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SYNTHESIS & INTEGRATION

Cross-system comparisons elucidate disturbance complexities and generalities

Debra P. C. Peters,[1,†] Ariel E. Lugo,[2] F. Stuart Chapin, III,[3] Steward T. A. Pickett,[4] Michael Duniway,[1] Adrian V. Rocha,[5] Frederick J. Swanson,[6] Christine Laney,[1,8] and Julia Jones[7]

[1]US Department of Agriculture-Agricultural Research Service, Jornada Experimental Range, Las Cruces, New Mexico 88003 USA
[2]US Department of Agriculture-Forest Service, International Institute of Tropical Forestry, Río Piedras, Puerto Rico 00928-5000
[3]Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775 USA
[4]Cary Institute of Ecosystem Studies, Millbrook, New York 12545-0129 USA
[5]The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543 USA
[6]US Department of Agriculture-Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331 USA
[7]Department of Geosciences, Oregon State University, Corvallis, Oregon 97331-5506 USA

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Abstract. Given that ecological effects of disturbance have been extensively studied in many ecosystems, it is surprising that few quantitative syntheses across diverse ecosystems have been conducted. Multi-system studies tend to be qualitative because they focus on disturbance types that are difficult to measure in an ecologically relevant way. In addition, synthesis of existing studies across systems or disturbance types is challenging because sufficient information needed for analysis is not easily available. Theoretical advances and improved predictions can be advanced by generalizations obtained from synthesis activities that include multiple sites, ecosystems, and disturbance events. Building on existing research, we present a conceptual framework and an operational analog to integrate this rich body of knowledge and to promote quantitative comparisons of disturbance effects across different types of ecosystems and disturbances. This framework recognizes individual disturbance events that consist of three quantifiable components: (1) environmental drivers, (2) initial system properties, and (3) physical and biological mechanisms of effect, such as deposition, compaction, and combustion. These components result in biotic and abiotic legacies that can interact with subsequent drivers and successional processes to influence system response. Through time, a coarse-scale quasi-equilibrial state can be reached where variation in drivers interacting with biotic processes and feedbacks internal to the system results in variability in dynamics. At any time, a driver of sufficient magnitude can push the system beyond its realm of natural variability to initiate a new kind of event. We use long-term data from diverse terrestrial ecosystems to illustrate how our approach can facilitate cross-system comparisons, and provide new insights to the role of disturbance in ecological systems. We also provide key disturbance characteristics and measurements needed to promote future quantitative comparisons across ecosystems.

Key words: disturbance event; disturbance type; drought; ecological theory; global change; hurricane; legacies; overgrazing; thresholds; wildfire.

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[8] Present address: Department of Biological Sciences, University of Texas, El Paso, Texas 79968 USA.

† **E-mail:** debpeter@nmsu.edu

Introduction

Disturbance is a ubiquitous force in ecological systems that shapes patterns and dynamics across a range of spatial and temporal scales (White and Pickett 1985). The ecological effects of disturbance may be the most well-studied phenomena in ecology with a long history grounded in succession (Pickett et al. 2011). Conceptualizations about the role of disturbance have shifted multiple times over the past century, from a driver that can push a system beyond its equilibrial state (Clements 1916) to a system component that affects natural variability and non-equilibrial dynamics at fine-scales with broad-scale consequences (Bormann and Likens 1979, Shugart 1984, Pickett and White 1985). A related paradigm shift moved from viewing disturbance as a broad-scale impact (e.g., Albertson and Weaver 1946) to the recognition that a disturbance regime consists of many events, each with its own characteristics that interact with system properties to influence recovery dynamics (Sousa 1984). More recently, attention has shifted to changes in disturbance regimes under the umbrella of "global change" that may result in novel ecosystems with consequences to ecosystem services (Hobbs et al. 2006, Williams and Jackson 2007, Raffa et al. 2008, Seastedt et al. 2008). The result of these major shifts is a large body of knowledge on the ecology of disturbance that is both deep for any given system and broad for multitude of diverse systems (e.g., Turner et al. 2003, Turner 2010).

Given the plethora of studies conducted on disturbance in ecological systems, there are surprisingly few synthetic treatments that rigorously compare ecosystem types, yet these syntheses are needed to push science forward through the development of generalities (Pickett et al. 2007, Carpenter et al. 2009, Peters 2010). Most studies seeking generalizations about the role of disturbance have either: (1) compared disturbance events or regimes across sites but within a biome or ecosystem type, for example temperate and tropical forests (e.g., Boose et al. 1994, Dale et al. 2001, Roberts 2004, Keane et al. 2009, Long 2009), (2) compared different types of disturbance, such as drought, grazing, fertilization, hurricanes, and/or wildfires, often within the same site (e.g., Collins 1987, Minshall 2003, Covich et al. 2006, Fuhlendorf et al. 2006, Houseman et al. 2008), or (3) provided a collection of case studies that illustrate common features of disturbance effects and system recoveries for different ecosystems (e.g., Pickett and White 1985, Turner et al. 2003, Johnson and Miyanishi 2007, Fraterrigo and Rusak 2008).

Because disturbances are expected to play an increasingly important role in the future (MEA 2005, IPCC 2007, Running 2008, Turner 2010), it is imperative that approaches be developed to promote general understanding and prediction of disturbance effects and system responses that can account for future conditions. Multi-site quantitative comparisons across different ecosystems and disturbance types provide one way to develop this generality. However, there are three major limitations that preclude these comparisons.

First, current definitions of disturbance are relatively vague. Although a number of definitions, conceptual frameworks, and theories have been developed (e.g., Clements 1916, Grime 1977, Sousa 1984, White and Pickett 1985), the most commonly used definition 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" (White and Pickett 1985:7). This definition, with minor modifications, has been applied extensively to both terrestrial and aquatic ecosystems (e.g., Collins 1987, Coffin and Lauenroth 1988, Resh et al. 1988, Palmer et al. 1996, Reich et al. 2001, Fraterrigo and Rusak 2008).

In many cases, this definition has been applied by focusing on disturbance types that are readily identified (e.g., drought, wildfire, hurricane), but often difficult to measure in ecologically relevant ways (Pickett et al. 1989, Johnson and Miyanishi 2007). Disturbance types are often compared using characteristics such as size, frequency of occurrence, and intensity of effect (e.g., Pickett and White 1985, Turner et al. 1993, 1997*b*, Reich et al. 2001). However, these characteristics can be insufficient to explain variation in ecological response that may be related to weather or environmental conditions at the time of the event (e.g., Coffin et al. 1996, Turner et al. 1997*b*). These characteristics also may not be able to determine the causal driver of a given pattern. For example, both windstorms and flooding can have similar effects when they involve similar mechanisms (e.g., sediment deposition) (Turner et al. 1997*a*); thus, observations of a similar intensity in different ecosystems can generate misleading interpretations about the drivers. Disturbance types also differ in their temporal and spatial scales, and interactions among types operating at different scales can generate complex system dynamics that are not accounted for in commonly used characteristics (Peters et al. 2004).

In addition, a disturbance type consists of multiple drivers, each with a set of characteristics, which are confounded when combined into a "type". For example, a drought refers to a period of abnormally dry weather that integrates low rainfall and high temperature (Wilhite and Glantz 1985). Meteorological indices, such as the Palmer Drought Severity Index (PDSI), used to characterize a drought, can be misleading ecologically: droughts with the same PDSI can have different consequences because of different precipitation and temperature (Palmer 1965).

Second, most disturbance research is specific to a biome or ecosystem type where differences in the physical environment and biota are minimized compared to multi-system responses (White and Jentsch 2001, Grman et al. 2010). For example, initial conditions important to the consequences of disturbance (Johnson and Miyanishi 2007) can be difficult to assess before natural disturbance events. Assuming similar initial conditions when comparing disturbance effects will certainly be violated when comparing across ecosystem types. Ecophysiological status of plants, species abundance, soil resource status, composition and structure of patches, and the spatial distribution of patch types are examples of initial system properties that can influence the resistance of an ecosystem to disturbance, and its resilience or ability to sustain its properties following a disturbance (Pickett et al. 2011).

