UNPACKING COMPLEXITIES OF DISTURBANCE: INSIGHTS FROM CROSS-SYSTEM COMPARISONS

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Abstract

Current use of definitions of disturbance limit quantitative comparisons of the effects of disturbance across different ecosystem types. These frameworks focus on comparing disturbance types (e.g., fire, hurricanes) that are difficult to characterize with ecologically relevant measures. We expand on current frameworks by defining a disturbance event based on quantifiable characteristics of environmental drivers, physical and biological mechanisms of impact, and initial system properties. A disturbance event results in short-term consequences that include legacies of the previous ecosystem state and long-term outcomes of ecosystem development that lead to future states. We use long-term data from the U.S. Long-Term Ecological Research Network as part of the EcoTrends project (http://www.ecotrends.info) to illustrate how this new approach can facilitate cross-ecosystem comparisons and provide new insights to ecosystem dynamics. We discuss the implications of this framework for future research, including issues in global change science, applications to management, and development of new cross-ecosystem experiments.

Keywords: disturbance, drought, ecological theory, global change, hurricane, overgrazing, thresholds, wildfire
Disturbances are ubiquitous in ecological systems and are major forces shaping patterns and dynamics (White and Pickett 1985). Disturbances are expected to play an increasingly important role in future ecosystem dynamics as global changes in drivers, such as precipitation and temperature, continue to alter disturbance regimes. Rising concentrations of greenhouse gases, such as carbon dioxide, in the atmosphere and oceans are projected to result in more extreme climatic disturbance events, including more frequent summer drought, more intense hurricanes and tropical cyclones, and an increase in flooding events (IPCC 2007). These climatic disturbance events interact with ecosystem properties to generate additional disturbance, such as the spread of wildfire, pests, invasive species, and pathogens (Pickett et al. 1999, Dale et al. 2001, Crowl et al. 2008). Because disturbance affects all ecosystems, generalizations about the role of disturbance based on comparisons across different ecosystem types are expected to be critical in projecting future ecological changes (White and Jentsch 2001). However, the lack of rigor in the use of the concept of disturbance thwarts quantitative comparisons across ecological systems (Pickett et al. 1989, Johnson and Miyanishi 2007).

Disturbance studies often compare different disturbance types, such as fire, hurricanes, or drought (Pickett and White 1985). But, a disturbance type is a way of classifying events consisting of more than one driver, each of which may have different effects on an ecosystem. Individual disturbance events have an onset, duration, and release that are related to the specific characteristics of its drivers (Pickett and Cadenasso 2009). For example, a drought refers to a period of abnormally dry weather (Wilhite and Glantz 1985). Meteorological indices, such as the Palmer Drought Severity Index (PDSI), are often used to characterize a drought, but droughts with the same PDSI can have very different weather patterns (Palmer 1965); thus comparing drought per se across ecosystems is difficult. However, unpacking a drought event into its
constituent climatic drivers of precipitation, temperature, and wind is a first step to comparing different drought events. Once the drivers are identified, then the processes by which those drivers operate, such as amount and timing, direction, intensity, and duration, can be assessed. Ultimately, the specific mechanisms of action of drought in an ecosystem, such as plant stress, provide measurable variables that can be compared across systems (Fig. 1a). Thus, disaggregating a disturbance event, as suggested by Bart and Hartman (2000) for anthropogenic activities, provides a more rigorous use of the term disturbance that can reduce uncertainties and improve predictions as the global environment continues to change.

A number of definitions, conceptual frameworks, and theoretical developments have been used to generalize disturbance effects and ecological responses (e.g., Clements 1916, Grime 1977, Sousa 1984, White and Pickett 1985). A definition of disturbance commonly used by ecologists is: “any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resource, substrate availability, or the physical environment” (p 7, White and Pickett 1985). This definition is sufficiently general and flexible to account for different types of disturbances within an ecosystem type: however, it also points to the need to account for the complexity of dynamics invoked by disturbances impacting different types of ecosystems operating under different drivers and time scales. Different disturbance types, such as windstorms and flooding, can generate similar mechanisms (e.g., sediment deposition), and thus have similar effects in different ecosystems (Turner et al. 1987). A given disturbance type, such as wildfire, can have very different effects across different wildfire events because of variation in climatic conditions which affect the processes of disturbance and interact with the system properties (Turner et al. 2003b) to determine the ability of mechanisms to alter a specific system (Fig. 1a). Because specific disturbances are often unanticipated events with serious consequences
for ecosystem properties and services (Peters et al. 2004, MEA 2005, Chapin et al. 2008), there is a critical need to refine existing conceptual frameworks to account for spatial and temporal variability in disturbance drivers, impacts, and system responses.

Here we build on existing frameworks and integrate a large body of knowledge in order to improve understanding and prediction about the role of disturbance in structuring ecosystem dynamics in the face of global change. Our goals are to: (1) expose the limitations and assumptions associated with common usage of the term disturbance, (2) develop and support a revised conceptualization of disturbance that is general, robust, and flexible, yet is sufficiently rigorous to apply to multiple disturbances operating across a wide range of ecological systems. To do this, we disaggregate disturbance into its component features of a disturbance event that includes a suite of environmental drivers and mechanisms (Bart and Hartman 2000) that interact with system properties to result in short-term consequences and long-term states (Fig. 1a). We then (3) use this framework to provide new insights about spatial and temporal variability in disturbance across ecosystem types, and (4) illustrate how this framework can be used to design new cross-ecosystem experiments and comparative observational studies, and to develop strategies for management in a world where both the drivers of disturbance and system properties are changing.

We focus on data collected by the U.S. Long-Term Ecological Research (LTER) Network. Sites in the LTER Network include terrestrial, aquatic, marine, urban, and polar ecosystems (http://www.lternet.edu) (Appendix I). Because this network was developed in the early 1980s and many sites access retrospective data spanning centuries, long records of disturbance drivers and ecological responses are available for cross-system comparisons (Turner et al. 2003a). However, the EcoTrends Project, a recent attempt to quantitatively compare LTER
disturbance datasets (http://www.ecotrends.info), demonstrated ambiguity in the ways that disturbances were conceptualized and studied such that quantitative comparisons and generalizations across ecosystems are difficult (Box 1). Thus, the EcoTrends project revealed the need for a new way of looking at disturbance within the context of disturbance events, outcomes, and consequences as part of an expanded conceptual framework.

