wide fluctuation in these rates, and average rates of NPP that exceeded any measured before in mature natural forests (21.6 $Mg \bullet ha^{-1} \bullet yr^{-1}$).

- The characteristics of ecosystems that lead to resilience were identified, including rapid turnover rate of nutrients, mass, and populations; biotic control of fluxes; high species richness at ecosystem interfaces (redundancy); high nutrient and carbon storage in soils; negative feedback at all levels of biotic interaction; and high species turnover followed by self-organization of new communities (Lugo and Scatena 1995).

- Successional changes after natural and anthropogenic disturbances were documented and compared. These studies demonstrated that succession was slower after anthropogenic disturbances than after natural ones (Aide et al. 2000, Zimmerman et al. 1995).

- Differences between ecological and geographic space were identified. After the hurricane, a dramatic geographic restructuring of environmental gradients was observed, resulting from the opening of the forest canopy. Animal populations then shifted in space location in response to changes in environmental conditions (Waide 1991, Willig and Camilo 1991). Ecological gradients are not spatially fixed, and organisms move in response to the distribution of suitable conditions regardless of geographical space.

Four new ways of analyzing the forest at Luquillo emerged. First, the relationship between turnover of biotic compartments, including the length of succession and time required to restore biomass, and the recurrence interval of disturbances was recognized. For example, a tabonuco *(Dacryodes excelsa)* stand matures in 60 years, coinciding with the recurrence interval of category IV–V hurricanes in the region (Scatena 1995).

Second, researchers realized that Caribbean forests share a common cadre of physiognomic and functional characteristics that are hurricane-induced and occur regardless of location. That is, dry, moist, wet, or rain forests share similar characteristics that are traceable to hurricane responses. Examples of these are canopy structure, species dominance, size class dominance, forest height (absence of emergent trees), low biomass, and capacity to sprout. These characteristics are associated with resistance and resilience to hurricanes.

Third, the complexity of the effects of a large-scale disturbance such as a hurricane was recognized (Boose et al. 1994). Like other large, infrequent disturbances, hurricanes produce a spatial mosaic of varying disturbance severities across the landscape that affect different ecosystem components (Turner et al. 1997, Foster et al. 1998). For example, a hurricane has wind and rain components that change in magnitude as they pass over the landscape and produce substantial heterogeneity in effects. Moreover, each of these forces affects a different component of the forest. Wind interacts mostly with the canopy, whereas rain largely affects the soil and stream ecosystems. Ecosystem response depends on the type of disturbance force that prevailed at the time of hurricane passage. By isolating the disturbance force for the affected ecosystem component, feedbacks operating at a landscape scale can be observed.

Fourth, in spite of recurrent hurricanes, ecological legacies acquired through anthropogenic changes persisted. Forests recovering from prior land use usually developed a structure, physiognomy, and function similar to that of forests not influenced by human land use. However, species composition and dominance were different between sites that had or had not experienced land use. These differences, which change very slowly, persisted even when hurricanes occurred (Zimmerman et al. 1995, Willig et al. 1996).

Hurricanes produce sudden, striking changes in forest ecosystems, including massive tree mortality (Lugo and Scatena 1996) and transfer of materials from the canopy to the forest floor (Lodge et al. 1991). Hurricanes shape forest structure and function and initiate a slow but continuous trajectory of change in which return to any precise predisturbance state is unlikely. Only through long-term ecological research can such continuous but slow change in ecosystems be assessed.

Long-term research provides understanding of disturbance scale and heterogeneity. Disturbances occur at different spatial and temporal scales, and many ecosystems experience a variety of different disturbances. Consequently, analysis of a single type of disturbance may be misleading because different kinds of disturbance may interact in space and time. Rather than focusing on a single disturbance type or event, long-term research has the luxury of focusing on the disturbance regime, the sum of all disturbances affecting an ecosystem in space and time (White and Jentsch 2001). Grassland ecosystems, for example, are subject to fire, periodic drought, and intense periods of herbivory by ungulates, invertebrates, and numerous species of small mammals. Other common disturbances in grasslands include soil mounds, fecal deposition, animal burrows, and bison wallows. Together these disturbances create spatial and temporal heterogeneity in resource availability, community structure, and ecosystem processes.

Research at grassland LTER sites has provided insight into how different disturbances affect these ecosystems. At the Konza Prairie LTER site, a tallgrass prairie in northeastern Kansas, the interactive effects of fire and grazing have been investigated experimentally (Knapp et al. 1998, 1999). Replicate watersheds at Konza Prairie have been burned at 1-, 2-, 4-, and 20-yr frequencies since 1972, and a free-ranging herd of bison was reintroduced to a subset of the area in 1987. Unlike hurricanes or invasive species, fire and grazing create a disturbance regime in which large- and small-scale disturbances recur at intervals that are much shorter than the life span of the dominant native species. These species thus exhibit numerous adaptations that allow them to survive and thrive under an intensive disturbance regime.