Effects of multiple, interacting disturbances are also particularly challenging when comparing across ecosystem types. 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, Krawchuk and Cumming 2011). In this case, previous disturbance determined the response of a system to subsequent disturbance. Historical events, including time lags, thresholds, and management history, are important sources of variation (e.g., Foster and Aber 2004, Fraterrigo et al. 2006) that can be difficult to standardize when comparing across ecosystems.

Another important comparison across ecosystems is to use disturbance regimes, defined as the suite of disturbance types that affect a particular system, each with multiple events through time. A disturbance event can interact with other events and with ecosystem properties to feed forward to generate additional disturbance (Pickett et al. 1999, Dale et al. 2001, Allen 2007, Crowl et al. 2008, Turner 2010). Because a large diversity of effects can occur, even in the case of a single type of disturbance (Cardinale et al. 2005), only qualitative comparisons across ecosystems of disturbance regimes with multiple disturbance types are often possible (Table 1; Fig. 1). In addition, disturbance regimes are changing with directional changes in climate, increases in atmospheric pollutants, invasion and loss of species, and modifications to land use that result in even greater challenges to cross-system comparisons (MEA 2005, Westerling et al. 2006, Raffa et al. 2008, Restrepo et al. 2009).

Third, sufficient information needed for statistical comparisons is typically not provided as part of a study. Notable exceptions exist where disturbance events are compared within an ecosystem type based on published information (e.g., Jones and Post 2004). However, a recent attempt to quantitatively compare disturbance types and effects across ecosystems in the US or funded by US agencies (forests, grasslands, desert, streams, lakes marine, urban, polar) demonstrated ambiguity in the ways that disturbance types are conceptualized and studied such that only general comparisons were possible (Table 1, Fig. 1) (Peters et al. 2011).

To address these limitations, we present an integrated framework to promote and guide quantitative comparisons of effects of disturbance on different types of ecosystems. Our goals were to: (1) provide a framework to organize and integrate the large amount of existing knowledge

Table 1. Characteristics of disturbance regimes for each LTER site based on a survey of principal investigators.

Site code and ecosystem type	Major disturbances (and recent trends)*	Drivers of change	Mechanism by which disturbance effects ecosystems	Consequences	Return interval (yr)	Median size (km^2)	Website
H.J. Andrews Experimental Forest[1] (coniferous forest)	Fire (↓)	Management policy/action (fire use, suppression)	Combustion	Mortality	50–500	.01–10^4	http://www.fsl.orst.edu/
	Logging (↓)	Federal land policy	Tree bole removal	Mortality	100 (formerly)	2	
Arctic (tundra)	Thermokarst (↑)	Climate warming	Physical stress	Severe erosion	NA	1 km^2	http://ecosystems.mbl.edu/ARC/
	Fire (↑)	Climate warming	Combustion	Mortality	300	1	
Baltimore Ecosystem Study (city)	Land conversion (↑ or ↓?)	Globalization; Human population redistribution	Altered social capital	Land conversion	50	.001	http://www.beslter.org/
	Sea level rise (↑)	Climate warming	Threatened properties		decades	global	
Bonanza Creek (boreal forest)	Fire (↑)	Climate warming	Combustion	Mortality	80	100	http://www.lter.uaf.edu/
	Insect outbreak (↑)	Climate warming	Consumption	Mortality	4	100	
Central Arizona-Phoenix (city)	Land change (↑)	Human population redistribution; Economic opportunity		Soil disruption; Altered hydrology	10	1	http://caplter.edu
	Drought (↑)	Climate change; Human appropriation		Mortality; Loss of habitat	50	100,000	
California Current Ecosystem (coastal)	ENSO (unclear trend)	Proximal causes: changes in Walker circulation; Winds	Increased water column stratification, Reduced nutrient supply	Faunal/floral displacements	2–7	Pacific basin	http://ccelter.sio.ucsd.edu/
	Coastal upwelling variability (↑)	Increased wind stress; Climate warming	Increased nutrient supply	Species change	3–10 days	100s of km	
Cedar Creek (grassland)	Fire (↓)	Human population redistribution; Fire suppression	Combustion	Mortality	1–3	1	http://www.lter.umn.edu/
	Drought (↑)	Climate change	Water; Heat stress	Mortality	50	50,000	
Coweeta (eastern deciduous forest)	Fire (↓)	Human population redistribution; Fire suppression	Combustion	Mortality	None in 70 yr	.01–.1	http://coweeta.ecology.uga.edu/
	Disease (↓)	Globalization	Defoliation	Mortality	decades	10000	
Florida Coastal Everglades (coastal wetland)	Flooding (↓)	Human population redistribution	Deposition	Biogeochemical change	10	2500	http://fcelter.fiu.edu/
	Fire (↑)	Human population redistribution	Combustion	Mortality	10	100	

Table 1. Continued.

Site code and ecosystem type	Major disturbances (and recent trends)*	Drivers of change	Mechanism by which disturbance effects ecosystems	Consequences	Return interval (yr)	Median size (km^2)	Website
Georgia Coastal Ecosystems (coastal wetland)	Severe drought (↑)	Climate change	Water, heat stress	Mortality; Biogeochemical change	3	10,000–100,000	http://gce-lter.marsci.uga.edu/
	Major storms (↑)	Climate change	Erosion-deposition	Mortality; Biogeochemical change	decades	10,000	
Hubbard Brook Ecosystem Study (eastern deciduous forest)	Logging (↓)	Globalization; Human population redistribution	Tree bole removal	Species change; Biogeochemical change	30–100	.001–.01	http://www.hubbardbrook.org/
	Snowpack duration loss (↓)	Climate change	Change in water quality, distribution, quantity	Hydrological and biogeochemical change	1	1000s	
Harvard Forest (eastern deciduous forest)	Land clearing (↓)	Human population redistribution	Landscape change	Species change	100	10,000	http://harvardforest.fas.harvard.edu/
	Logging (no Δ)		Tree bole removal	Mortality	10	.01	
Jornada Basin[2] (desert grassland)	Drought (↑)	Climate change	Water, heat stress	State change	30–50	100s	http://jornada-www.nmsu.edu
	Grazing (↓)	Management	Grass consumption	State change	1	100s	
Kellogg Biological Station (agricultural)	Drought (↑)	Climate change	Water, heat stress	↓ NPP	3–10	10s	http://lter.kbs.msu.edu/
	Exotic pest (invasive species) (↑)	Globalization	Defoliation	↓ NPP	10–20	100s	
Konza Prairie (mesic grassland)	Fire (↓)	Human population redistribution; Fire suppression	Combustion	Woody plant expansion; Land cover change	5	.1–1.0	http://www.konza.ksu.edu/
	Grazing (↑)	Human population redistribution	↑ consumption	↓ Landscape heterogeneity	1	10	
Luquillo (tropical forest)	Hurricanes (↑)	Climate change	Defoliation	Biomass transfer from canopy to soil surface	50–60	100	http://luq.lternet.edu/
	Drought (↑)	Climate change; Landuse change	Water stress; Loss of connectivity	Population and community change	1–10	100	
McMurdo Dry Valleys[3] (Antarctica)	Summer air temperatures (↓)	Ozone hole		Microbial abundance (↓)	??	$>10^4$ km^2	http://www.mcmlter.org/
	Floods	Air temperature; Melting ice	Soil wetting; Sediment to lakes		10		
Moorea Coral Reef (coral reef)	Ocean acidification (pH ↓)	Atmospheric CO_2 levels; Climate change	(↑) Mortality (↓) Growth		100–1000??	Global	http://mcr.lternet.edu/

Table 1. Continued.

