

Long-Term Ecological Research and Evolving Frameworks of Disturbance Ecology

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Detecting and understanding disturbance is a challenge in ecology that has grown more critical with global environmental change and the emergence of research on social–ecological systems. We identify three areas of research need: developing a flexible framework that incorporates feedback loops between social and ecological systems, anticipating whether a disturbance will change vulnerability to other environmental drivers, and incorporating changes in system sensitivity to disturbance in the face of global changes in environmental drivers. In the present article, we review how discoveries from the US Long Term Ecological Research (LTER) Network have influenced theoretical paradigms in disturbance ecology, and we refine a framework for describing social–ecological disturbance that addresses these three challenges. By operationalizing this framework for seven LTER sites spanning distinct biomes, we show how disturbance can maintain or alter ecosystem state, drive spatial patterns at landscape scales, influence social–ecological interactions, and cause divergent outcomes depending on other environmental changes.

Keywords: disturbance, LTER, ecological theory, social–ecological studies, ecological research networks

Ecologists have long recognized that disturbances can drive ecological system dynamics (Pickett and White 1985, Peters et al. 2011, Grimm et al. 2017). As a result, disturbance, defined as “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett and White 1985), is a familiar component of explanatory and predictive models in ecology (e.g., Lucash et al. 2018). However, several challenges remain for the ecological study of disturbance. First, the general definition above requires detailed specification to translate to particular models and experiments. Specifying disturbance processes in nature is difficult because responses to disturbance events occur across interacting levels of ecological organization and at varying spatial and temporal scales (Pickett et al. 1999). Deriving theoretical and empirical generality from such complex processes can be aided by flexible conceptual frameworks that detail process elements and their connections. Second, the term disturbance is often associated with negative ecological responses or events that increase vulnerability to other global change drivers, particularly in human-dominated ecosystems. Disturbance can reduce ecosystem vulnerability to other environmental changes through information and material legacies

(Johnstone et al. 2016), which is modifying how resilience is conceptualized in disturbance ecology. Understanding how or why disturbances might enhance or reduce ecosystem vulnerability is an important area of inquiry as ecosystems are faced with rapid-paced environmental changes. Third, because disturbance is the interaction between an event and a particular ecological system, the effect of a disturbance can be modified as systems and their environments change (i.e., feedback loops). Feedback loops between these system components—event and ecosystem—are important. To document and understand event–ecosystem feedback loops requires persistent research to quantify changes in type, intensity, or frequency of drivers of disturbance as well as temporal changes in the sensitivity of systems to disturbance (Ratajczak et al. 2018). Across many ecosystems, the drivers of disturbance and the resilience or resistance of systems to disturbance are shifting or projected to shift because of global change (e.g., Dale et al. 2001, Turner et al. 2016, Ummenhofer and Meehl 2017). Fluctuations and directional changes in climate and atmospheric chemistry, and the extent and intensity of urbanization, agriculture, or other resource uses suggest that addressing the three challenges of studying disturbance will be increasingly necessary to guide expectations of how ecosystems may change in the future

(Franklin et al. 2016) and to manage for resilience (Sasaki et al. 2015).

Long-term ecological research (LTER) is uniquely positioned to address the three challenges of disturbance ecology (Likens 1989). Long-term studies can capture spatiotemporal variability in ecosystem dynamics at many scales, can measure the effects of potentially multiple disturbances on that variability, and can observe infrequent events. Long-term studies also often unite field observations, manipulative experiments, historical reconstruction, modeling, and cross-site comparisons to inform mechanisms of social-ecological response to disturbance (Turner et al. 2003). The US Long Term Ecological Research Network currently consists of 28 sites representing a wide variety of ecosystems, including temperate and tropical forests; grasslands, shrublands, and deserts; alpine, arctic, and Antarctic ecosystems; freshwater lakes and streams; urban ecosystems; and coastal and marine ecosystems. This distributed network of place-based, long-term studies allows for comparisons of disturbance types and ecological responses to promote a general understanding of disturbance and its outcomes (e.g., Boose et al. 1994, Gholz et al. 2016, Kranabetter et al. 2016). The US LTER Network has contributed to the development of disturbance ecology theory as a tool for comparing long-term dynamics across different ecosystem types exposed to a variety of disturbance types (Peters et al. 2011, Grimm et al. 2017). However, a common framework is needed to guide interpretation of disturbance as a process across diverse ecosystems and disturbance types.