Early studies at Konza Prairie focused primarily on fire frequency. Long-term research has shown that as fire frequency increases in tallgrass prairie, plant species diversity, community heterogeneity, and nitrogen (N) availability decline, while annual net primary production increases. Burning results in N losses to the atmosphere; thus, N availability declines as fire frequency increases. Nitrogen is a key limiting resource in tallgrass prairie, and the negative relationship between N availability and production is highly unusual (figure 3; Turner et al. 1997). At Konza Prairie, increases in production following fire result from the removal of the litter layer, which allows growth of the dominant C_4 grasses to begin earlier in the growing season compared with unburned sites (Knapp and Seastedt 1986). Work at the Cedar Creek LTER site has shown that the dominant C_4 grasses are powerful competitors under low-N conditions (Tilman and Wedin 1991). This increase in production by the perennial grasses results in development of a dense canopy and intense shading, leading to the competitive exclusion of many forbs and to a reduction in plant species diversity (Tilman 1984, Collins et al. 1995).

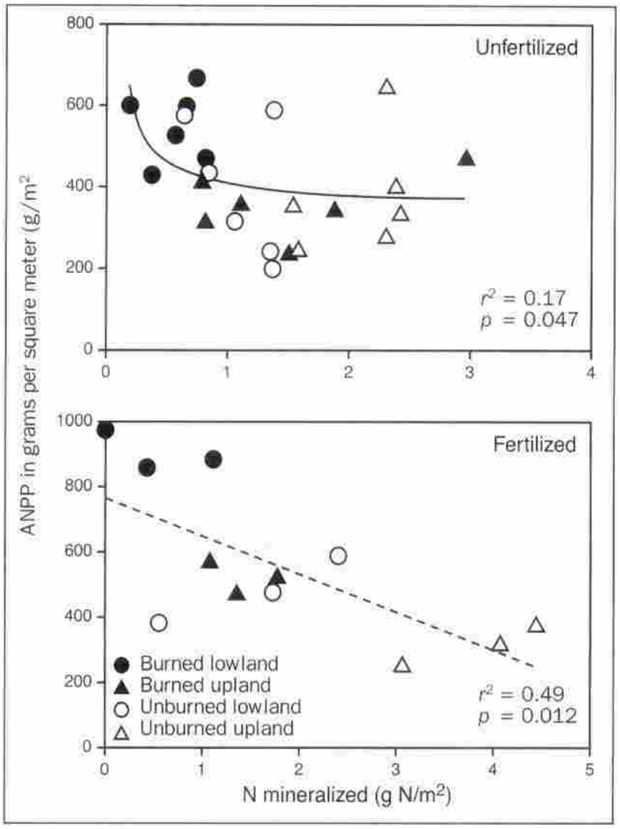

Figure 3. Annual aboveground net primary production (ANPP) as a function of cumulative nitrogen mineralized (N_{min}) in unfertilized and fertilized, burned and unburned tallgrass prairie, Konza Prairie LTER site. Unfertilized: ANPP = 354.2 + 54.9/(N_{min}), $r^2 = 0.17$, P = 0.047. Fertilized: ANPP = –116.2 (N_{min}) + 767, $r^2 = 0.49$, P = 0.012 (redrawn from Turner et al. 1997).

Although spring burning results in relatively clear responses at Konza Prairie, these responses do not reflect the full impact of the disturbance regime that now characterizes natural or managed tallgrass ecosystems. Further research at Konza Prairie and elsewhere has shown that light to moderate grazing by ungulates, either bison or domestic cattle, alters many of the patterns produced by burning (Knapp et al. 1999). Nitrogen availability increases in grazed areas because nutrient cycles are more rapid, and less aboveground production is lost during fire in grazed areas than in ungrazed areas. Grazing reduces the dominance and competitive ability of the C_4 grasses, which leads to higher plant species diversity and greater spatial heterogeneity (Collins et al. 1998). In addition, ungulates enhance spatial heterogeneity by wallowing and by creating grazing lawns within areas of ungrazed vegetation. These grazing lawns form around urine deposition sites, which are small patches of high productivity (Steinauer and Collins 1995, 2001). These small patches serve as focal sites for the formation of larger grazing lawns. Thus, small nutrient-rich patches create larger-scale heterogeneity in grazed landscapes.

The role of disturbances like fire and grazing varies regionally. Although burning is common in eastern tallgrass prairie, it is less common in western shortgrass steppe, where less aboveground production limits fuel loads that can sustain fire. Water constrains production in these systems more than N availability (Lauenroth 1979). Moreover, in shortgrass steppe, grazing seems to have little impact on ecosystem structure and function (Milchunas and Lauenroth 1993, Milchunas et al. 1998). Thus, shortgrass steppe is highly resistant to disturbance, whereas tallgrass prairie is less resistant but perhaps more resilient (i.e., better able to recover from a given disturbance) (Coffin et al. 1996, Baer et al. 2000).