Site code and ecosystem type	Major disturbances (and recent trends)*	Drivers of change	Mechanism by which disturbance effects ecosystems	Consequences	Return interval (yr)	Median size (km^2)	Website
	Coral bleaching (↑)	Climate change; Irradiance and SST		(↑) mortality	50–100	Local–Global	
North Temperate Lakes (lakes)	Invasive species (↑)	Human transport		Species change	Not cyclic	0.01–10	http://limnosun.limnology.wisc.edu/
	Eutrophication (↑)	Agricultural practices; Land disturbance		Change in nutrient cycles; Water quality; Species	Not cyclic	100–1000	
Niwot Ridge[4] (alpine tundra)	Gopher activity (no Δ)	Unknown	Burrowing	Species change	Decadal	10–100 m^2	http://culter.colorado.edu/NWT/
	Snow amount/duration (↑)	Climate change	Deposition	Species change	1	100s	
Niwot Ridge[5] (forest-tundra ecotone)	Snow amount/duration (no Δ)	Climate change	Deposition	Tree and patch distribution change	1	100–500	http://culter.colorado.edu/NWT/
	Wind (no Δ)	Climate change	Temperature stress	Tree and patch distribution change	1	1000s	
Palmer Station (Antarctic marine)	Snowfall (↑)	Sea ice retreat		Seabird mortality ↑	1	100	http://pal.lternet.edu/
	Sea ice retreat (↑)	Climate warming		Albedo change; Trophic change	1	1000	
Plum Island (coastal)	Land-use change (↑)	Human population redistribution		Hydrologic change	1	1000	http://ecosystems.mbl.edu/PIE/
	Storms (↑)	Climate change	Erosion	Shoreline change	Decadal	100s	
Santa Barbara Coastal[6] (coastal)	Large wave events (↑)	Climate change		Mortality	2	100	http://sbc.lternet.edu/
	Episodic grazing (↑)	Climate change; Fishing		Mortality	3–5	1	
Santa Barbara Coastal (terrestrial)	Fire (↑)	Human population redistribution; Warming	Combustion	Mortality	15	1	http://sbc.lternet.edu/
	Grazing (↓)	Globalization	↓ Consumption		50	100	
Sevilleta[7] (semiarid grassland)	Drought (↑)	Climate change	Water; Heat stress	Mortality	2–3	1000	http://sev.lternet.edu/
	Fire (↑)	Human population redistribution	Combustion	Mortality	8–10	.1	
Shortgrass Steppe[8] (semiarid grassland)	Plowing (↓)	Human policies	Altered landscape composition/connectivity	Species loss	>50	.2	http://sgs.cnr.colostate.edu/
	Prairie dogs (↑)	Introduction of exotic disease	Burrowing; Plant consumption	Altered species composition (flora/fauna); Soil redistribution; Change in nutrient cycling	2–20	1	

Table 1. Continued.

Site code and ecosystem type	Major disturbances (and recent trends)*	Drivers of change	Mechanism by which disturbance effects ecosystems	Consequences	Return interval (yr)	Median size (km^2)	Website
Virginia Coast Reserve (coastal)	Storms (↑)	Climate change	Erosion-accretion of sediment; Water transport	Mortality, Change in hydrologic and biogeochemical cycles; Geomorphic change	5–40	10s to 100s	http://www.vcrlter.virginia.edu/

Note: Superscripted numbers in the left column refer to sources: 1, Morrison and Swanson (1990), Garman et al. (1999); 2, Fredrickson et al. (1998), Yao et al. (2006); 3, Doran et al. (2002), Foreman et al. (2004); 4, Walker et al. (1993), Seastedt et al. (2004), Sherrod et al. (2005), Litaor et al. (2008); 5, Malanson et al. (2007); 6, Eberling et al. (1985), Harrold and Reed (1985), Reed et al. (2008); 7, Parmenter (2008); 8, Augustine et al. (2008).

*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 shown. Both naturally-occurring and anthropogenic disturbance can be listed.

about disturbance in a coherent way, (2) use this framework to provide new insights about the role of disturbance, and illustrate how it can be used to design new experiments and strategies for management when both the drivers of disturbance and system properties are changing beyond the limits of historical variability, and (3) document the measurements and characteristics that need to be reported in future studies such that quantitative cross-ecosystem syntheses can be conducted.

Putting Disturbance to Work: an Integrated Conceptual Framework

Current conceptualizations focus on disturbance types that interact with system properties, often described in terms of life history traits, to determine system response; successional processes interacting with environmental drivers result in dynamics through time that eventually may lead to a persistent state of the system (Fig. 2A) (Pickett and White 1985, Pickett et al. 2011). To support comparisons across systems, we propose that the complexities of a disturbance event need to be disaggregated into three measurable components that emerge from the literature: (1) environmental drivers and their associated characteristics that interact with (2) initial properties and spatial structure of a given ecological system to determine (3) physical and biological mechanisms that result in a change in system properties (Figs. 2B, 3). These components are similar to those proposed for anthropogenic activities (Bart and Hartman 2000). Legacies of a disturbance, including remnant abiotic and biotic properties, interact with subsequent drivers and successional processes to shape the ecological response (Foster et al. 1998). Through time, a coarse-scale quasi-equilibrial state may be reached where variation in drivers interacting with mechanisms and feedbacks internal to the system results in natural variability in ecological dynamics. At any time, a driver may be of sufficient magnitude to push a system beyond its realm of natural variability to initiate a new kind of event. Because the suite of disturbance events occurring through time comprises the disturbance regime of an ecosystem, comparisons among regimes are also facilitated.

Drivers

Four main classes of drivers influence ecological systems and, through feedbacks, can be affected by these systems in the future: (1) climate and atmospheric chemistry, such as wind, temperature, precipitation, ozone, and atmospheric deposition, (2) physical, such as soil additions or losses, (3) biotic, such as species invasions, pests, and pathogens, and (4) anthropogenic, such as land use (Fig. 3). Each driver has a set of characteristics, such as amount, duration, and timing, which can be measured and compared across events and ecosystems. Note that similar criteria are commonly used to classify disturbance types (Table 1). However, unmea-

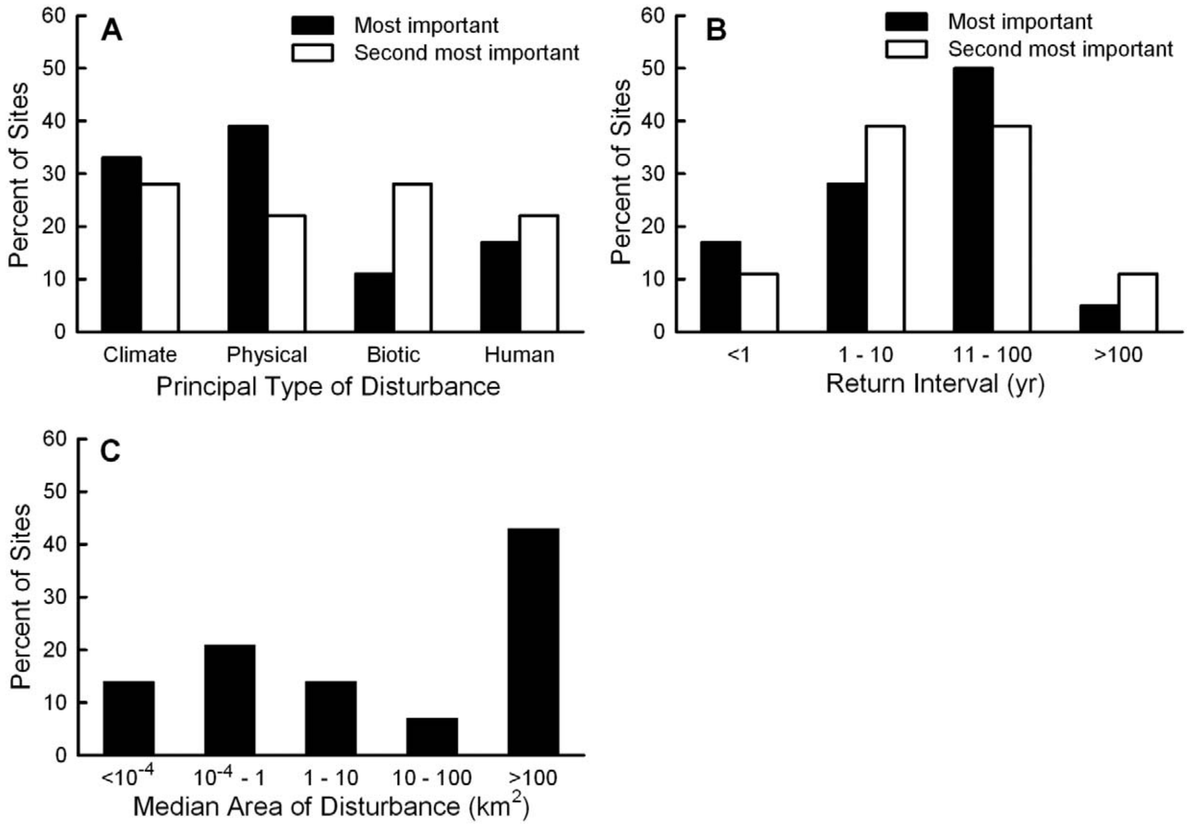


Fig. 1. Spectrum of disturbance across ecosystems. Data from ecosystems represented by 26 sites in the US Long-Term Ecological Research (LTER) network were used to qualitatively compare disturbance regimes (⟨http://www.ecotrends.info⟩). Additional information is provided in Table 1. (A) Climate (e.g., severe storms) and climate-related physical disturbances (e.g., fire) were viewed as the predominant disturbance at most sites; biotic (e.g., insect outbreaks) and anthropogenic disturbance (e.g., eutrophication) were also important at many sites. (B) The most important 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 (Peters 2010). In some ecosystems, frequent disturbances ($<$10 yr return interval) were particularly important. (C) There was a bimodal distribution in size of the most important disturbances, with most being either quite large ($>$100 km^2) or relatively small ($<$1 km^2).

sured variation in drivers within a disturbance type often precludes quantitative comparisons across sites and ecosystems except at the most general level of relative importance (Fig. 1A).