This article approaches the aforementioned challenges by three paths. First, we review recent developments in the literature examining how LTER research, both within and among research sites, has advanced the understanding of disturbance as a process. Second, building on existing disturbance frameworks (Peters et al. 2011, Grimm et al. 2017), we articulate a refined theoretical social-ecological framework that explicitly links interactions among social and ecological responses and their feedback loops to disturbance. Such a framework for understanding complex, path-dependent, and layered disturbances is an important step toward improving the study of disturbance and the comparison of disturbance across systems. Third, building on the earlier review by Turner and colleagues (2003), we apply this framework to seven LTER sites representing diverse social-ecological ecosystems to provide insights on how disturbance modifies and is influenced by dynamic interactions between social and ecological responses occurring over decadal or longer timescales.

Long-term ecological research: Synthesis of social-ecological disturbance

Despite a recognition that disturbance plays an important role in the long-term dynamics of ecosystems, we lack a theoretical framework to guide expectations for how individual and cumulative disturbance events and types interact to produce observed patterns and processes in social-ecological

systems. Turner (2010) synthesized research on disturbance with an emphasis on fundamental contributions to contemporary theory in landscape and ecosystem ecology. Her analysis pointed out knowledge gaps that could be addressed through long-term ecological research, including the need to quantify the role of disturbance in catalyzing rapid ecological change, evaluate if and how multiple disturbances interact synergistically or antagonistically through time, address relationships between disturbance and society, and determine the role of feedback loops among disturbance and other global drivers of environmental change. This last recommendation is particularly pressing, because global change is creating new spatial patterns, novel trajectories of ecosystem change (Kominoski et al. 2018), and interactions among environmental drivers that lead to altered disturbance regimes (Johnstone et al. 2016, Ummenhofer and Meehl 2017, Peters et al. 2018).

A conceptual framework that depicts responses of social and ecological systems to disturbance, and their interactions and feedback loops to disturbance drivers may guide interpretation of the process of disturbance in ways that address these four recommendations for advancing disturbance theory. We focused on long-term observational and experimental research because of its potential to generate data on ecosystem processes occurring on multiple timescales that capture changing drivers of variability and trajectories of ecosystem change, including nonlinear or abrupt responses to disturbance (e.g., Bestelmeyer et al. 2011, Kominoski et al. 2018, Ratajczak et al. 2018). Moreover, long-term ecological studies can uniquely address how disturbance events may have different consequences depending on prior conditions and legacies (Moorhead et al. 1999, Foster et al. 2003, Kulakowski et al. 2013, Johnstone et al. 2016). Long-term studies of disturbance provided insight into the effects of events that operate on shorter (pulse) and longer (press) timescales (Collins et al. 2011), and how disturbance legacies integrate spatiotemporal scales (Pickett et al. 1999), driving the direction and magnitude of change in ecological systems (Grimm and Fisher 1989). In addition to driving integrative place-based research, long-term collection of core data sets across diverse ecosystems enables synthesis of disturbance via cross-site comparisons of disturbance effects on structural and functional changes that support ecosystem services, how disturbance events propagate differently through hierarchical levels of ecological organization (Pickett et al. 1989), and the effects of disturbance events as a function of existing system properties (e.g., physical structure, biological productivity, extent of land use change), and the connectivity of system properties to one another (e.g., biological sensitivity to abiotic change, ecosystem service dependency). Long-term, place-based data provide important insight into the disturbance process particularly when coupled with large-scale experimental manipulations of disturbance (Knapp et al. 2012) and subsequent recovery (e.g., McGlathery et al. 2012). The need to advance studies of human interactions with nonlinear