Resilience has been well demonstrated in efforts to reestablish native vegetation through ecological restoration. The Curtis Prairie at the University of Wisconsin Arboretum serves as the prototype system for ecological restoration of grasslands (Jordan et al. 1987). Many grassland restorations have been conducted, but one difficulty has been the maintenance of native species diversity in restored prairie (Kindscher and Tieszen 1998). At Konza Prairie, an experiment was initiated to determine whether resource heterogeneity enhances species diversity during ecological restoration. Results thus far show that native species have been more abundant and diversity higher on restoration plots where N availability was reduced by carbon (C) amendments. Thus, long-term integrated research on grassland ecosystems has provided fundamental understanding needed for the restoration of biotic diversity as regional patterns of land use change from production agriculture to conservation.

The value of long-term research for understanding disturbance dynamics

The LTER Network enhances understanding of the importance and role of natural disturbances in ways that are qualitatively different from sites or programs that lack a long-term perspective and funding base. The preceding examples illustrated scientific contributions from site-based research to general understanding. Here we discuss several key ways in which the overall LTER program significantly enhances the ability to study disturbance.

The LTER Network encompasses ecosystems subject to a wide range of disturbances. Only a subset of sites is susceptible to any particular disturbance type, but collectively many important ecological disturbances occur across the network of sites (table 1). For example, Luquillo, Harvard Forest, and Coweeta are forested sites that have experienced hurricanes; Konza Prairie, Jornada, Sevilleta, and Shortgrass Steppe are all grazed by ungulates; Bonanza Creek experiences crown fires; and H. J. Andrews, Hubbard Brook, and Coweeta have all been subjected to forest harvest. Various sites experience floods in forested streams, many sites have exotic species present or likely to invade in the near future, and many bear the legacies of prior human land use. The LTER Network enhances opportunities for sampling major disturbances, and comparative studies across sites can sometimes even examine the same event in different ecosystems. For example, Hurricane Hugo affected Luquillo, Harvard Forest, and North Inlet (an estuarine site in South Carolina, formerly an LTER site); LTER scientists engaged in productive collaborative study of these disturbances (e.g., Boose et al. 1994).

Long-term data provide a valuable baseline against which to detect change and measure ecosystem responses to disturbance. Even dramatic ecological changes might go undetected without long-term studies. In many cases, extensive predisturbance data on ecosystem structure or function are lacking when a disturbance occurs (e.g., the 1988 Yellowstone fires, the Exxon Valdez oil spill). Long-term data have been crucial to understanding the response of tropical and temperate forests to hurricanes, floods, and droughts. Long-term observations at Bonanza Creek have identified the importance of annual sedimentation to floodplain successional dynamics (Van Cleve et al. 1991, 1996) and the importance of major flooding events (Yarie et al. 1998). Understanding of the effects of the 1996 flood at H. J. Andrews was enhanced by preflood data on channel geometry, riparian vegetation, and aquatic biota (Swanson et al. 1998). Detection and monitoring of the exotic species invading the North Temperate Lakes emerged directly from long-term observations. Long-term studies at the Shortgrass Steppe site documented plant community changes in response to changing climate (Alward et al. 1999). LTER data provide a rich resource for interpretation of system response following a disturbance.

Long-term research permits observation of slow or infrequent events that are only apparent over longer time scales. As the number of sites in the LTER Network has grown and the duration of study has lengthened, the opportunity for direct sampling of infrequent, major disturbance events has also increased. For example, hurricanes only rarely affect inland regions of the Appalachian Mountains. The center of Hurricane Opal passed over southeastern Tennessee on 5 October 1995, however, causing high winds and heavy rainfall in much of the southern Appalachians, including the Coweeta LTER basin. The unusual size and strength of Opal produced broad-scale tree damage to inland forests, followed by subsequent salvage logging. Although forest disturbance has been a main focus of research at Coweeta for decades, this was the first opportunity to study the effects of catastrophic wind damage on vegetation dynamics in the basin. The long-term

Table 1. Examples of disturbance processes that are represented within the Long Term Ecological Research (LTER) Network for selected ecosystem types.

Ecosystem type	LTER site	Fire	Flood or drought	Hurricane	Insect pests	Exotic species	Land use
Forest only	HRV			X	X	X	A, F
Forest and stream	AND, BNZ,	X	X				F, R
	CWT, HBR, LUQ		X	X	X	X	F, R
Forest and lake	NTL		X				F, R
Grassland, shrub, and tundra,	JRN		X				A, G
Grassland, shrub, tundra, and stream	KNZ	X	X				G
Grassland, shrub, tundra, and lake	ARC	?					
Lakes	NTL		X			X	

Notes: Site abbreviations are as follows: ARC, Arctic Tundra; AND, H. J. Andrews; BNZ, Bonanza Creek; CWT, Coweeta; HBR, Hubbard Brook; HRV, Harvard Forest; JRN, Jornada; KNX, Konza Prairie; NTL, North Temperate Lakes.