Characteristics of drivers vary from place to place and from time to time, and can interact to generate nonlinear ecological dynamics (Frelich and Reich 1999). Climatic drivers, for instance, are modified in intensity and duration by such processes as global and regional atmospheric circulation patterns, or shifts in storm tracks. Likewise, biotic drivers can be altered by species invasions and population cycles. Multiple drivers can also interact, either synchronously or sequentially (Allen 2007). Biotic disturbances can have direct effects on physical processes, such as animal activity that creates bioturbation in soils (Yoo et al. 2005) or sediments (Moore 2006). Climate influences invasive species and insect outbreaks, and often interacts with properties of the biota, such as insect population size and host species identity (Lovett et al. 2006, Raffa et al. 2008, Bentz et al. 2010). Because drivers are common across multiple disturbances and ecosystem types, this approach provides a direct link to studies of global change (IPCC 2007).

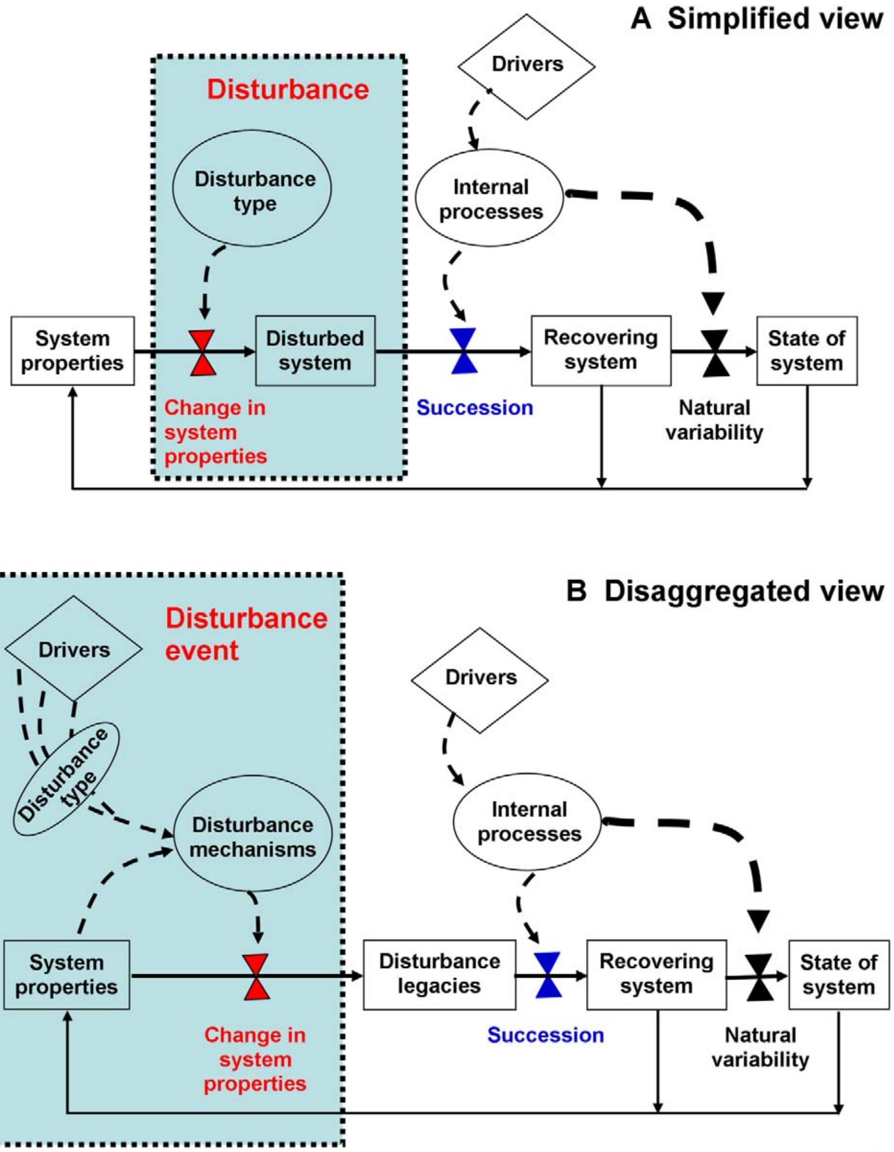
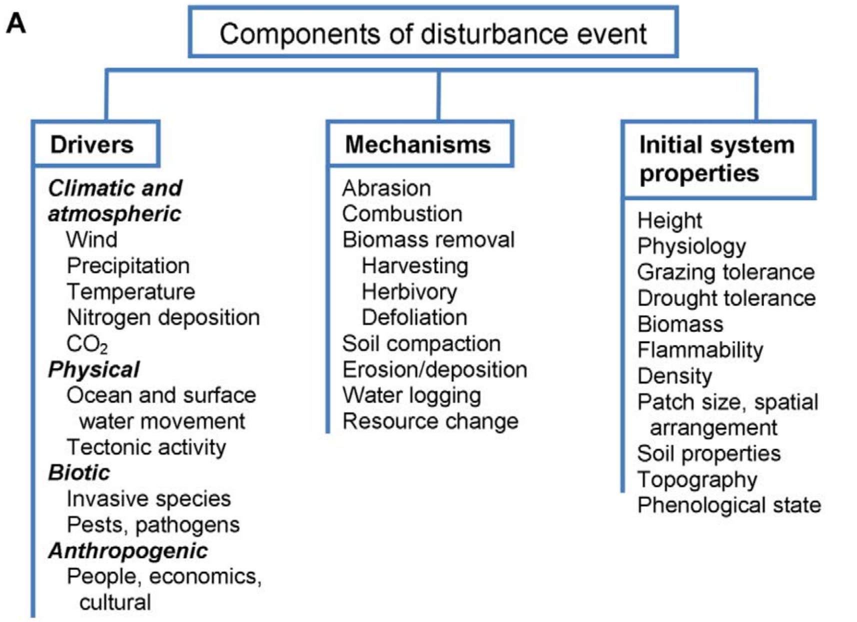


Fig. 2. Simplified and integrated views of disturbance. In both views, a disturbance regime consists of multiple events of a single or multiple types that influence an ecological system through time. The two views differ in their focus on disturbance (in blue box), either as an event or a type. (A) Simplified view of disturbance focuses on disturbance types, including spatial and temporal characteristics, interacting with initial system properties to result in a disturbed state with consequences for ecosystem change followed by future states through time. Comparisons within and across disturbance types typically focus on properties of the disturbed state which confound the multiple drivers, initial system properties, and mechanisms of effect. (B) Disaggregated view of disturbance based on an event consisting of three measurable components: environmental drivers, initial system properties, and physical and biological mechanisms of effect. These components interact to result in a disturbed state with legacies: abiotic and biotic properties that interact with subsequent drivers and successional processes to influence system response. Through time, a quasi-equilibrial state can be reached where variation in drivers interacting with biotic processes and feedbacks internal to the system can result in natural variability in ecological dynamics. At any time, a driver can push the system beyond its realm of natural variability to initiate a new event. A disturbance type, such as wildfire, consists of multiple drivers and mechanisms.