**Limitations and assumptions of existing frameworks**

Three main short-comings of current use of the disturbance concept limit cross-ecosystem comparisons and generalizations. *First*, disturbances are often defined by their type, such as hurricane or wildfire, which does not provide information on measurable characteristics that can be compared across ecosystems (Fig. 1b). Most disturbance studies across ecosystems have compared responses to the size, frequency of occurrence, and/or intensity of effects created by similar or different disturbance types (Pickett and White 1985). However, these comparisons have limited usefulness because of high variability in responses that can not be attributed to differences among disturbance types. Furthermore, disturbance types differ in their temporal and spatial scales, and interactions among disturbance types operating at different scales can generate complex system dynamics (Peters et al. 2004). Climatic drivers, such as precipitation, temperature, and wind speed, are common features of disturbance types that can be measured and compared. The specific features of the drivers are the processes by which disturbance occurs. Biotic disturbances, such as invasive species and insect outbreaks, operate through climatic drivers interacting with properties of the biota, such as insect population size and species identity. Because drivers are common across multiple disturbances and ecosystem types, an approach that focuses on drivers, and the processes that are associated with them, has large
potential to allow comparisons over ecosystem types and provides a direct link to studies of global changes in drivers (IPCC 2007).

Second, comparisons of the consequences of a disturbance are limited because they often use characteristics of the disturbance type with less attention devoted to the role of initial conditions associated with ecosystem properties (Johnson and Miyanishi 2007). Ecophysiologica|status of plants, species abundance, composition and structure of patches, and the spatial distribution of patch types are examples of system properties that can influence the resistance of an ecosystem to disturbance and its resilience or ability to sustain its properties following a disturbance. In some cases, previous disturbance can determine the response of a system to another disturbance. For example, high-intensity grazing by domestic livestock from ca. 1880 to 1935 disrupted the spatial continuity of herbaceous vegetation and altered the spread of wildfires in the southwestern U.S. (Allen 2007). These fire effects provided a feedback to influence future fire and grazing events, similar to vegetation-disturbance feedbacks in other systems (Chapin et al. 2008). Thus, comparisons of the effects of multiple, interacting disturbances are particularly challenging under current frameworks.

Third, a disturbance regime consists of individual or multiple disturbance types, each with its own set of characteristics. Comparison of disturbance regimes among ecosystems is hindered by the great diversity of characteristics of disturbance effects, even in the case of a single type of disturbance. Comparative analysis of disturbance effects would be facilitated by considering the specific mechanisms experienced by organisms, regardless of the drivers. For example, when organisms are buried by deposition of inorganic material by volcanic ashfall, river deposition on floodplains, and landslides, the mechanism of disturbance (burial) is common in all cases, though the processes differ by driver. Therefore, studies that explicitly examine
commonalities or differences in biotic response to similar mechanisms are a more useful basis for comparison rather than comparing disturbance types per se.

**Putting Disturbance to Work: An Expanded Conceptual Framework**

The conventional study of disturbance emphasizes the type of disturbance as a controlling feature (Fig. 1b), but it does not explicitly consider the drivers of a disturbance, the mechanisms by which disturbance alters the ecological system, and interactions among disturbance characteristics with ecosystem properties. To support comparisons across systems, the complexities of a disturbance must be “unpacked” or disaggregated into its five components (Figs. 1a, 2): a disturbance event that consists of (1) environmental drivers and their associated processes, (2) a set of mechanisms that influence the target system, and interact with the (3) characteristics and spatial structure of a given ecological system. These interactions result in (4) consequences that include legacies and colonizers that shape the (5) future states of the system.

Disturbance type consists of drivers and mechanisms.

**1. Drivers**

A disturbance event, such as a particular fire or hurricane, consists of a suite of drivers that influence ecological systems and, through feedbacks, can be affected by these systems in the future. There are five main classes of drivers: (1) climatic drivers such as wind, temperature, and precipitation, (2) atmospheric chemistry drivers such as ozone and atmospheric deposition, (3) physical drivers such as soil and nutrient additions and losses, (3) biotic drivers such as invasive species, pests, and pathogens, and (4) anthropogenic drivers such as land use that are ultimately controlled by human actions (Fig. 2). Each driver has a set of characteristics, such as amount,
duration, and timing, which can be measured and compared across ecosystems and events. The processes of disturbance are the features of drivers that can vary from place to place and from time to time. Climatic drivers, for instance, are modified in intensity and duration by such processes as global and regional cycles, or shifts in storm tracks. Likewise, biotic drivers can be altered by species migrations and population cycles, for example.

, and a suite of processes, such as erosion and deposition, that can be measured and compared across ecosystems and events.

2. Mechanisms
Organisms respond to disturbance mechanisms, which may be physical, such as thermal stress, erosion-deposition, and abrasion, or biological, such as foliage removal by consumer organisms (Fig. 2) (Swanson and Major 2005). Mechanisms of disturbance often have a gradient of intensities – for example, different depths of burial or degrees of heating or cooling that are affected by system properties. A single disturbance type can involve one or more mechanisms, one of which may be most limiting to the biotic response. In addition, the same mechanism of disturbance can be associated with a wide range of disturbance types. Defoliation, for example, is a disturbance mechanism that can result from windstorms, wildfire, outbreaks of insects, or drought. Thus, unpacking a disturbance into its mechanisms facilitates comparative analysis across different ecosystems, enhances predictive power, and opens the opportunity for experimentation, such as testing species response to gradients of disturbance intensity for different mechanisms.

3. System properties
Key system properties cause the effects of various disturbance events to differ. System properties can be defined at the scale of individuals that differ in properties such as height, and at the scale
of populations that differ in drought or stress tolerance (Fig. 2). At broader scales, properties include species abundance and composition and the spatial arrangement of patches of variable composition, size, shape, and connectedness with other patches.