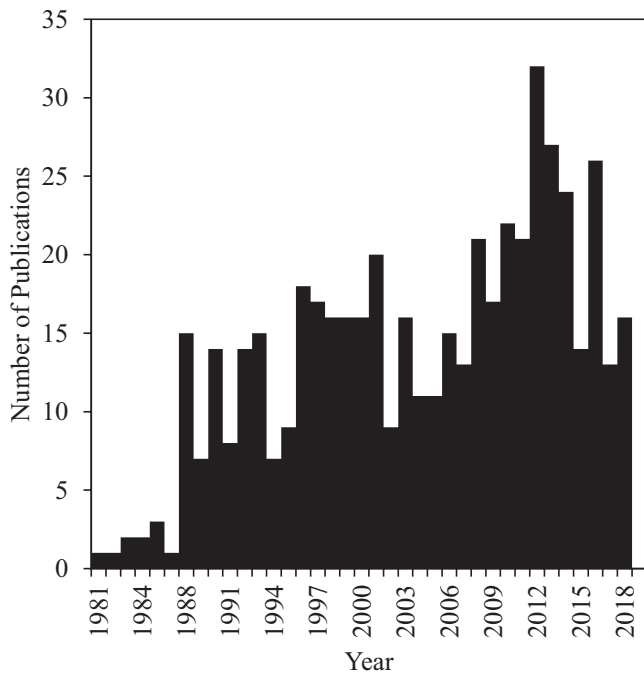


Figure 1. Number of publications about disturbance each year from 1982 to 2018 listed in the publication database of the U.S. Long Term Ecological Research Network.

disturbance processes brought social–ecological systems to the forefront and the addition in 1988 of agricultural (Kellogg Biological Station) and in 1997 of urban (Baltimore Ecosystem Study and Central Arizona–Phoenix) research sites. These and several other LTER sites have expanded the LTER mission to address land-use and land-cover change and human–environment interactions (Collins et al. 2011), and the subsequent research has broadened our understanding of social–ecological feedback loops to disturbance.

Because of this dedication to data collection across common core areas, the US LTER Network has generated numerous data sets that capture disturbance and disturbance interactions across multiple spatiotemporal scales. A 2019 literature review identified 457 LTER publications to date (2019) that include *disturbance* in the title, and 78 of these describe data or observations from more than one site. The number of publications about disturbance has been increasing through the mid-2000s (figure 1). Well-known examples of long-term research on disturbance include the influence of nonnative aquatic species on long-term ecological dynamics in north temperate lakes, the interactions of multiple hurricanes on the landscape dynamics of tropical forests in Puerto Rico, and vulnerability of prairies to future disturbances across spatial scales of prior disturbances (Turner et al. 2003). These studies highlight the potential for long-term core data sets to inform how disturbance regulates ecosystem dynamics across a wide variety of ecosystem types, particularly by providing data on long-term spatiotemporal variability before and after disturbance.

These studies also underscore the need for much longer time series to capture the outcome of multiple, potentially interacting disturbance events that occur on different spatial and temporal scales, and call into question the utility of defining a predisturbance or baseline condition suggestive of equilibrium. Although unexpected phenomena, novel events, and ecological surprises remain a serious challenge to ecological prediction (Likens 1989, Lindenmayer et al. 2010, Dodds et al. 2012), improved quantitative and mechanistic understanding of multiple disturbance events and their interactions across multiple scales may increase the accuracy of ecological forecast models and their successful application to management strategies (Dale et al. 1998).