B

Driver	Disturbance mechanism								
	Abra	Comb	Harv	Herb	Defo	Comp	Ero/dep	Water logging	Resource change
Wind	X	X			X		X		X
PPT		X					X	X	X
Temp		X		X	X				
N-dep				X	X				X
CO_2									X
Physical						X	X	X	X
Biota				X	X				X
People	X	X		X	X	X	X	X	X

Abra: abrasion; Comb: combustion; Harv: harvest
Herb: herbivory; Defo: defoliation; Comp: compaction
Ero/dep: erosion/deposition; PPT: precipitation; Temp: temperature
N-dep: nitrogen deposition

Fig. 3. Components of a disturbance event. (A) A disturbance event consists of environmental drivers, mechanisms of effect, and initial 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. (B) Each driver has a suite of potential mechanisms, and similar mechanisms occur with more than one driver.

Initial system properties

System properties of importance are those that either make possible or constrain the initiation and spread of a disturbance (Fig. 3A). These properties include both abiotic site conditions and properties of the biota (Halpern 1989, Rydgren et al. 2004, Bruelheide and Luginbühl 2009). System properties can be defined at different spatial scales or levels of organization in a biological hierarchy (Pickett et al. 1989). Because we are interested in comparing ecosystems, we focus on properties that have consequences for dynamics following disturbance.

Variation in initial system properties can cause effects of drivers to differ among events (Minshall 2003, Turner 2010). The importance of these system properties can also vary as a disturbance spreads through time and space (Peters et al. 2004). Seemingly simple system properties can lead to complexity in disturbance spread. For example, fire that begins at an individual tree can either ignite that tree, or the fire can go out (Allen 2007). If the tree burns, fire can spread to other trees through flammable herbaceous vegetation 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. Fire burning with extremely high intensity can show little variation in effect with system properties such as topographic position (Moritz 1997). Similar complexities may exist in other processes, for example in systems experiencing disease as disturbance (McCallum 2008).

Disturbance mechanisms

Disturbance mechanisms may be physical such as combustion, erosion-deposition, and abrasion, or biological such as foliage removal by consumers (Fig. 3A) (Swanson and Major 2005). A single disturbance type can involve one or more mechanisms (Fig. 3B), one of which may dominate the response. For example, under some conditions, a drought results in high plant mortality as a result of extreme water stress (McDowell et al. 2008) whereas in other conditions mortality results from burial by sand: as plant cover is reduced, wind erosion and deposition become the dominant process on erosive dryland soils (Okin et al. 2009). Similarly, the same mechanism can be associated with a range of disturbance types (Fig. 3B). Defoliation, for example, is a mechanism that can result from windstorms, wildfire, outbreaks of insects, or drought. The realization of a mechanism is a measure of the severity of an event that depends on characteristics of the drivers and system properties. Severity is often expressed as a change in biomass, nutrients, or soil. For example, the process of combustion is common to all wildfires, but the amount of biomass lost in a given fire depends on the fuel load of the system and the weather. Thus, disaggregating a disturbance into its mechanisms opens the opportunity for experimentation, such as testing species response to gradients of disturbance severity for different mechanisms. Different mechanisms can also play out as the dominant process shaping ecosystem dynamics, even for the same disturbance type.

Legacies

Initial system properties interact with drivers and mechanisms to result in legacies of the event (Fig. 2B). In the fire example above, legacies are surviving individual herbaceous plants and trees, and soil properties, such as amount of soil organic matter and water repellency. System properties and timing of a disturbance event can influence severity of effect and the resulting legacy (Cooper-Ellis et al. 1999). Recruits from legacy plants can be important colonizers that influence short- and long-term outcomes of a disturbance (Myster and Pickett 1990, Elmqvist et al. 2001). These legacy effects can be relatively short-term, transitional states of a system that persist for days or weeks, such as initial response to wildfire in forests. These effects can also persist through multiple disturbance events, such as the effects of drought in desert grasslands that lead to greater susceptibility of the system to additional disturbance (Herbel et al. 1972, Drewa and Havstad 2001, Rocha and Goulden 2010).

Future states

System responses through various transitional stages depend on legacies interacting with subsequent drivers and successional processes (Fig. 2B). Time lags, thresholds, and differential response rates can be related to both positive and negative feedbacks among the biota, soils, and drivers (Viles et al. 2010). Through time, the importance of legacies can diminish (Rydgren et al. 2004, Bruelheide and Luginbühl 2009), and mechanisms and feedbacks internal to the post-disturbance system can become increasingly important. Eventually, a quasi-equilibrial state may be reached where natural variability in ecological dynamics reflects variation in drivers (e.g., Bernhardt and Willard 2009). We use the term "quasi-equilibrial state" to refer to a persistent assemblage of species and associated soil properties, although other levels in the biological hierarchy may also be important (Pickett et al. 1989). This quasi-equilibrial state may or may not reflect the initial state of the system. Recovery to a previous state through succession is one possible pathway (Pickett et al. 2011), 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 et al. 2010).

New Insights to Understanding Dynamics across Ecosystem Types

Separating disturbance into its components provides a powerful way to both understand variability in ecological responses to past disturbance and to predict future dynamics under global change. In this section, we show how the disaggregation of common disturbance types into their component features (Fig. 2B) can provide new insights into multi-system dynamics.

Disaggregating a hurricane disturbance

A hurricane is a disturbance type that combines multiple drivers, each with multiple mechanisms, interacting with spatially heterogeneous vegetation to generate complex dynamics in time and space. Because hurricanes are destructive forces that are difficult to predict far in advance, this framework (Fig. 2B) can be used to identify and manage for key features of drivers or system properties to either limit negative effects or promote ecological responses following a hurricane.

Comparisons of hurricanes often use meteorological indices of storm 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/⟩) (Lugo 2008), or they use visible effects on the vegetation to estimate strength (e.g., Stanturf et al. 2007). However, even a single hurricane can have effects that are either spatially heterogeneous in ways that are not related to a particular driver (Fig. 4A) or 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 ecosystems (Lugo 2008). Based on the framework (Fig. 2B), measures of the dominant drivers (wind, rainfall amount and intensity) and spatial structure of the land surface or vegetation 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, initial ecological properties, and mechanisms of hurricane effects in different ecosystem types (Hopkinson et al. 2008).

In addition, hurricanes can generate a cascade of disturbance effects that can be accounted for in this framework. For example, landslides are a secondary disturbance type often associated with hurricanes. In hurricanes with high rainfall intensity and/or in locations with low tree cover, large amounts of water saturate the soil and reduce soil strength, making the system vulnerable to landslides in mountainous areas (Fig. 4B). In this example, rain is the primary driver which interacts with system properties of slope, soil type, and tree cover to result in the mechanism of massive soil erosion and landslides. Water logging of soils in locations without landslides can also have deleterious effects due to chemical changes such as nutrient leaching and physiological changes, including anaerobic soil conditions, both of which alter post-disturbance resource availability (Heartsill-Scalley et al. 2007). In addition, variation in wind intensity during a hurricane can be independent of rainfall intensity. Wind intensity can influence defoliation patterns that interact spatially with the physico-chemical processes and consequences associated with rainfall. Disaggregating and measuring the individual components of these multiple, inter-related drivers and mechanisms would allow direct comparisons among hurricane events that would be valuable in the future under projected changes in hurricane intensity

Fig. 4. Hurricane effects in a forest can be either spatially homogeneous or heterogeneous as a result of interactions between drivers and initial system properties. Forest in Puerto Rico one week after Hurricane Hugo (18 September 1989) shows how wind and rainfall affect forests independently and differently (Photos by A. E. Lugo). (A) At broad scales, the role of topography (aspect) in creating a disturbance legacy is demonstrated by patchiness of brown and green canopies defoliated by wind. (B) At finer scales, heavy rains can trigger landslides with overwhelming effects on forest legacies.

(IPCC 2007).

Wildfire: different outcomes in similar or different ecosystems

Wildfire is a disturbance common to many ecosystems, yet variability in drivers and initial system properties often dictate its variable effects in different ecological systems, and even among wildfires in the same system (Fig. 2B). Temperature, precipitation, wind speed and direction are the primary climate drivers of a wildfire regime. These drivers influence other drivers, such as relative humidity or vapor pressure deficit, thunderstorm occurrence, and lightning frequency as well as fuel moisture and spatial distribution of the vegetation to determine rates and patterns of fire spread. A number of primary and secondary mechanisms are involved that include combustion, but also defoliation, erosion and deposition, soil compaction, and resource inputs, particularly nitrogen.