The importance of system properties can change as a disturbance spreads through time and space (Peters et al. 2004). For example, fire that begins at an individual tree can either ignite that tree, or the fire can go out depending on the flammability properties of the tree. If the tree burns, fire can spread to other trees through flammable herbaceous vegetation at the tree base or by inter-canopy properties that connect adjacent trees. Spread of fire among patches of vegetation is affected by the continuity in fuel load determined by patch type, density, and spatial arrangement, and topographic position relative to wind speed and direction. Contiguous, high-fuel-load patches can spread fire across large landscapes whereas strong, fire-affected winds can carry embers many kilometers to ignite far away trees or patches.

4. Consequences

System properties interact with disturbance drivers and mechanisms to influence the initial outcome and future consequences (Fig. 1a). In the fire example above, greater fuel loads in the understory of a forest can result in an increase in fire intensity and severity. Legacies of a disturbance in the form of surviving individuals and initial soil properties, such as amount of compaction, soil organic matter, and water repellency, along with new recruits that colonize the site can influence short-term outcomes of a disturbance (Fig. 2). These consequences can occur abruptly and be relatively short-term, transitional states of a system that may persist for days or weeks, such as initial response to wildfire in forests, or can persist for years to decades, such as response to drought in arid systems.

5. Future states
The accumulated effects of drivers, mechanisms, system properties, and consequences through time eventually result in a future state of the system (Fig. 1a). We use the term state to refer to a persistent assemblage of species and associated soil properties that may or may not reflect the initial state of the system at the time of the disturbance event. Recovery to a previous state through succession is one possible pathway (Pickett et al. 2010), although alternative states are possible, especially if the disturbance modifies propagules or soil properties to result in novel ecosystems with threshold dynamics (Schlesinger et al. 1990, Hobbs et al. 2006, Johnstone and Chapin 2006).

**New Insights to understanding dynamics across ecosystem types**

Although the framework presented here basically expands and refines existing ideas, we believe that unpacking disturbance into its components provides a powerful way to both understand variability in ecological responses to past disturbance and predict future dynamics under global change. In this section, we illustrate new insights about multi-system dynamics using this framework.

**Unpacking a hurricane disturbance**

Hurricanes illustrate how this framework can unpack the complexities of a disturbance event to provide new insights when comparing different ecosystem types. Comparisons of hurricanes often use meteorological indices of strength, such as the Saffir Simpson scale which includes wind velocity, atmospheric pressure at the center of the storm, and height of tidal surge ([http://www.nhc.noaa.gov/](http://www.nhc.noaa.gov/)) (Lugo 2008), or they use visible effects on the vegetation to estimate strength (e.g., Stanturf et al. 2007). However, effects of even the same hurricane can be either spatially heterogeneous in ways that are not related to a particular driver (Fig. 3a) or can be spatially homogeneous in ways that are not related to properties of the ecosystem. As a result,
most ecological studies of hurricanes lack rigor in comparisons of effects within and across ecosystem types (Lugo 2008). Based on this framework (Fig. 1a), measures of the dominant drivers (wind, rainfall amount and intensity) and spatial structure of the land surface affected by hurricanes would improve quantitative comparisons of the effects of hurricanes on different systems. In particular, measuring energy dissipation of wind and water through the canopy as related to driver strength and patterns in biotic structure would be one way to link drivers, structure, and mechanisms of hurricane effects in different ecosystem types (Hopkinson et al. 2008).

In addition, hurricanes can generate a cascade of disturbance impacts that can be accounted for in this framework. For example, independent of wind intensity different intensities of rainfall accompany hurricanes and if rainfall intensity is high, this increases the amount of water reaching the forest floor. This water saturates the soil and makes it vulnerable to mechanical effects of landslides in mountainous areas (Fig. 3b) and triggers chemical effects such as nutrient leaching and physiological effects including anaerobic soil conditions (Heartsill-Scalley et al. 2007). Without unpacking the components of these multiple, inter-related drivers and mechanisms, comparisons among hurricanes as a type of disturbance could lead to incorrect conclusions about how hurricanes affect ecosystems or how projected changes in hurricane intensity (IPCC 2007) might affect ecosystems.

**Wildfire: event with different outcomes in different ecosystems**

Wildfire is a disturbance event common to many ecosystem types, yet variability in drivers and system properties often dictate both the role of fire and its impacts on ecological systems (Fig. 1a). Temperature and precipitation are the primary climate drivers of wildfire regime. These
drivers influence relative humidity, fuel moisture, thunderstorm occurrence, and lightning frequency. The relative importance of climate drivers to ecosystem dynamics based on fire return interval changes nonlinearly across terrestrial ecosystems in the LTER network. Fire return intervals are shortest for mesic grasslands (Konza; 5 y) and dry forests (Bonanza Creek; 80y) compared with deserts (Jornada; 100 y) and moist forests (H.J Andrews; centuries). The effectiveness of climate in fostering wildfire ultimately depends on system properties, such as quantity of aboveground biomass for fuel load, allocation to leaves and twigs as structural determinants of flammability, and plant chemistry that determines chemical flammability. For example, deserts, despite having a hot, dry, windy climate conducive to the spread of fire, typically have insufficient fuel to carry a fire. By contrast, moist forests, despite a large fuel load, have leaves with too much water and too little resin and terpene to carry fire under most conditions. This variation in system properties results in high spatial variability in the spread of fire in dry grasslands and wet forests compared to more complete burns with high-intensity fires in mesic grasslands and dry forests (Fig. 4).

In some cases, alteration of drivers under global change can lead to different successional trajectories than occurred historically. For example, in mesic tallgrass prairie, hot and dry conditions during the summer, frequent thunderstorms, and abundance of fine fuels in the form of grass leaves and litter led to a pre-European fire return interval of less than 10 years. Recent fire suppression has lengthened the fire return interval, allowing juniper invasion and the potential conversion of grassland to forest (Briggs et al. 2005). By contrast, in boreal forests, low fuel moisture and thunderstorms occur infrequently, leading to a fire return interval of 50-150 years. Here, fire adaptations are closely related to plant life history traits and the capacity of plants to survive or colonize burned sites. Recent warming has led to unusually dry conditions
and to wildfires that consume more of the surface peat layer, producing a seedbed that is more favorable to deciduous trees and initiating a new successional trajectory to deciduous forest (Johnstone and Chapin 2006).