Peters and colleagues (2011) recognized the need for a common framework to drive synthesis of disturbance dynamics across long-term research programs. They developed a conceptual framework that depicts disturbance as a process that includes interactions among disturbance drivers, initial system components, and the physical and biological mechanisms of disturbance effects. This framework acknowledges interactions among abiotic and biotic ecosystem components across spatial scales, and the influence of prior disturbance legacies (Pickett et al. 1999, Pickett and Cadenasso 2009). The *discreteness* of an event could be defined on the basis of the onset, duration, or release of a driver, or the time over which a mechanism operates relative to the lifespan of key organisms. The quantification of *disruption* requires an appropriate model or reference state, which is often elusive when disturbances interact at relatively short return intervals. Finally, Peters and colleagues (2011) challenged future research to use this strategy of disaggregating disturbance types into measurable drivers, mechanisms, and initial system properties to understand how global change is altering disturbance effects, to guide more informative and generalizable experimental manipulations across sites, and to incorporate the role of human actions and decisions on managing vulnerability to disturbance. The incorporation of human dimensions research into the US LTER Network has advanced understanding of the relevance of disturbance to both ecology and society, and therefore requires an expansion of the Peters and colleagues (2011) theoretical framework. This expansion is the primary goal of our article.

A refined conceptual framework of social–ecological disturbance

In studying social dimensions of disturbance, ecologists have moved beyond the tendencies to characterize humans solely as agents of disturbance (e.g., via land-use land cover change, hydrologic changes) and to narrowly define *disturbed ecosystems* as those dominated by humans. Instead, the field is increasingly recognizing the human ecosystem as an organizing concept (Machlis et al. 1997) and that people are important components responding to, interacting with, and influencing disturbance processes in many ecosystems (McDonnell and Pickett 1993). To advance disturbance

ecology theory for social–ecological systems, In the present article, we conceptualize the role of humans as both drivers of and responders to long-term disturbance dynamics. If disturbance theory is to help address the changes of the Anthropocene (Newman 2019), such refinement is urgently needed.

The US LTER Network arrived at this cultural shift in the mid-1990s and began to integrate human dimensions into long-term studies by incorporating ecosystem services, planning and design, governance, and human preferences into strategic documents and publications (see Collins et al. 2011). Indeed, 20 years ago, Pickett and colleagues (1997) endorsed the study of human-dominated ecosystems by integrating humans into ecological research in human-occupied areas. This conceptual advance stood on the shoulders of research in European urban ecology (Sukopp 1990) and early dialogue on humans as components of the ecosystems that they inhabit (McDonnell and Pickett 1993). Grimm and colleagues (2017) put forward a general conceptual framework for disturbance in urban social–ecological–technological systems, that built on the Peters and colleagues (2011) framework, to understand disturbance as a process rather than as a discrete event, by involving the disturbance event, its effects, and the system response. In their synthesis, Grimm and colleagues (2017) suggested that a contemporary conceptualization of disturbance should include quantification of structural disruption, characterized by effects relative to an explicit definition of system boundaries, composition, and interactions; the intensity or magnitude, spatial extent, duration, and timing; and the spatiotemporal pattern of disturbance regimes (to embrace interactions and legacies of multiple disturbances). By disaggregating the social, ecological, and technical (SET) aspects of the disturbance process, their framework allows any driver to be an agent of disturbance to a dynamic—but bounded—SET system. This avoids conflating *urban* with *disturbance*.