Abbreviations used for land use effects are A, agriculture; F, forestry; R, roads; G, grazing.

predisturbance data on forest structure and function at Coweeta provided a valuable baseline for tracking the response of the ecosystem to Hurrican Opal. Insights gained from the hurricane studies at Luquillo and Harvard Forest also informed hypothesis testing at Coweeta.

As the period of study continues to grow across the LTER Network, we can expect additional opportunities to detect and study infrequent events. For example, fire is the key disturbance that has shaped ecosystems of the Bonanza Creek LTER site in the boreal forests of Alaska. With an increasing duration of study, long-term ecological research will most likely provide the opportunity to observe and study an infrequent large crown fire in that system. Similarly, the introduction of invasive species is likely to be detected and studied at many LTER sites. The LTER Network provides a range of sites in different ecosystems that are likely to sample large and infrequent events.

The LTER structure facilitates the use of multiple research approaches. Disturbance research at LTER sites benefits from a wide variety of approaches, including field observations, manipulative experiments, historical reconstruction, modeling, and cross-site studies. This plurality of approaches is fostered by focusing the attention of many investigators with different perspectives on a given site, by creating long-term databases and making them available online, and by having a network of sites at which similar questions can be addressed.

The diversity of approaches is nicely illustrated by the hurricane research developed over more than a decade at the Harvard Forest LTER site in central Massachusetts. Harvard Forest researchers began with retrospective analysis of effects of the 1938 hurricane on forests of New England, compiling records from archival sources and analyzing those data geographically. Further study led to development of two alternative models: a meteorological model that reconstructed hurricane wind velocity and damage on a regional scale, and a topographic exposure model that assessed terrain effects at a landscape scale. The models were then tested against observed effects and combined with extensive historical records to reconstruct hurricane impacts in both New England and Puerto Rico since European settlement (Boose et al. 2001). In addition to observation and modeling studies, experiments were conducted to simulate hurricane damage by toppling trees with winches, and the ecological responses were carefully studied (Foster et al. 1997). The experimental hurricane revealed that only a fraction of toppled trees died immediately, and there was significant continuity of cover by live trees and shrubs through the postdisturbance period. Consequently, despite dramatic alteration of forest structure, there was little change of many ecosystem processes such as nitrogen cycling, nutrient availability, and soil respiration (Foster et al. 1997). Thus, understanding of the disturbance regime has been informed by observation, experiment, modeling, and historical analysis.

Among the many approaches used to study disturbance, the ability to conduct long-term landscape-scale experiments is a hallmark of research at LTER sites. Several of the forested LTER sites (e.g., Coweeta, Hubbard Brook, and H. J. Andrews) had a history of experimental manipulation (usually clearcutting) implemented by the US Forest Service before the LTER program began. Tremendous insights continue to be gained through the long-term monitoring of these experiments (e.g., Swank and Crossley 1988, Likens and Bormann 1995, Elliott et al. 1997). An understanding of the characteristics and dynamics of canopy gaps (small disturbances common in eastern deciduous forest) has emerged from experimental studies at Coweeta (e.g., Clinton and Boring 1993). Landscape experiments are also being conducted at Konza Prairie, where replicated sets of small watersheds have been burned in the spring at varying intervals since 1972 (Knapp et al. 1998). After 25 years, this burning regime has created a landscape of patches subjected to different frequencies of disturbance by fire. Understanding the response of tallgrass prairie communities to different burning frequencies and the mechanisms creating that response would not have been possible without the long-term experimental approach and the integrated research that is a general characteristic of the LTER program.

Long-term research provides a focus for modeling disturbance dynamics. Disturbance models have produced unique insights into ecosystem and landscape dynamics at LTER sites. For example, the hurricane exposure model developed for Harvard Forest and Luquillo underscored the importance of landscape position for predicting disturbance severity (Boose et al. 1994). Spatial modeling of forest cutting alternatives in the Cascades Mountains in Oregon identified significant time lags in the response of landscape pattern to changes in the disturbance regime (Wallin et al. 1994). Modeling of the causes, patterns, and effects of disturbance is facilitated within the LTER program because detailed long-term data sets exist for specific ecosystems and because a variety of investigators focus on the same site or group of sites. Research at the Bonanza Creek LTER site in the boreal forest of Alaska illustrates how important modeling contributions can be facilitated through long-term research.

Fire is the major disturbance factor in the boreal forest (Wright 1974, Payette 1992), and postfire succession dominates vegetation dynamics (Zackrisson 1977, Payette 1992). Succession varies widely across the region in response to stochastic variability in disturbance and species recruitment (Mann and Plug 1999). Research at the Bonanza Creek LTER site, begun in 1987, has produced valuable insights about disturbance and successional patterns and rates in the region. Current research addresses how changes in climate and disturbance regime might alter the function of the Alaskan boreal forest. For example, fire frequency influences patterns of energy partitioning (Chapin et al. 2000) and carbon dynamics (Kasischke et al. 1995).