Changes in fire regime may also occur in response to global changes in drivers. For example, extended periods of El Niño in Indonesia, 8-year drought in southern Australia, and permafrost thaw and dry conditions in tundra all cause wildfire to occur more extensively and/or become more difficult to suppress (IPCC 2007). The consequences of fire in systems where it is a novel disturbance may be quite different than in historically fire-prone systems. Even rare fires can have huge effects in systems without a fire history. These effects include mortality of non-fire-adapted plants with resulting effects on herbivores, and spread of fires from rural to urban areas. Similarly, changes in system characteristics with global change, such as invasion of introduced species or changes in fuel loads, can lead to fires that are more intense, severe, or extensive than in the past, causing large changes in ecosystem dynamics.

**Clearcutting: event with similar outcomes for different ecosystems**

Removal of trees from forests by logging shows how similar mechanisms associated with a driver can overwhelm contrasts in system properties to result in similar dynamics across different ecosystem types. Hydrological responses to effects of clearcut logging have been studied in forested ecosystems across the U.S. Cross-site comparisons of small watersheds has revealed interesting and, in some cases, surprising patterns of streamflow response to forest removal and regrowth over seasons or successional time (Jones and Post 2004).

Forest types in different parts of the U.S. from the Pacific Northwest, Southeast, and Northeast exhibit a broad range of climate drivers, biotic conditions, and disturbance histories.
Climate drivers contrast in degree of snowiness and seasonality of wet and dry periods, biotic conditions range from deciduous to evergreen, coniferous vegetation, and disturbance history is reflected in the age class of forest in the “reference” watershed (Jones and Post 2004). Despite this diversity of conditions, the sites exhibit surprisingly similar responses to clearcutting. In all three forest types, flow of water in streams increases in response to clearcutting because absence of vegetation reduces evapotranspiration. As vegetation regrows in disturbed watersheds, flow decreases toward that expected from the relationship with the reference watershed (Fig. 5; Jones and Post 2004). After a decade or so, flow from many treated watersheds “overshoots” where low flows dip below the reference watersheds for a decade or two before achieving a closer return to the discharge expected from the reference watershed. Note that vegetation in the “reference” watershed is also changing in response to succession and climate on the time scale of these studies. The similarity in hydrologic response to clearcutting in forests with strikingly different system properties may reflect a common suite of biophysical mechanisms. A reduction in evapotranspiration and soil binding with vegetation removal links a similar disturbance event, in this case clearcutting, to similar responses of water and sediment discharge. In addition to common responses across sites, differences in other response measures, such as the magnitude and timing of streamflow change, reflect variation in site productivity, stage of succession in the reference watershed, and various climatic factors (Fig. 5).

**Desertification: event with scale-dependent outcomes**

Conversion from perennial grasslands to degraded shrublands shows how outcomes are scale – dependent and governed by drivers at broad scales and by system properties at plant to landscape scales. This desertification event has occurred in arid and semiarid regions globally over the past
several centuries with consistent results: loss of biodiversity and production (Peters et al. submitted), spread of invasive introduced species (Masters and Sheley 2001), and wind and water erosion of soil and nutrients (Okin et al. 2009). Although the broad-scale outcome of desertification is the same, spatial and temporal variations in rates and patterns of woody plant invasion across landscapes have led to alternative hypotheses regarding key drivers (e.g., Archer 1994). Our disturbance framework (Fig. 1) provides improved understanding of these dynamics by focusing on interactions of multiple drivers with variation in system properties across a range of scales.

Drought and livestock grazing are proposed to cause desertification globally, and conceptualizations of their effects on grasslands follow typical models of disturbance (Fig. 6a) (Schlesinger et al. 1990, Archer 1994). In contrast, the new framework considers drought to consist of a suite of climate drivers, including low rainfall, high temperature, and low relative humidity, and considers livestock grazing to be the result of land management decisions and socio-economic drivers (Fig. 6b). Although climatic and socio-economic drivers are highly variable in time and space, in general, broad-scale grassland-to-shrubland conversion occurs globally as a result of similar disturbance mechanisms (Fig. 6b, blue) and system properties and consequences (Fig. 6b, green, black, respectively). For example, desert grasslands were historically the predominant ecosystem type throughout the Southwestern U.S. and were likely resistant to periodic droughts. Overgrazing by livestock in the late 1880s would have resulted in high grass mortality and low herbaceous cover that made these systems vulnerable to high winds, high temperatures, and low rainfall during the extended droughts in the 1910s, 1930s, and 1950s (Fig. 6b). In contrast, unpalatable shrubs in this system are resistant to grazing and can be dispersed by livestock; thus overgrazing would have set up conditions favorable to shrub
expansion during drought. In addition, shrubs have deep roots that, if water is available in deeper soil layers, confer tolerance to hot, dry surface conditions and continued production of seeds, thus further promoting shrub expansion at the expense of grasses. Finally, shrubs accumulate soil and nutrients in resource islands beneath their canopy such that bare interspaces between shrubs are nutrient-poor with little or no grass recovery. These shrub-soil feedbacks maintain degraded shrubland states through time (Schlesinger et al. 1990). Although different grass and shrub species occur in arid and semiarid regions globally, and livestock grazing occurs concurrently with drought in many cases, similar mechanisms and processes are likely operating to allow conversion to woody plant dominance (Archer 1994).

However, landscape-scale variation in woody plant invasion is more difficult to explain and involves both variability in drivers and their interactions with heterogeneity in system properties (Peters et al. 2006). Precipitation is highly variable in time and space, and livestock grazing varies both within and among pastures as a result of variation in forage quality and quantity. Horizontal and vertical heterogeneity in soil properties interact with precipitation variability to affect patterns of plant-available water with often differential impacts on grasses and shrubs resulting in complex relationships between vegetation and soil patterns (McAuliffe 1994, Gibbens et al. 2005). Spatial context of a location is important, both for distance to seed sources for shrubs, and for connectivity by wind among bare soil patches and by water between upland and lowland topographic positions (Yao et al. 2006, Peters et al. 2006, Okin et al. 2009).