To further integrate the human dimensions of disturbance into our conceptualization of social–ecological systems, we refined the Grimm and colleagues (2017) framework by adding both intentional and unconscious feedback loops manifesting in changes to laws, policies, values, and behaviors, which in turn affect the ecosystem template affecting future disturbance. We also include a model reset and recalibration to capture the temporal (sometimes cyclical) nature of disturbance and system response (figure 2). Importantly, this recalibration does not imply that the system returns to the state it occupied prior to the disturbance (i.e., equilibrium), but rather that the next disturbance operates on the properties of the system that may include legacies of the prior disturbance as well as other ongoing changes (a nonequilibrium model). The human dimension components interact with each other (figure 2, upper right), with disturbance event drivers and system properties (left panel), with internal processes and drivers of disturbance processes (center panel), and with the new state of the system (lower right), through consequences that may be either intended

or unintended. Our refinement of the Grimm and colleagues (2017) framework retains their process-based framing, incorporates human dimensions, feedback loops, and nonequilibrium dynamics that allow the transition to new system states, and finally, subdivides the general processes into more specific types, emphasizing social–ecological system components (Childers et al. 2014).

To understand the consequences, legacies, and feedback loops of disturbance relevant in coupled social–ecological systems (e.g., management activities, economic disruption), they must be dissected and closely examined. For example, land cover conversion (e.g., from forest to farmland) is intentional, but many of its consequences are unintentional (e.g., erosion and downstream eutrophication) with long-term legacies for biophysical (e.g., water quality, food webs) and human (e.g., governance, economic) dimensions (supplemental table S1). The consequences of agricultural activities have led to the creation of new government agencies, research programs, and policies intended to reduce the detrimental effects of agriculture on water quality. Similarly, urban development processes have intentionally resulted in economically productive urban hubs, whereas unexpected disruptions to urbanization have resulted in unintended consequences for urban biodiversity (supplemental table S1). Studies of beaver overharvesting and the expansion of nonnative Asian carp across the United States elucidate similar insights into the coupled consequences of disturbance to both social and ecological systems. The more we recognize that social and ecological systems are inextricably linked, the more critical the need becomes for disturbance studies to examine the role of humans as both agents of and subjects of disturbance legacies and feedback loops.

Application of our framework to LTER sites

In the present article, we apply our new conceptual framework to seven sites in the US LTER Network, characterized by a wide range of disturbance types and levels of human intervention (figure 3) to evaluate the utility of the framework for advancing knowledge of disturbance effects and interactions, and social–ecological feedback loops. These sites include temperate coniferous forest, urban, subtropical coastal wetland, temperate deciduous forest, desert grassland, temperate kelp forest, and temperate barrier island ecosystems. Below, we provide a detailed interpretation of a process-focused example of disturbance at each site, using our conceptual framework (figure 2) as a guide; each case study begins with a description of system properties and disturbance drivers, types, and mechanisms (disturbance event, green box), followed by a description of the disturbance effect and processes of recovery and reorganization (disturbance process, blue boxes), followed by a description of human dimensions (gray box), including social–ecological feedback loops (dotted arrows) and recalibration or recovery (red arrow) to a new or former state. After describing the disturbance process for each case study, we synthesize our