The relative importance of fire based on return interval varies across terrestrial ecosystems, and depends in large part on interactions between long-term climate and vegetation type (Table 1). Fire return intervals are shortest for mesic grasslands (Konza; 5–10 y) and dry forests (Bonanza Creek; 80 y) compared with deserts (Jornada; 100 y) and perennially moist forests (H. J Andrews; centuries). The effectiveness of climate in fostering a wildfire event ultimately depends on initial 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, desert grasslands, despite having a hot, dry, windy climate conducive to fire spread, typically have insufficient fuel to carry a fire (Drewa et al. 2001). 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 pre-fire system properties results in high spatial variability in fire spread in dry grasslands and wet forests compared to more complete burns with high-intensity fires in mesic grasslands and dry forests (Fig. 5). Examining effects of wildfire as a disturbance type across ecosystems without measuring ecological properties and characteristics of individual drivers, is limited to qualitative comparisons, and is insufficient for quantitative predictions.

In some systems, trends in drivers and changes in management are needed in addition to information about historical disturbance regimes. For example, in mesic tallgrass prairie, hot and dry conditions during the summer, frequent thunderstorms, and abundance of fine fuels in 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 fire or to rapidly colonize burned sites. Recent warming has led to drier conditions and to wildfires that consume more of the surface peat layer, producing a seedbed that is more favorable to deciduous trees compared to conifers, and initiating a new successional trajectory to deciduous forest (Johnstone et al. 2010).

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, to become more difficult to suppress, or both (IPCC 2007). Rare fires can have huge effects in systems without a fire history, such as 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 (IPCC 2007).

Clearcutting: similar outcomes in different ecosystems

Removal of trees by logging shows how similar mechanisms associated with the same driver can overwhelm contrasts in initial system properties to result in similar dynamics across different ecosystems. Studies of effects of clearcut logging in forests across the U.S. have revealed

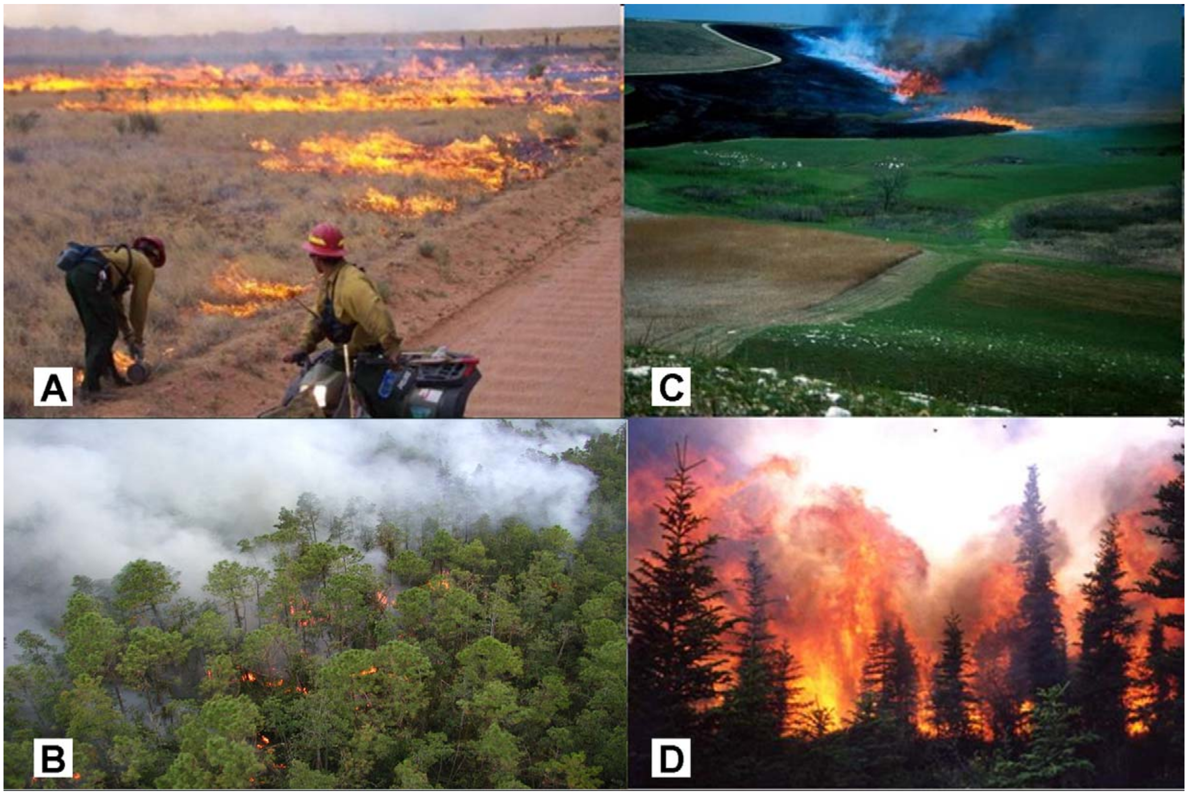


Fig. 5. Effects of wildfire often depend on initial system properties: fires are patchily distributed in (A) dry grasslands with low fuel loads (Photo from ⟨http://www.sev.lternet.edu⟩) and (B) wet forests with vegetation high in moisture content (Photo by R. D. Ottmar). Fires burn more completely with high intensity in (C) mesic grasslands (Photo by A. K. Knapp) and (D) dry boreal forests (Photo by L. DeWilde).

surprisingly similar patterns of streamflow response to forest removal and regrowth that can be explained using the framework (Fig. 2B).

Forest types in different parts of the U.S. 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: late summer flow of water in streams increases in response to clearcutting for ca. 8 years, and then flow decreases toward that expected from the reference watershed based on pretreatment conditions (Fig. 6; Jones and Post 2004). The similarity in response of summer flows to clearcutting may reflect a common suite of biophysical mechanisms in these temperate systems: vegetation removal initially reduces evapotranspiration water loss to the atmosphere, thus increasing stream flow, and then regrowth of vegetation increases water flux to the atmosphere and streamflow diminishes to pre-cut levels, regardless of local site conditions.

Desertification: scale-dependent outcomes

Conversion from perennial grasslands to dominance by xerophytic woody plants shows how outcomes following disturbance are scale-dependent, and governed by climatic and anthropogenic drivers at broad scales and by initial system properties interacting with drivers at plant to landscape scales. Because environmental degradation associated with this "desertification" influences ecosystem services to an estimated 250 million people globally (MEA 2005, Reynolds

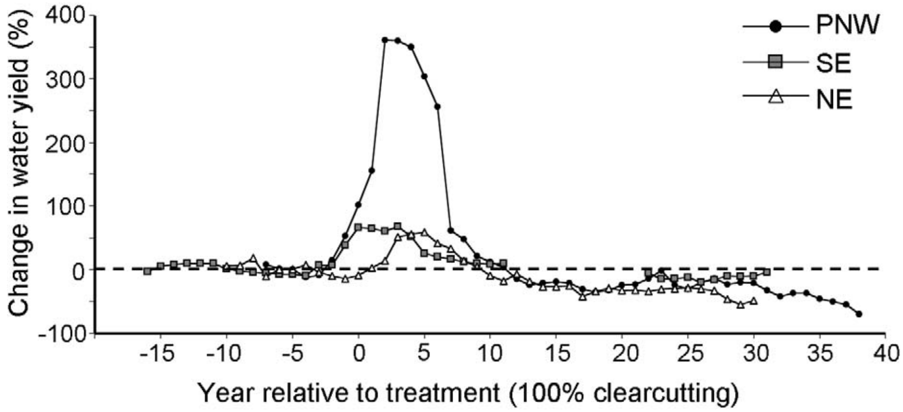


Fig. 6. Effects of clearcutting of trees on water yield for three forest types in different parts of the U.S.: PNW (Pacific Northwest: 460-yr-old evergreen conifer forest; HJ Andrews Experimental Forest), SE (Southeast: 36-yr-old deciduous forest at the Coweeta Experimental Forest), and NE (Northeast: 50-yr-old mixed deciduous forest at the Hubbard Brook Experimental Forest). Five-year running mean of percentage changes in water yield relative to the pre-treatment period in clearcut versus control watersheds for the minimum flow period (September 1–15). Adapted from Jones and Post (2004).

et al. 2007), a better understanding of the drivers of these dynamics is critically needed for the diversity of systems potentially affected.