Thus, even within a site, complex patterns in shrub expansion following disturbance are possible that require knowledge of drivers, mechanisms, and system properties. In this case, similar mechanisms are operating, but they are overwhelmed by effects of variation in system properties.
Warming and wildfire: threshold responses depend on drivers and system properties

The occurrence and severity of a disturbance event often relies on thresholds of ecosystem properties and climatic drivers. Climate change will impose novel disturbances or a higher frequency of rare disturbances on many ecosystems. For example, fires are currently a rare phenomenon in the Arctic with 3% of Alaskan tundra burned between 1950 and 2005 (Higuera et al. 2008). The low fire frequency is attributed to few ignition sources, low fuel load, and high fuel moisture. However, these conditions are expected to change as global warming favors an increase in lightning strikes, productivity, and aridity in the Arctic (Higuera et al. 2008). Consequently, climate change may elicit threshold responses in the fire regime and ecology of the Arctic that are currently difficult to predict under the traditional view of disturbances as types rather than as events.

Conditions during the 2007 summer season demonstrated the importance of environmental thresholds in regulating Arctic fire activity and post-fire climate forcing. This summer was one of the warmest, driest, and most lightning-active years in the past two decades. These conditions created three lightning-induced fires within 110 km of each other that differed in extent of area burned and post-fire ecosystem states (Fig. 7). Differences between the three disturbance events in the extent of area burned and consequences suggests that a suite of environmental conditions controlled how the drivers and their mechanisms interacted with the system properties to result in different consequences.

The extent of area burned depended on thresholds in system properties related to fire timing during the summer season and vegetation community composition in 2007. Vegetation cover was highest next to the large Anaktuvuk River fire ignition source and lowest next to the
two smaller fires, suggesting variability in fuel loads (Fig. 7a). Vegetation moisture was high during the start of the Anaktuvuk and Kuparuk fires and kept the areas burned low for several weeks after ignition (Fig. 7c). High vegetation moisture content and low vegetation cover likely resulted in the extinguishing of the Kuparuk fire by mid-August, while high vegetation cover allowed the Anaktuvuk River fire to persist. The Anaktuvuk River fire burned larger areas as the vegetation dried out, as indicated by decreases in vegetation moisture, whereas high wind speeds and low relative humidity during the later part of the growing season fueled the fire and resulted in a 10-fold increase in area burned (Fig. 7b,c). The Sagavanirktok fire started in early September and burned mostly during the period of high winds and low relative humidity. Snowfall during the first week of October increased surface moisture and extinguished both the Anaktuvuk River and Sagavanirktok fires.

Interactions of drivers with ecosystem properties among these fires produced different consequences that may influence the future state of the system (Fig. 7d). Surface albedo was reduced in burned tundra, especially in the severely burned Anaktuvuk River fire, where more organic matter was consumed in the fire (Rocha and Shaver 2009). Burn severity can also influence the future state of the system. Leaf area recovery at a severely burned area was lower than at a moderately burned area within the Anaktuvuk River area during the 2008 growing season (Rocha and Shaver 2009). High-severity fires may favor the establishment of low albedo shrub species rather than more reflective tussock sedges (Racine et al. 2004) (Fig. 7d). Increased shrub abundance would result in a positive feedback to climate warming through the reduction of albedo and increased fuel load, illustrating the importance of understanding thresholds and feedbacks in order to predict future states in the Arctic.
Future Research

Implications for Global Change Research. Characteristics of many disturbances are expected to change as their drivers continue to respond to increases in greenhouse gases (e.g., Dale et al. 2001, Webster et al. 2005, Lavorel et al. 2007). Although attempts are being made to reduce future emissions, trajectories of change have been nonlinear over the past century and will likely continue in that way in the near future (Smith et al. 2009). In addition, properties of ecological systems are changing with spread of invasive species, and changes in climate and land use (MEA 2005). Disaggregating disturbance into drivers, mechanisms, and system properties could provide major advances in comparing disturbance events among ecosystems of the world.

Management implications. Future management decisions can benefit from this new framework. Management decisions are often made at scales that encompass multiple ecosystems having multiple states that are potentially subject to multiple disturbance events (Dale et al. 1998). This framework can be used to identify commonalities among disturbances and ecosystems and highlight where society acting through policy and implementation has the potential to mitigate some of the undesired consequences of disturbance and possibly keep some ecosystems from moving to an undesired state. Under some circumstances, changes in land management can lead to a system with more resilient ecosystem characteristics, thereby reducing system vulnerabilities to disturbance. Management can also focus on preserving or restoring system properties that increase ecosystem resilience to known disturbance mechanisms or to projected occurrence of novel disturbances (Seastedt et al. 2008). Managing for ecosystem resilience can include strategies that facilitate or emulate natural disturbances regimes with consequences that provide some of the desired system properties. In some instances, such as the warming of the Arctic tundra and resultant altered fire regimes, there are no clear opportunities
for managing system properties to minimize disturbance impacts; thus, society is left with post hoc interventions, such as fire suppression or acceptance of the novel disturbance regime and resulting ecosystem properties.

**Cross-site experiments.** Most disturbance studies have focused on comparing either effects of, or ecological responses to, disturbances of different characteristics, such as size, type, and frequency of occurrence. Generalizations across ecosystem types are difficult because of variability in both disturbance events and ecological responses. An expanded framework guides cross-system studies in the driver, mechanisms, and system properties to be compared or manipulated for different disturbance events. Manipulations of drivers and vegetation structure have commonly been used in ecology (e.g., Fay et al. 2000, Herrick et al. 2006). However, this framework shows that manipulations of mechanisms may provide the strongest comparative approach across ecosystem types. Because different disturbance events, such as drought and clearcutting, may impose similar mechanisms, conducting experiments on mechanisms may provide the necessary quantitative information to compare both disturbance events and ecosystem types.