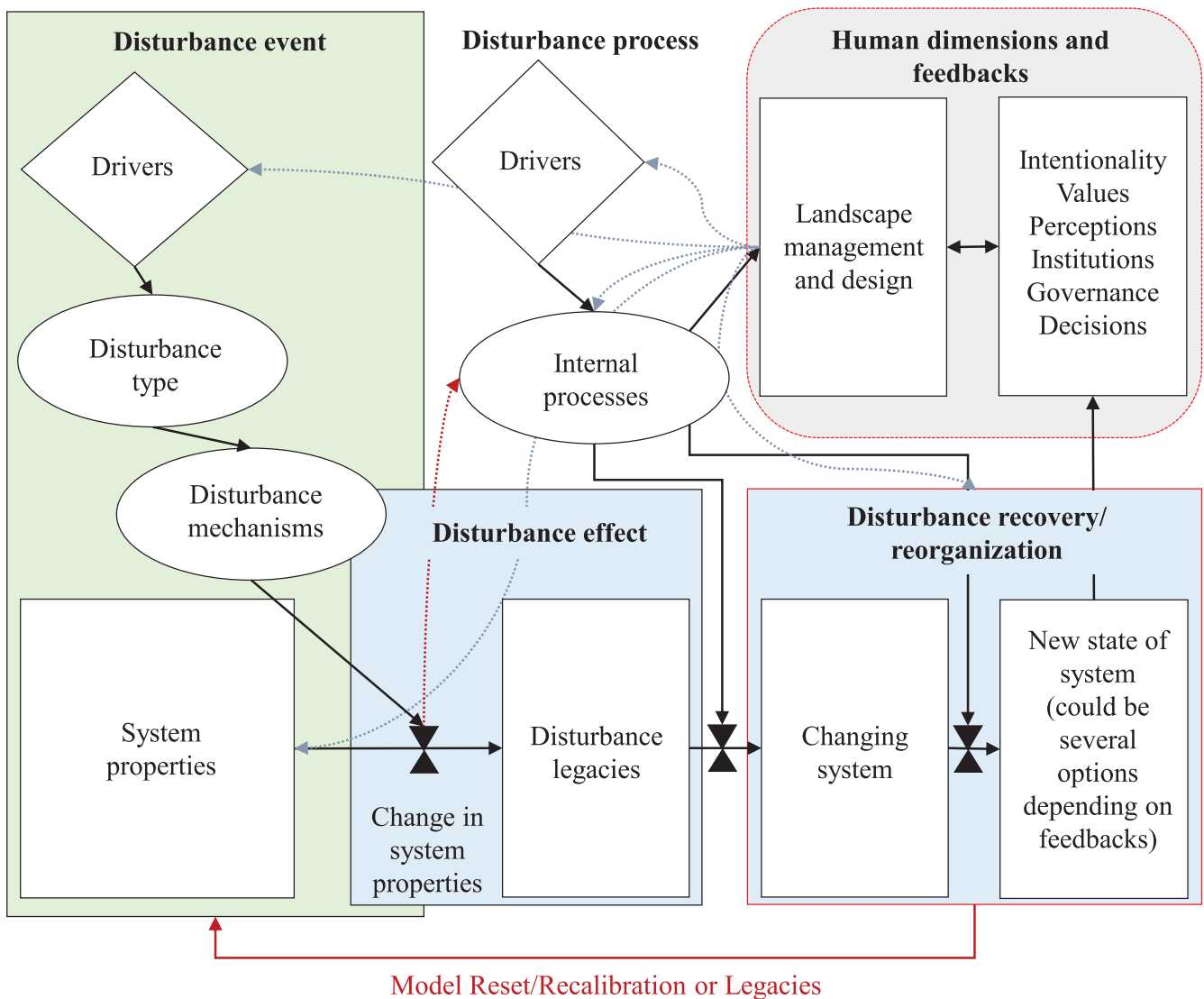


Figure 2. Conceptual framework for guiding long-term research on disturbance, and for describing links between disturbance events, their effects, and recovery trajectories (modified from Grimm et al. 2017). New elements include the explicit highlight of the human dimensions of disturbance (gray box) and their feedback loops (including intended or unintended consequences, dotted blue lines) and the effect of legacies of past disturbance or ongoing change on the next disturbance event and process (red lines).

findings across the four areas of research needs that were recommended by Turner (2010).

Temperate coniferous forest: Andrews Forest. In the Andrews Forest, and the surrounding western Cascade Mountains of Oregon, broadscale vegetation patterns have been shaped by multicentury cycles of fire disturbances in forest landscapes (supplemental figure S1; Morrison and Swanson 1990, Rasmussen and Ripple 1998, Weisberg and Swanson 2003, Zald et al. 2016) in conjunction with more recent timber harvesting activities. Fire severity, extent, and timing are determined by source of ignition (nonanthropogenic or anthropogenic), weather, fuels, and topography. In addition, fuels vary with environmental

gradients determining productivity and successional status, such as elevation, aspect, soils, landform, and history of other disturbances at the Andrews Forest, such as wind (Harmon and Pabst 2019), debris flows (Bigelow et al. 2007), and flooding (Johnson et al. 2000). Spatial heterogeneity in fire heat generation and combustion lead to spatial variation in tree survival, dead wood retention, and vegetation regeneration (Freund et al. 2014, Tepley et al. 2014, 2017). Disturbance recovery is then dominated by multiple successional pathways arising from stand-replacing and non-stand-replacing fires (Tepley et al. 2013), which contribute to both immediate and long-term landscape variability in structure and composition after fires (e.g., Brown et al. 2013).