The relatively simple disturbance regime and well-studied successional dynamics of the Alaskan boreal forest made it ideal for computer simulations of climate–vegetation–fire interactions at broad scales. A spatially explicit frame-based model (ALFRESCO) was developed to simulate the response of subarctic and boreal ecosystems to a changing climate and fire regime (Rupp et al. 2000a, 2000b). Model development was based on the knowledge of successional dynamics acquired and synthesized by a cadre of scientists studying the boreal forest over the past 20 to 30 years. LTER data sets served both to parameterize and to test ALFRESCO. Application of ALFRESCO to the forest–tundra ecotone suggested that long-term rates and patterns of vegetational change could be influenced by specific events leading to legacies that cannot be explained by current climate (Rupp et al. 2000b). Model simulations also suggested that a warming climate in Alaska would cause a steady increase in the proportion of early successional deciduous forest across the landscape. In turn, this increase might reduce the predicted decline in regional albedo and thus moderate the positive feedback to climate warming (Rupp et al. 2000b, 2001).

The Bonanza Creek modeling studies have generated some surprising results regarding the response of terrestrial ecosystems to predicted future climate. ALFRESCO was used to simulate an instantaneous 2-degree Celsius increase in growing-season temperature from currently observed climate with two different precipitation regimes (a 20% increase and 20% decrease from current precipitation) to explore the influence of climate change on long-term boreal ecosystem dynamics. Both warming scenarios predicted an increase in the total number of fires compared to current climate. However, the distribution of fire sizes was surprising (figure 4). As expected, the warmer and drier scenario resulted in fewer small fires (burning 0%–5% of total area) and an associated shift towards larger fires (burning > 5% of total area). Also as expected, the warmer and wetter scenario resulted in fewer large fires and an associated shift towards smaller fires. However, the distribution of very large fires (burning > 25% of total area) was unexpected (figure 4). The warmer and wetter climate scenario produced more very large fires compared to the warmer and dryer scenario. The warmer and dryer scenario produced frequent medium-sized fires, which prevented fuels from building up across the landscape and limited the number of large fires. In contrast, the warmer and wetter climate scenario led to frequent small fires, which allowed the development of well-connected, highly flammable late-successional stands across the landscape. Interestingly, similar results were obtained with a very different model for the landscape of Yellowstone National Park, Wyoming (Gardner et al. 1996). The regional implications of alternative climate warming scenarios for landscape structure and function are significant.

With long-term research, the interplay between models and data can be substantially enhanced. Model predictions can be tested against observations of the system over an extended time period. Models also serve as a research tool for scientists, allowing for the generation and testing of alternative hypotheses. In addition, model parameterization and calibration are much more feasible when extensive data are available and when there is a critical mass of investigators and collective knowledge available for the system.

Disturbance-related LTER studies contribute to land and resource management. Long-term disturbance research is making significant contributions to important issues in land and resource management. There is substantial interest among land managers in using natural disturbance regimes to guide future management plans, with the implicit assumption that maintenance of ecological processes will be more likely under these regimes. For example, considerable discussion has addressed whether the spatial patterns produced by natural disturbances can serve as a model for the pattern and timing of human disturbances such as forest harvest (Hunter 1993, Attiwill 1994, Holling and Meffe 1996). Clearly, this requires understanding historical disturbance patterns and processes. The concepts considered under the rubric of "range of natural variation" are especially important in land management. Two of these concepts are (1) that disturbance-driven spatial and temporal variability is a vital attribute of nearly all ecological systems, and (2) that past conditions and processes provide context and guidance for managing ecological systems today (Landres et al.

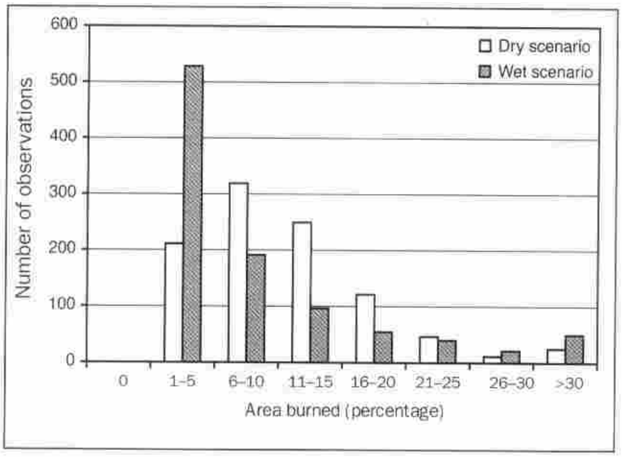

Figure 4. Histogram showing the size distribution of fires under two different climate warming scenarios using a simulation model developed for the Bonanza Creek LTER site. Growing-season temperature was instantaneously increased by 2 degrees Celsius in both scenarios. The dry scenario (white bars) represents a precipitation regime 20% less than currently observed. The wet scenario (gray bars) represents a precipitation regime 20% more than currently observed. Results are for a 1000-year simulation period, replicated 100 times.