**Summary and Conclusions**

The definition of disturbance proposed when disturbance ecology was a relatively young subfield of ecology (White and Pickett 1985) can be used to focus insights from the comparative studies and concepts summarized here. Two phrases in the original definition in particular resonate with this expanded conceptual framework (Fig. 1) and warrant further theoretical and observational studies. One is the need to specify exactly how disturbances are “relatively discrete” in time. Most ecologists have related the discreteness of potential disturbances to the times between such events, or to the length of time it takes for the system to recover from a disturbance. Thus, for
mesic forest successions lasting several centuries, the creation of canopy gaps is relatively
discrete, with recurrence intervals of slightly longer than a century, which is short relative to the
lifespan of the dominant trees. In contrast, the interaction of decades-long severe drought,
overgrazing, and wind erosion shifting woody composition and creating large bare soil patches in
desert systems is discrete compared to the several-century dynamic of this grazing system since
the Spanish colonial era. Our framework suggests that discrete events should be defined based
either on the onset, duration or release of a driver, or on the time over which a mechanism
operates relative to the lifespan of organisms dominating system behavior.

The second point indicated by this framework that deserves further refinement is the need
to specify “disruption” relative to a system property in time and space. Prior attempts have been
made to clarify this issue, by identifying a reference state. This reference state may be a long-
term mean or other persistent state (Rykiel 1985), or a system model, whether graphical, verbal,
or quantitative, that represents system components and their interactions (Pickett et al. 1989).
The requirement for a reference model is equally true for populations, communities, ecosystems,
and landscapes. Based on our framework, a disruption is an alteration of the system by removing
or adding structural components through the effects of drivers and mechanisms interacting with
system properties to result in outcomes that differ form the reference state.

Using examples from long-term research, the unpacked framework presented here
illustrates that similar disturbance events can have similar or different impacts on different
ecosystems because they have similar or different interactions among drivers, mechanisms, and
system characteristics. An explicit consideration of drivers and mechanisms provides
opportunities to design cross-system experiments to test understanding and to devise
management interventions to minimize undesirable outcomes. Finally, our focus on drivers,
mechanisms, and system properties rather than disturbance types provides a direct link to global change studies of climate and land use.
Acknowledgements

Support was provided by the National Science Foundation to the Long Term Ecological Research Programs at the Jornada Basin (DEB-0618210), Bonanza Creek (DEB-0620579), Luquillo (DEB-0620910), Baltimore Ecosystem Study (DEB-0423476), Arctic (DEB-0423385), and HJ Andrews Experimental Forest (DEB-0823380). Support was also provided by the LTER Network Office (DEB-0236154) to the EcoTrends Disturbance Working Group. We thank Principal Investigators from the 26 LTER sites for providing disturbance information from their site.
References Cited


Peters DPC, Yao J, Sala OE. Climate change and potential reversal of a regime shift in desert ecosystems. PNAS (submitted).


Box and Figures Legends

Box 1. Spectrum of disturbance across ecosystems

The broad range of ecosystem types in the US Long-Term Ecological Research (LTER) network can be used to qualitatively compare disturbance regimes. We surveyed the 26 sites in the LTER network to determine which disturbances are most important in shaping temporal and spatial variation in ecosystem structure and functioning. The two most important disturbances (shown as #1, #2) and their characteristics (primary driver, return interval, median area, and cause of change in disturbance characteristics) were provided by each site. Additional information on drivers, mechanisms, responses and return interval, and areal extent are in Appendix I.

(a) Climate (e.g., flood, severe storms) and climate-related physical disturbances (e.g., fire) were viewed as the predominant disturbance at most sites, although biotic disturbance (e.g., insect outbreaks, over-grazing, alien species) and anthropogenic disturbance (e.g., eutrophication, land-use change) were also important at many sites.

(b) Critical disturbances recurred most commonly at multi-decadal intervals, indicating the importance of infrequent events in shaping ecosystems and of long-term research in understanding the causes and consequences of these events. In some ecosystems (e.g., aquatic), however, frequent disturbances (<10 yr return interval) were particularly important.

(c) There was a bimodal distribution in size of the most critical disturbances, with most disturbances being either quite large (>100 km²) or relatively small (<1 km²).

(d) Recent changes in disturbance regimes are altering the dynamics of most LTER sites, with direct human impacts and climate change being the most prominent causes of altered disturbance regime.
Fig. 1. Modified and traditional views of disturbance. (a) “Unpacked” view of disturbance includes a suite of drivers, each with associated processes having spatial and temporal characteristics, and a set of mechanisms that interact with system properties to result in a disturbance event with consequences for ecosystem development followed by future states through time. Abbreviations are Anthro (anthropogenic), PPT (precipitation), and TEMP (temperature). Processes are the actions associated with each driver, such as speed and direction for wind, amount and duration for precipitation, or mode of anthropogenic change. Particular disturbance types can combine the processes associated with one or more drivers into mechanisms with sufficient strength to interact with the properties of a target system. See Fig. 2 for details on drivers, mechanisms, and system properties. (b) Traditional view of disturbance focuses on disturbance types, including spatial and temporal characteristics, interacting with system properties to result in consequences for ecosystem change followed by future states through time.

Fig. 2. Components of a disturbance. A disturbance event consists of broad-scale drivers, mechanisms of impact, and system properties. Examples of each component are shown; the list is not exhaustive. Drivers are listed in general categories, although a driver can be in more than one category, and drivers can interact. A disturbance type can be defined by its drivers and mechanisms (Fig. 1a).

Fig. 3. Hurricane impacts in a forest. Impacts can be either spatially homogeneous or heterogeneous as a result of interactions between drivers and system properties. Forest in Puerto Rico one week after the passage of Hurricane Hugo in September 18, 1989 (Photos by A.E. Lugo). (a) At broad scales, the role of topography (aspect) in creating system response is demonstrated by patchiness of brown and green (defoliated) canopies. (b) In other instances,
heavy rains associated with low-pressure systems trigger landslides with overwhelming effects on forests at smaller spatial scales. The wind and rainfall components of hurricanes affect forests independently and differently.