The traditional view of desertification is that drought and overgrazing by livestock are two types of disturbance with similar mechanisms that affect grassland-to-woody plant conversion in arid and semiarid ecosystems globally (Fig. 7A) (Schlesinger et al. 1990, Archer 1994). However, this view is insufficient to either determine the levels of grazing and degree of drought required for a shift in lifeform dominance or to explain landscape-scale variation in woody plant expansion and dominance. The framework that identifies a suite of drivers and mechanisms associated with each disturbance type (Fig. 2B) provides insights that can be used to mitigate effects of drought or to modify livestock management to maintain current grasslands and minimize the consequences of desertification.

For example, in the American Southwest, human decisions led to overgrazing by livestock in the mid to late 1800s and early 1900s that resulted in high grass mortality and low herbaceous cover, and a system vulnerable to high winds, high temperatures, and low rainfall during the extended droughts in the 1890s, 1900s, 1910s, and again in the 1930s and 1950s (Herbel and Gibbens 1996, Fredrickson et al. 1998) (Fig. 7B). Unpalatable shrubs resistant to grazing and dispersed by livestock expanded during and following drought to result in a broad-scale conversion of grasslands to shrublands throughout the Southwest that has continued to present day (Buffington and Herbel 1965, Gibbens et al. 2005).

However, landscape-scale variation in woody plant invasion is more difficult to explain, and involves multiple drivers and their mechanisms that are variable through time and space (Fig. 7B), and interact 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 effects 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 are possible that require knowl-

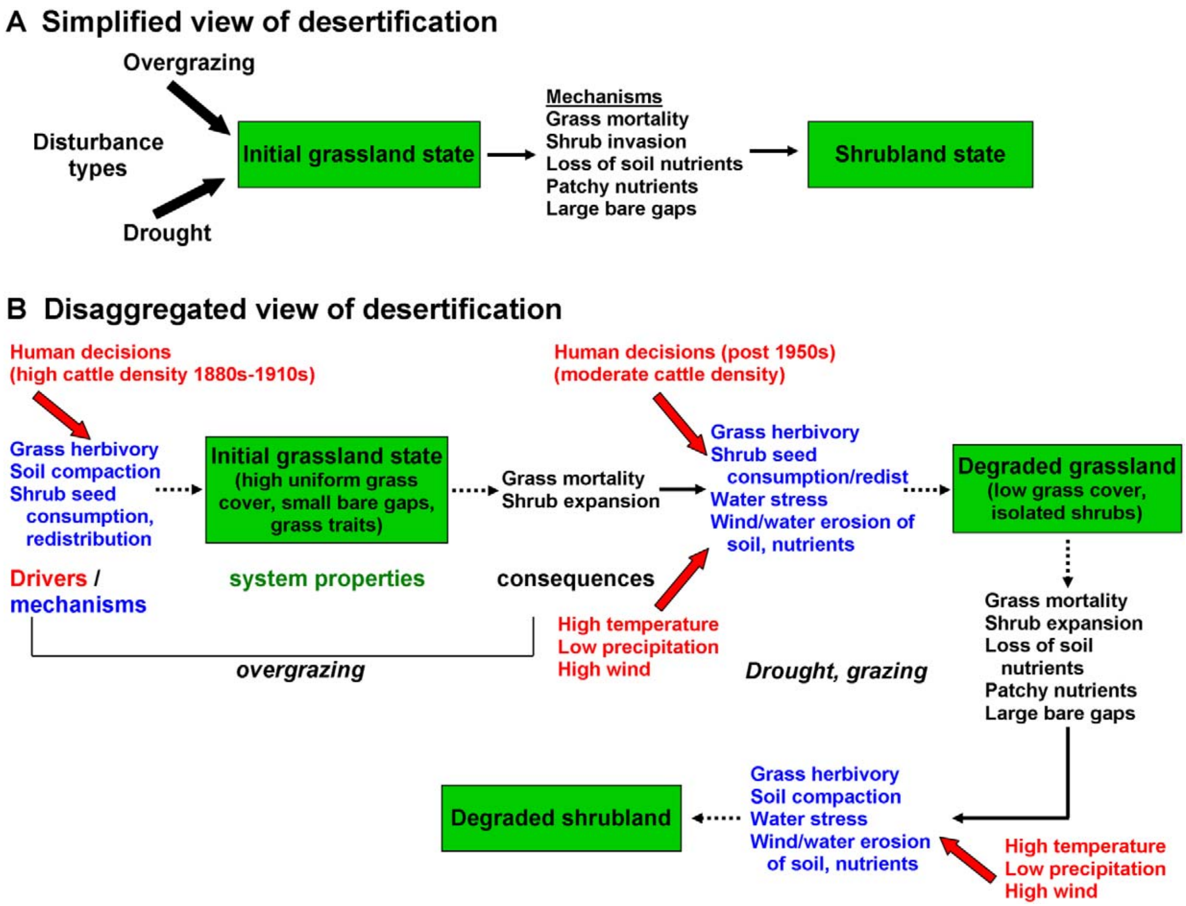


Fig. 7. Views of disturbance in grassland-shrubland transitions leading to desertification. (A) Traditional view of overgrazing and drought as disturbance types that shift grasslands to shrublands in arid and semiarid ecosystems. (B) Disaggregated view in which each disturbance has multiple drivers (red text) that vary through time and space to interact with mechanisms (blue text) and system properties (black text in boxes) to result in a shift to shrublands though time. This view explicitly accounts for each driver, mechanism, and system property as interacting factors in a state change.

edge of drivers, mechanisms, and initial system properties. In this case, similar mechanisms are operating, but they are overwhelmed by effects of fine-scale variation in system properties interacting with multiple drivers.

Climate change and wildfire: threshold responses depend on drivers and system properties

Directional changes in climatic drivers through time can trigger threshold responses to other drivers with consequences for ecosystem dynamics. For example in the Arctic, warming associated with climate change is changing the frequency of wildfires. Historically, wildfires occurred infrequently in these systems: only 3% of Alaskan tundra burned between 1950 and 2005 (Higuera et al. 2008). Low fire frequency is attributed to infrequent ignition sources, low fuel load, and high fuel moisture. However, these conditions are changing as increasing air temperature is leading to increases in lightning strikes, productivity, and aridity (Higuera et al. 2008). These factors influence the initiation and spread of wildfires, and interact with additional drivers of wildfire such as wind to result in a suite of mechanisms of effect. Consequently, climate change may trigger threshold responses in the fire regime that are currently difficult to