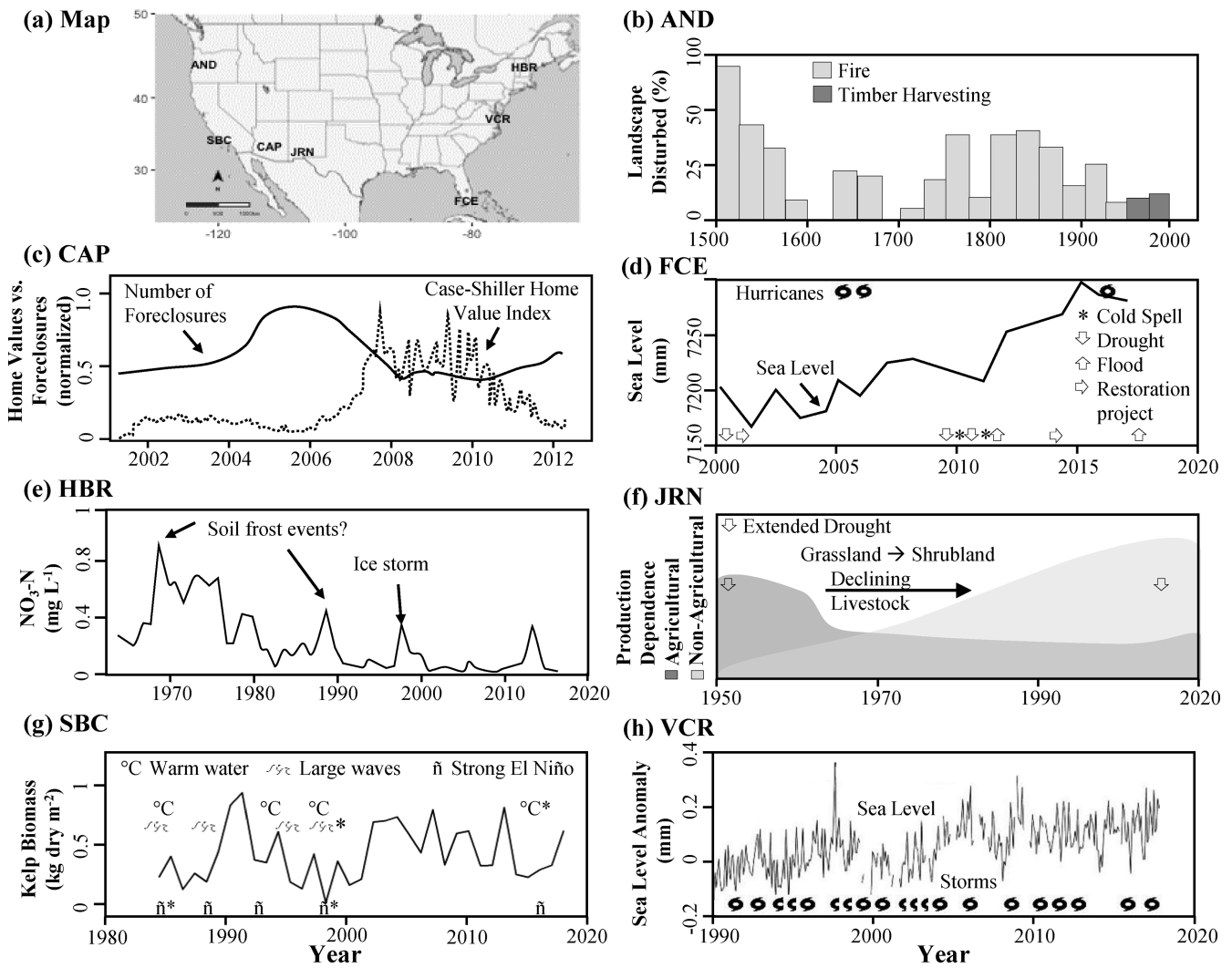


Figure 3. (a) Map of the seven US LTER sites highlighted in this article, all subject to multiple interacting disturbances that include human dimensions of change. (b) Percentage of the landscape effected by major disturbances in the Andrews Forest (AND) including fire (1492–1952; Teensma 1987) and timber harvesting (1945–1995; Seidl et al. 2014). (c) Timeline of foreclosures and home values from Central Arizona–Phoenix (CAP) showing the effect of the 2008 Great Recession on the Phoenix Metro Area (note that foreclosures peaked about 2 years before 2008, whereas the precipitous decline in home values began in late 2010). (d) History of major disturbances in the Florida Coastal Everglades (FCE) from 2000 to 2017, including the long-term increase in sea level (y-axis) punctuated by tropical cyclones, severe to extreme droughts (Palmer Index) and floods, cold spells (defined by extreme magnitude and duration, Boucek and Rehage 2014), and major shifts in managed freshwater flows into the FCE domain. (e) The long-term record of stream nitrate concentrations at the Hubbard Brook (HBR), showing the effect of soil frost and ice storm disturbances over water years (beginning June 1). These disturbances are taking place against a background of declining nitrate export or nitrogen oligotrophication that alters ecosystem response to disturbance. In the later stages of this record, soil frost events and experimental ice storms have produced very small, or undetectable responses in stream nitrate (Campbell et al. 2019). (f) History of production dependence on agriculture and nonagricultural production in the Chihuahuan Desert grasslands and shrublands of the Jornada (JRN), characterized by a history of droughts (with a 40–50-year return interval) and shifts toward woody plant dominance during