1999). Natural variability is defined as spatial and temporal variation in the ecological conditions that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal (Landres et al. 1999). Improved understanding is needed of how natural disturbance-generated landscape mosaics differ from human-generated mosaics. The LTER program can contribute valuable insights to this discussion, as illustrated by contributions from the H. J. Andrews LTER site in Oregon.

At the Andrews LTER site, wildfires during the period AD 1500–1900 strongly shaped the current landscape distribution of forest age classes. Regional synthesis of fire history studies in forest types characteristic of the Andrews Forest indicates periods of high and low forest fire extent reflecting century-scale climate variability and human influences. There has been no stationary reference period against which to index future forest conditions, but land managers can still incorporate what is known about past disturbances into their planning. For example, information on historic frequency, severity, and spatial pattern of wildfire disturbance was incorporated into a new management plan for a 23,900 ha area of the Willamette National Forest formally designated for innovative adaptive management (Cissel et al. 1999). This disturbance-based management plan was compared with a plan that employed dispersed-patch clearcutting and a plan that emphasized reserves and matrix prescriptions for multiple species. The disturbance-based plan produced more old-growth habitat and more natural diversity of structure and composition at stand and landscape scales, and appeared to be superior for sustaining native species and processes. The data from LTER sites can be a valuable resource for managers of sites within the same region.

Challenges and future directions

The LTER approach is particularly valuable for understanding disturbance dynamics over long time periods and placing those dynamics in a regional context. The LTER Network offers unique opportunities for time series observations on a wide array of disturbances and ecosystems. What promising new research directions should be pursued? Opportunities abound within the LTER program for synthetic analyses that compare disturbances and ecological responses at different sites and across spatial and temporal scales. Because sites differ so widely in the types of organisms present and the frequency of disturbance, scaling by organism life histories (e.g., Addicott et al. 1989) and spatial and temporal attributes of disturbance and succession (e.g., Turner et al. 1993) might be especially useful for synthesis and integration. Many of the large-scale, long-term experiments at LTER sites provide an excellent context for understanding evolutionary processes in response to disturbance frequency and intensity. In addition, comparisons could be expanded to non-LTER sites characterized by a rich history of disturbance-related studies. For example, LTER sites have made important contributions to a synthetic treatment of large, infrequent disturbances (Foster et al. 1998, Turner et al. 1998), and further collaborations and comparisons among sites should be strongly encouraged. Non-LTER sites may also serve as valuable locations for independently testing hypotheses generated by LTER.

Disturbance-related LTER studies should capitalize on the diversity of ecosystems represented in the network (table 1) to further understanding of the mechanisms and implications of changes in natural and anthropogenic disturbances. Biotic mixing has been identified as a major challenge in global ecosystems research, and the LTER program should provide valuable documentation of species invasions and effects by asking questions such as: Do aquatic and terrestrial systems respond similarly to invasions by exotic species? Are invasions by animal species similar or different to invasions by plants? Enormous changes in species composition will continue in the future in response to increasing human effects on the planet. In addition, climate-induced changes in disturbance regimes may profoundly affect ecosystem structure and function. Ecologists have a responsibility to anticipate the consequences of these changes, and LTER sites are in a unique position to study these events effectively.

Disturbance regimes encompass an extremely wide range of temporal and spatial scales. Understanding the spatial heterogeneity in disturbances, and how this is manifest at different scales, is also a fruitful direction for continued work across the LTER Network. Spatial variation in disturbance effects may lead to important functional patterns across ecosystems, and understanding such variation may be important to drive complex system models. The ecosystem response to disturbance may influence future disturbance patterns and dynamics, and long-term studies could elucidate such feedbacks. The LTER program's traditional emphasis on understanding temporal variation can be augmented by an increasing integration of spatial and temporal variation. Additional cross-site studies are likely to yield important new insights and should receive high priority. Long-term research is crucial to gaining understanding of past, present, and future disturbance dynamics and ecological responses, and the LTER Network is poised to make continuing contributions to this goal.

Acknowledgments

Funding for this research has been provided by the Long Term Ecological Research Program of the National Science Foundation. We thank James R. Miller, Tania L. Schoennagel, John Hobbie, members of the LTER Coordinating Committee, and two anonymous reviewers for constructive comments on this manuscript.

References cited

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA. 1987. Ecological neighborhoods: Scaling environmental patterns. Oikos 49: 340–346.

Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano Vega H. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration. Restoration Ecology 8: 328–338.

Alward RD, Detling JK, Milchunas DG. 1999. Grassland vegetation changes and nocturnal global warming. Science 283: 229–231.

Attiwill PM. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. Forest Ecology and Management 63: 247–300.

Baer SG, Rice CW, Blair JM. 2000. Assessment of soil quality in fields with short and long term enrollment in the CRP. Journal of Soil and Water Conservation 55: 142–146.

Boose ER, Foster DR, Fluet M. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs 64: 369–400.

Boose ER, Chamberlin KE, Foster DR. 2001. Landscape and regional impacts of hurricanes in New England. Ecological Monographs 71: 27–48.