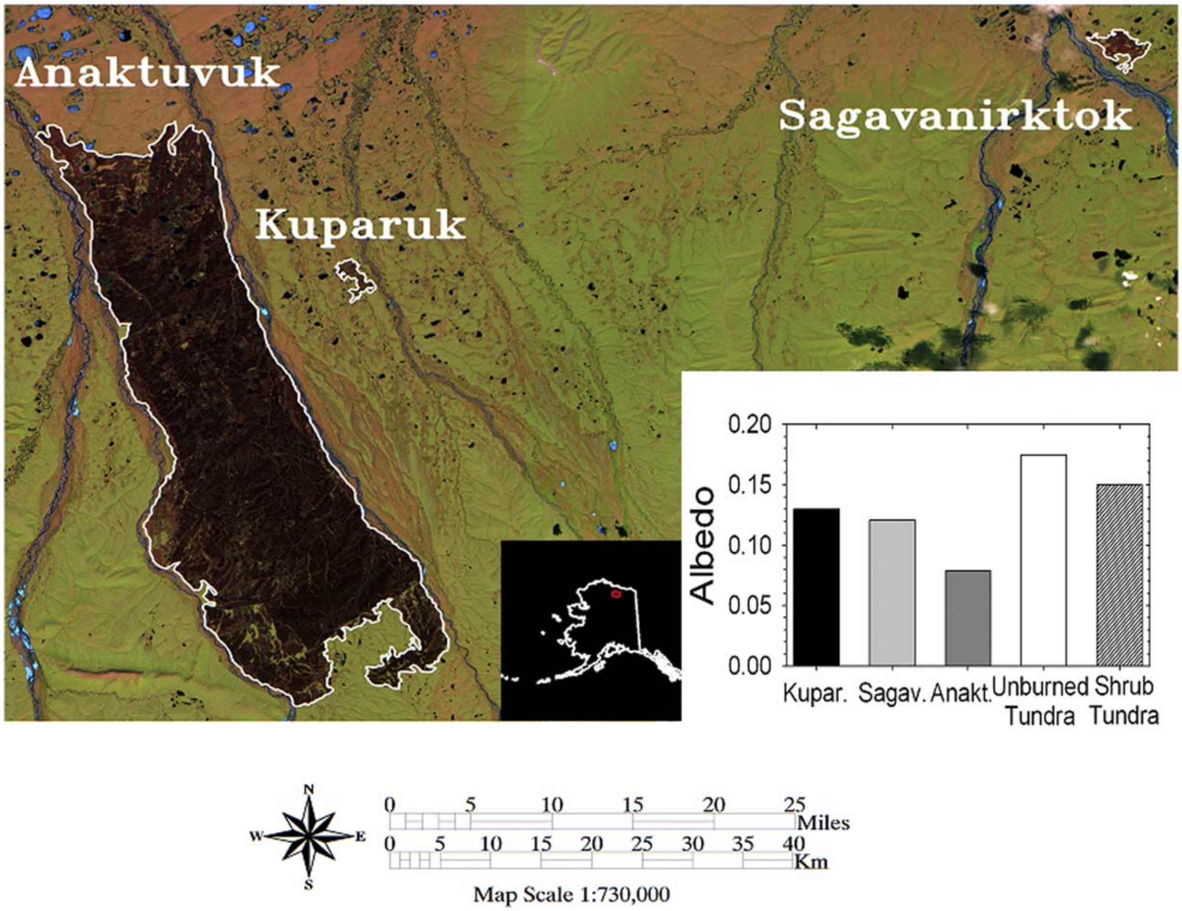


Fig. 8. Environmental conditions and ecological consequences of three 2007 summer wildfires on the North Slope of Alaska. White lines represent fire perimeters derived from two false color Landsat images in July, 2008. (inset) Surface albedo for each fire and unburned tundra calculated from a 1 km^2 MODIS product on July 3, 2008; albedo for shrub tundra from Chapin et al. (2005). Kupar = Kuparuk; Sagav = Sagavanirktok, Anakt = Anaktuvuk.

interpret or predict unless the drivers, mechanisms, and initial system properties are distinguished and quantified (Dale et al. 2001) (Fig. 2B).

Conditions during the 2007 summer season demonstrate the importance of thresholds in regulating Arctic fire activity. This summer was one of the warmest, driest, and most lightning-active years in the previous two decades. These conditions created three lightning-induced fires that differed in extent of area burned and post-fire legacies (Fig. 8). The extent of area burned depended on thresholds in pre-fire system properties related to fire timing during the summer and vegetation composition. Vegetation cover was highest next to the ignition source of the large Anaktuvuk River fire and lowest next to the two smaller fires, suggesting the importance of variability in fuel loads in determining fire spread. High vegetation moisture content and low vegetation cover likely resulted in the extinguishing of the Kuparuk fire by mid-August to result in a small burned area whereas high vegetation cover allowed the Anaktuvuk River fire to persist and burn a much larger area. The Sagavanirktok fire started in early September and burned mostly during the period of high winds and low relative humidity to result in a small burned area.

Interactions of drivers with ecosystem properties produced different consequences that may influence the future state of the Arctic system (Rocha and Shaver 2010). High-severity fire, such as the large Anaktuvuk fire, may favor the establishment of low-albedo shrub species rather than more reflective tussock sedges (Racine et al. 2004) (Fig. 8). Increased shrub abundance following fire would reduce albedo and increase fuel load to result in a positive feedback to climate warming and future fires (Rocha and Shaver 2009).

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 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). More widespread use of the research strategy of disaggregating disturbance into measurable drivers, mechanisms, and initial system properties would provide major advances in understanding disturbance-ecosystem interactions. This strategy would facilitate comparing events among ecosystems of the world, particularly when conditions fall outside the historical range of variability.

Management implications

Future land management decisions can benefit from this integrated framework. Management decisions are often made at scales that encompass numerous ecosystems having multiple states that are potentially subject to many different disturbance events (Dale et al. 1998). This framework can be used to identify commonalities among disturbance events and ecosystems, and to highlight where policy and implementation have the potential to mitigate undesired consequences of disturbance to keep ecosystems from moving to an undesired state. Under some circumstances, changes in land management can lead to a system with more resilient ecosystem characteristics, such as a reduction in livestock grazing that increases perennial grass cover, thereby reducing vulnerabilities to disturbance by wind erosion (Okin et al. 2009). Management can also focus on preserving or restoring system properties that increase resilience to disturbance mechanisms or to projected occurrence of novel disturbances (Seastedt et al. 2008). Managing for ecosystem resilience includes strategies that facilitate or emulate natural disturbances regimes with consequences that provide desired system properties (e.g., Baer et al. 2002). In some instances, such as warming of the Arctic tundra with altered fire regimes, there are no clear opportunities for managing system properties to minimize disturbance effects; thus, society is left with post hoc interventions, such as fire suppression or acceptance of the novel disturbance regime and resulting ecosystem properties (Suding et al. 2004).

Cross-site experiments

The framework described here guides cross-system studies in the drivers, mechanisms, and system properties to be compared, manipulated, and measured 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 suggests that experimental manipulations of disturbance mechanisms may provide the strongest comparative approach across ecosystems. 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 ecosystems.

Operationalizing Cross-System Comparisons

Conducting syntheses of disturbance effects and system response across diverse ecosystems will require standardized attributes and units of measures to be reported for all future studies. Based on this framework (Fig. 2B), these attributes and measurements are directly related to drivers and initial system properties associated with the mechanisms operating in each event. At

Table 2. Key attributes to be measured and reported pre- and post-event as part of disturbance studies to allow future synthesis activities.

Disturbance event	Driver	System property
Wildfire	Precipitation Temperature Wind speed Relative humidity Fire intensity	Biomass Litter Soil moisture Soil nitrogen
Drought	Precipitation Temperature Wind speed Relative humidity	Biomass Litter Soil moisture Soil temperature
Overgrazing	Precipitation Temperature Wind speed Relative humidity Stocking rate	Biomass defoliation ANPP defoliation Soil compaction Soil nitrogen (fertilization)

a minimum, the magnitude and timing of each driver involved in the disturbance effect should be defined (Table 2). For most disturbance events, this list will include climatic drivers recorded annually (precipitation, temperature, wind speed, relative humidity), although the drivers should be recorded at the finest resolution necessary for predicting ecological responses and for the duration of the event. System properties measured prior to the event should be selected to represent both the expected influence of the disturbance event on the state variables of interest (e.g., vegetation, soils, animals, microbes, nutrients), and the projected responses of interest as the abiotic and biotic legacies. Examples of the attributes needed for several disturbance types are shown in Table 2.

Redefining Disturbance

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 integrated conceptual framework (Fig. 2B), 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 disturbance to the times between events or to the length of time it takes for the system to respond. 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 integrated 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. Furthermore, these measures of time need to be reported in published studies.

The second point indicated by this integrated 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 this framework (Fig. 2B), a disruption is an alteration of the system that removes or adds structural components through the effects of drivers and mechanisms interacting with initial system properties to result in outcomes that differ from the reference state. The magnitude of change from the reference state is a measurable attribute that can be reported as part of a study.

Conclusions

Using examples from long-term research, the integrated framework presented here illustrates that similar disturbance events can have similar or different effects on different ecosystems because they have similar or different interactions among drivers, mechanisms, and system characteristics. An explicit consideration and measurement of drivers and mechanisms provides opportunities to design cross-system experiments to test understanding, and to devise management interventions to minimize undesirable outcomes. A relatively small list of key attributes should be measured and reported for all disturbance studies to promote cross-system synthesis activities. 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.

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