**Fig. 4.** Wildfire is a disturbance with variable impacts across different ecosystem types. Impacts of wildfire often depend on system properties: fires are patchily distributed in (a) dry grasslands with low fuel loads in desert grasslands (photo from [http://www.sev.lternet.edu](http://www.sev.lternet.edu)) and (b) wet forests with vegetation with high moisture content (Photo by R.D. Ottmar). Fires burn more completely with high intensity in (c) mesic grasslands at Konza (Photo by A. K. Knapp) and (d) dry boreal forests (Photo by L. DeWilde).

**Fig. 5** Effects of clearcutting of trees on water yield for three forest types at LTER sites in the U.S.: AND (HJ Andrews Experimental Forest [460-yr-old evergreen conifer forest in western Oregon]), CWT (Coweeta Experimental Forest [36-yr-old deciduous forest in Georgia]), and HBR (Hubbard Brook Experimental Forest [50-yr-old mixed deciduous forest in New Hampshire]). Five-year running mean of percent changes in water yield relative to the pretreatment period in clearcut vs. control watersheds for (a) the water year (October-September), and (b) the minimum flow period (September 1-15). Maximum increases in annual water yield occurred in the first five years after clearcutting and ranged from 110% at AND to 2% at CWT. Maximum decreases in annual water yield occurred in the most recent record, 30 to 40 years after clearcutting. Adapted from Jones and Post (2004).

**Fig. 6.** Views of disturbance in grassland-shrubland transitions. (a) Traditional view of overgrazing and drought as disturbances that shift grasslands to shrublands in arid and semiarid ecosystems. (b) Unpacked view in which each disturbance has multiple drivers (red) that interact with mechanisms (blue) and system properties to result in a recovering state of the system.
followed by a shift to shrublands though time. This view explicitly accounts for each driver, mechanism, and system property as interacting factors in a state change.

Fig. 7. Environmental conditions and ecological consequences of three 2007 summer wildfires on the North Slope of Alaska. Map on the left is derived from two false color Landsat images from July of 2008, and the white lines represent fire perimeters derived from the images. Panels a-c illustrate environmental conditions during the 2007 summer fires. Prefire Enhanced Vegetation Index (EVI) was derived from MODIS imagery from a 6.25 km\(^2\) area next to the fire ignition source on 7/11/2007 [a]. Daily Maximum Wind Speed (Max WS) and Minimum Relative Humidity (Min RH) were measured at Toolik lake (40 miles to the southeast) at 5 m and smoothed with an 8 day moving average [b]. The Normalized Difference Water Index (NDWI; Gao 1996) was calculated during the 2007 summer in unburned and cloudless areas within the map perimeter (red square within map of Alaska), while burned area was calculated from MODIS false color images [c]. Surface albedo for the three fires and unburned tundra was calculated from the 1km\(^2\) MODIS product on 7/3/2008, while albedo for shrub tundra was derived from the literature (Chapin et al. 2005).
(b) Traditional disturbance

(a) “unpacked” disturbance

Drivers
PPT
Nitrogen
Anthro
Temp
Invasive species

Disturbance Type

System properties

Consequences

Future State

Disturbance event
System recovery
Components of disturbance event

Drivers
- Climatic
  - Wind
  - Precipitation
  - Temperature
- Atmospheric
  - Nitrogen dep.
  - CO₂
- Physical
  - Soil resource addition & loss
- Biotic
  - Invasive species
  - Disease
- Anthropogenic
  - Land Use

Mechanisms
- Abrasion
- Combustion
- Herbivory
- Defoliation
- Soil compaction
- Water infiltration
- Transfer of biomass
- Erosion/deposition
- Water logging

System properties
- Height
- Physiology
- Grazing tolerance
- Drought tolerance
- Biomass
- Flammability
- Density
- Patch size, spatial arrangement
(a) Traditional view of grazing and drought in desert grasslands

Overgrazing

Grassland → Grass mortality
Shrub invasion
Loss of soil nutrients
Patchy nutrients
Large bare gaps → Shrubland

Drought

(b) Unpacked view of grazing and drought in desert grasslands

Human decisions (high cattle density 1880s-1950s)

Grass herbivory
Soil compaction
Shrub seed consumption, redistribution

Grassland (high uniform grass cover, small bare gaps, grass traits)

Grass mortality
Shrub expansion

Human decisions (post 1950s) (moderate cattle density)

Grass herbivory
Shrub seed consumption/redist
Water stress
Wind/water erosion of soil, nutrients

Degraded grassland (low grass cover, isolated shrubs)

Driver/mechanisms → system properties/states → consequences

Overgrazing → High temperature
Low precipitation
High wind

Drought, grazing → Grass mortality
Shrub expansion
Loss of soil nutrients
Patchy nutrients
Large bare gaps

Degraded shrubland

Grass herbivory
Soil compaction
Water stress
Wind/water erosion of soil, nutrients

High temperature
Low precipitation
High wind
Appendix I. Characteristics of disturbance regimes for each LTER site based on a survey of principal investigators.