Chapin FS III, McGuire AD, Randerson J, Pielke R Sr, Baldocchi D, Hobbie SE, Roulet N, Eugster W, Kasischke E, Rastetter EB, Zimov SA, Running SW. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biology 6 (suppl. 1): 211–223.

Cissel JH, Swanson FJ, Weisberg PJ. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9: 1217–1231.

Clinton B, Boring LR. 1993. Characteristics of canopy gaps and drought influences in oak forests of the Coweeta Basin. Ecology 74: 1551–1558.

Coffin DP, Lauenroth WK, Burke IC. 1996. Recovery of vegetation in semiarid grassland 53 years after disturbance. Ecological Applications 6: 538–555.

Collins SL, Glenn SM, Gibson DJ. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: Decoupling cause and effect. Ecology 76: 486–492.

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280: 745–747.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1309.

Elliott KJ, Boring LR, Swank WT, Haines BR. 1997. Successional changes in plant species diversity and composition after clearcutting a southern Appalachian watershed. Forest Ecology and Management 92: 67–85.

Farnsworth EG, Golley FB, eds. 1974. Fragile Ecosystems: Evaluation of Research and Applications in the Neotropics. New York: Springer-Verlag.

Foster DR, Aber JD, Melillo JM, Bowden RD, Bazzaz FA. 1997. Forest response to disturbance and anthropogenic stress. BioScience 47: 437–445.

Foster, DR., Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large infrequent forest disturbances. Ecosystems 1: 497–510.

Gardner RH, Hargrove WW, Turner MG, Romme WH. 1996. Climate change, disturbances and landscape dynamics. Pages 149–172 in Walker B, Steffen W, eds. Global Change and Terrestrial Ecosystems. Cambridge (United Kingdom): Cambridge University Press.

Hobbie J, Carpenter S, Grimm N, Gosz J, Seastedt T. 2003. The US Long Term Ecological Research program. BioScience 53: 21–32.

Holling CS, Meffe GK. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10: 328–337.

Hrabik TR, Magnuson JJ. 1999. Simulated dispersal of exotic rainbow smelt *(Osmerus mordax)* in a northern Wisconsin lake district and implications for management. Canadian Journal of Fisheries and Aquatic Sciences 56 (suppl. 1): 35–42.

Hrabik TR, Magnuson JJ, McLain AS. 1998. Predicting the effects of rainbow smelt on native fishes in small lakes: Evidence from long-term research on two lakes. Canadian Journal of Fisheries and Aquatic Sciences 55: 1364–1371.

Hunter ML Jr. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65: 115–120.

Jordan WR, Gilpin ME, Aber JD, eds. 1987. Restoration Ecology. Cambridge (United Kingdom): Cambridge University Press.

Kasischke ES, French NF, Bourgeau-Chavez LL, Christensen NJ. 1995. Estimating release of carbon from 1990 and 1991 forest fires in Alaska. Journal of Geophysical Research 100: 2941–2951.

Kindscher K, Tieszen LL. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. Restoration Ecology 6: 181–196.

Knapp AK, Seastedt TR. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36: 662–669.

Knapp AK, Briggs JM, Hartnett DC, Collins SL, eds. 1998. Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie. Oxford (United Kingdom): Oxford University Press.

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49: 39–50.

Landres PB, Morgan P, Swanson FJ. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179–1188.

Lauenroth WK. 1979. Grassland primary production: North American grasslands in perspective. Pages 3–24 in French NR, ed. Perspectives in Grassland Ecology. New York: Springer-Verlag.

Likens GE, Bormann FH. 1995. Biogeochemistry of a Forested Ecosystem. New York: Springer-Verlag.

Lodge DJ, Scatena FN, Asbury CE, Sánchez MJ. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. Biotropica 23: 336–342.

Lodge DM, Kratz TK, Capelli GM. 1986. Long-term dynamics of three crayfish species in Trout Lake, Wisconsin. Canadian Journal of Fisheries and Aquatic Sciences 43: 993–998.

Lodge DM, Taylor CA, Holdich DM, Skurdal J. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: Lessons from Europe. Fisheries 25 (8): 7–20.

Lugo AE, Scatena FN. 1995. Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the tabonuco forest. Pages 59–108 in Lugo AE, Lowe C, eds. Tropical Forests: Management and Ecology. New York: Springer-Verlag.

Lugo AE, Scatena FN. 1996. Background and catastrophic tree mortality in tropical moist, wet, and rain forests. Biotropica 28 (4a): 585–599.

Mann DH, Plug LJ. 1999. Vegetation and soil development at an upland taiga site, Alaska. Ecoscience 6: 272–285.

McLain AS. 1991. Conceptual and empirical analyses of biological invasion: Non-native fish invasion into north-temperate lakes. PhD dissertation, University of Wisconsin, Madison.

Milchunas DG, Lauenroth WK. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63: 327–366.

Milchunas DG, Lauenroth WK, Burke IC. 1998. Livestock grazing: Animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. Oikos 83: 65–74.