<table>
<thead>
<tr>
<th>Site code and ecosystem type</th>
<th>Major disturbances (and recent trends)*</th>
<th>Drivers of change</th>
<th>Mechanism by which disturbance impacts ecosystems</th>
<th>Consequences</th>
<th>Return interval (yr)</th>
<th>Median size (km²)</th>
<th>Website</th>
</tr>
</thead>
<tbody>
<tr>
<td>H.J. Andrews Experimental Forest¹ (coniferous forest)</td>
<td>Fire (↓)</td>
<td>Management policy/ action (fire use, suppression)</td>
<td>thermal stress</td>
<td>mortality</td>
<td>50-500</td>
<td>0.01 - 10⁴</td>
<td><a href="http://www.fsl.orst.edu/">http://www.fsl.orst.edu/</a></td>
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<tr>
<td>Logging (↓)</td>
<td>Federal land policy</td>
<td>Tree bole removal</td>
<td>mortality</td>
<td>100 (formerly)</td>
<td>2</td>
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<tr>
<td>Arctic (tundra)</td>
<td>Thermokarst (↑)</td>
<td>Climate warming</td>
<td>Physical stress</td>
<td>Severe erosion</td>
<td>NA</td>
<td>1 Km²</td>
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<tr>
<td>Fire (↑)</td>
<td>Climate warming</td>
<td>Combustion</td>
<td>mortality</td>
<td>300</td>
<td>1</td>
<td></td>
<td></td>
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<tr>
<td>Baltimore Ecosystem Study (city)</td>
<td>Land conversion (↑ or ↓?)</td>
<td>Globalization; Human population redistribution</td>
<td>Altered social capital</td>
<td>Land conversion</td>
<td>50</td>
<td>.001</td>
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<tr>
<td>Sea level rise (↑)</td>
<td>Climate warming</td>
<td>Threatened properties</td>
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<td>decades</td>
<td>global</td>
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<td></td>
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<td>Bonanza Creek (boreal forest)</td>
<td>Fire (↑)</td>
<td>Climate warming</td>
<td>Combustion</td>
<td>mortality</td>
<td>80</td>
<td>100</td>
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<td>Insect outbreak (↑)</td>
<td>Climate warming</td>
<td>Consumption</td>
<td>mortality</td>
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<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central Arizona-Phoenix (city)</td>
<td>Land change (↑)</td>
<td>Human population redistribution; economic opportunity</td>
<td>Soil disruption, altered hydrology</td>
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<tr>
<td>Drought (↑)</td>
<td>Climate change; human appropriation</td>
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<td>mortality, loss of habitat</td>
<td>50</td>
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<td>proximal causes are changes in</td>
<td>increased water column stratification, reduced nutrient supply</td>
<td>Faunal/floral displacements</td>
<td>2-7 y</td>
<td>Pacific basin</td>
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<td>(coastal)</td>
<td>Walker circulation, winds</td>
<td>Coastal upwelling variability (↑)</td>
<td>Increased nutrient supply</td>
<td>Species change</td>
<td>3-10 days</td>
<td>100s of km</td>
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<td>Cedar Creek (grassland)</td>
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<td>Human population redistribution, fire suppression</td>
<td>Increased wind stress, climate warming</td>
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<td>Water, heat stress</td>
<td>mortality</td>
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<td>Coweeta (eastern deciduous forest)</td>
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<td>Human population redistribution, fire suppression</td>
<td>Increased nutrient supply</td>
<td>Species change</td>
<td>3-10 days</td>
<td>100s of km</td>
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<td>Disease (↓)</td>
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<td>mortality</td>
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<td>100</td>
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<td>Mortality, biogeochemical change</td>
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<td>Erosion-deposition</td>
<td>Mortality, biogeochemical change</td>
<td>decades</td>
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<td>Hubbard Brook Ecosystem Study (eastern deciduous forest)</td>
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<td>Globalization, Human population redistribution</td>
<td>Tree bole removal</td>
<td>species change, biogeochemical change</td>
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<td>Snowpack duration loss (↓)</td>
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<td>Landscape change</td>
<td>species change</td>
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References:
http://www.lter.umn.edu/
http://coweeta.ecology.uga.edu/
http://fcelter.fiu.edu/
http://gce-lter.marsci.uga.edu/
http://www.hubbardbrook.org/
http://harvardforest.fas.harvard.edu/
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<td>State change</td>
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<td>management</td>
<td>Grass consumption</td>
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<td>Kellogg Biological Station (agricultural)</td>
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<td>Water, heat stress</td>
<td>↓ NPP</td>
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<td>Exotic pest (invasive species) (↑)</td>
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<td>defoliation</td>
<td>↓ NPP</td>
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<td>Konza Prairie (mesic grassland)</td>
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<td>combustion</td>
<td>Woody plant expansion, land cover change</td>
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<td>↓ landscape heterogeneity</td>
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<td>Luquillo (tropical forest)</td>
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<td>Population and community change</td>
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<td>McMURDO Dry Valleys³ (Antarctica)</td>
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<td>Ozone hole</td>
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<td>Atmospheric CO₂ levels – climate change</td>
<td>(↑) mortality (↓) growth</td>
<td>100-1000??</td>
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<td>Climate change – irradiance</td>
<td>(↑) mortality</td>
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<td>Invasive species (↑)</td>
<td>Human transport</td>
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<td>Agricultural practices, land disturbance</td>
<td>Change in nutrient cycles, water quality, species</td>
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<td>100-1000</td>
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<td>unknown</td>
<td>burrowing</td>
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<td>Decadel 10-100 m²</td>
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<td></td>
<td>Snow amount/duration (↑)</td>
<td>climate change</td>
<td>deposition</td>
<td>Species change</td>
<td>1 100s</td>
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<tr>
<td>Niwot Ridge (forest-tundra ecotone)</td>
<td>Snow amount/duration (no Δ)</td>
<td>Climate change</td>
<td>deposition</td>
<td>Tree and patch distribution change</td>
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<td>Snowfall (↑)</td>
<td>Sea ice retreat</td>
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<td>Climate warming</td>
<td>Albedo change; trophic change</td>
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<td>Land-use change (↑)</td>
<td>Human population redistribution</td>
<td>Hydrologic change</td>
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<td></td>
<td>Storms (↑)</td>
<td>Climate change</td>
<td>Erosion</td>
<td>Shoreline change</td>
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<td>Santa Barbara Coastal (coastal)</td>
<td>Large wave events (↑)</td>
<td>Climate change</td>
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<td>Human pop. redistrib., climate warming</td>
<td>Combustion</td>
<td>mortality</td>
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<tr>
<td></td>
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<td>Globalization</td>
<td>↓ consumption</td>
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<td>Sevilleta (iarid)</td>
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<td>Water, heat stress</td>
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<td></td>
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<td>Human</td>
<td>Combustion</td>
<td>mortality</td>
<td>8-10 .1</td>
</tr>
</tbody>
</table>
Major disturbances are defined as those having the greatest importance in recent decades in shaping the structure and long-term (decades to centuries) dynamics of a site. These disturbances could be small in extent and frequently occurring or large in extent or infrequent. The trend (positive, negative, no change) over the past decades is also no change) over the past decades is also shown. Both natural-occurring and anthropogenic disturbance can be listed.