Payette S. 1992. Fire as a controlling process in the North American boreal forest. Pages 145–169 in Shugart HH, Leemans R, Bonan GB, eds. A Systems Analysis of the Global Boreal Forest. Cambridge (United Kingdon): Cambridge University Press.

Rupp TS, Starfield AM, Chapin FS III. 2000a. A frame-based spatially explicit model of subarctic vegetation response to climatic change: Comparison with a point model. Landscape Ecology 15: 383–400.

Rupp TS, Chapin FS III, Starfield AM. 2000b. Response of subarctic vegetation to transient climatic change on the Seward Peninsula in northwest Alaska. Global Change Biology 6: 541–555.

———. 2001. Modeling the influence of topographic barriers on treeline advance at the forest-tundra ecotone in northwestern Alaska. Climatic Change 48: 399–416.

Scatena FN. 1995. Relative scales of time and effectiveness of watershed processes in a tropical montane rain forest of Puerto Rico. Pages 103–111 in Costa JE, Miller AJ, Potter KW, Wilcock PR, eds. Natural and Anthropogenic Influences in Fluvial Geomorphology. Washington (DC): American Geophysical Union. Geophysical Monograph 89.

Scatena FN, Larsen MC. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 317–323.

Scatena FN, Moya S, Estrada C, Chinea JD. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28: 424–440.

Spies TA, Ripple WJ, Bradshaw GA. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4: 555–568.

Steinauer EM, Collins SL. 1995. Effects of urine deposition on small-scale patch structure in prairie vegetation. Ecology 76: 1195–1205.

———. 2001. Feedback loops in ecological hierarchies following urine deposition in tallgrass prairie. Ecology 82: 1319–1329.

Swank WT, Crossley DA Jr, eds. 1988. Forest hydrology and ecology at Coweeta. New York: Springer-Verlag.

Swanson FJ, Johnson SL, Gregory SV, Acker SA. 1998. Flood disturbance in a forested mountain landscape. BioScience 48: 681–689.

Tilman D. 1984. Plant dominance along an experimental nutrient gradient. Ecology 65: 1445–1453.

Tilman D, Wedin D. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72: 1038–1049.

Turner CL, Blair JM, Schartz RJ, Neel, JC. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology 78: 1832–1843.

Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. Landscape Ecology 8: 213–227.

Turner MG, Dale VH, Everham EE III. 1997. Fires, hurricanes, and volcanoes: Comparing large-scale disturbances. BioScience 47: 758–768.

Turner MG, Baker WL, Peterson C, Peet RK. 1998. Factors influencing succession: Lessons from large, infrequent natural disturbances. Ecosystems 1: 511–523.

Van Cleve K, Chapin FS III, Dyrness CT, Viereck LA. 1991. State factor control of element cycling in taiga forests. Bioscience 41: 1–10.

Van Cleve K, Viereck LA, Dyrness CT. 1996. State factor control of soils and forest succession along the Tanana River in interior Alaska, USA. Arctic and Alpine Research 28: 388–400.

Waide RB. 1991. Summary of the response of animal populations to hurricanes in the Caribbean. Biotropica 23: 475–480.

Walker LR, Silver WL, Willig MR, Zimmerman JK, eds. 1996. Special issue: Long-term responses of Caribbean ecosystems to disturbance. Biotropica 28 (4a): 414–613.

Wallin DO, Swanson FJ, Marks B. 1994. Landscape pattern response to changes in pattern generation rules: Land-use legacies in forestry. Ecological Applications 4: 569–580.

White PS, Jentsch A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62: 399–499.

White PS, Pickett STA. 1985. Natural disturbance and patch dynamics: An introduction. Pages 3–13 in Pickett STA, White PS, eds. The Ecology of Natural Disturbance and Patch Dynamics. New York: Academic Press.

Willig MR, Camilo GR. 1991. The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest of Puerto Rico. Biotropica 23: 455–461.

Willig MR, Moorhead DL, Cox SB, Zak JC. 1996. Functional diversity of soil bacterial communities in the tabonuco forest: Interaction of anthropogenic and natural disturbance. Biotropica 28: 471–483.

Wilson KA. 2001. Impacts of the invasive rusty crayfish *(Orconectes rusticus)* in northern Wisconsin lakes. PhD dissertation. University of Wisconsin, Madison.

Wright HE. 1974. Landscape development, forest fires, and wilderness management. Science 186: 487–495.

Wu J, Loucks OL. 1995. From balance of nature to hierarchical patch dynamics: A paradigm shift in ecology. Quarterly Review of Biology 70: 439–466.

Yarie JL, Viereck A, Van Cleve K, Adams P. 1998. Flooding and ecosystem dynamics along the Tanana River. BioScience 48: 690–695.

Zackrisson O. 1977. Influence of forest fires on the North Swedish boreal forest. Oikos 29: 22–32.

Zimmerman JK, Aide TM, Rosario M, Serrano M, Herrera L. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. Forest Ecology and Management 77: 65–76.