periods of aridity (Fredrickson et al. 1998) with modern levels of managed grazing that began in the 1980s (Peters et al. 2015). (g) History of major disturbances to giant kelp from 1982 to 2018 at the Santa Barbara Coastal (SBC) ecosystem (Bell et al. 2017), including strong El Niño periods (Multivariate ENSO Index [MEI] ≥ 2 ; Wolter and Timlin 2011), large wave events (maximum significant wave height, H_s , anomaly of at least 1 meter; Reed et al. 2016), and periods of anomalously warm water (sea surface temperature [SST] anomaly of at least 2 degrees Celsius; Reed et al. 2016). Asterisks indicate extreme El Niño (MEI ≥ 3), waves (H_s anomaly of at least 2 meters), and warm water (SST anomaly of at least 3 degrees Celsius). (h) History of sea level anomalies, and storms (tropical storms, hurricanes, and northeasters) influencing the Virginia Coast Reserve (VCR) since the 1980s.

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Immediate and long-term effects of fire on landscape heterogeneity in structure and composition in the western Cascades Mountains interacted with societal needs and values to set the context for forest management and governance, especially on public lands. Disturbance regimes have changed through time as fire suppression largely removed wildfire from the landscape, followed by periods of dispersed patch clear-cutting (1950–1990) leading to declining prevalence of old-growth forests, and later thinning operations in harvested patches following the 1994 Northwest Forest Plan, which prioritized old-growth conservation (Davis et al. 2015, Harris 2018). Regional assessments of forest structure and restoration needs (DeMeo et al. 2018) and the record of fire and harvesting disturbance at the Andrews Forest (figure 3b) indicate that area disturbed by timber harvesting is comparable to historical fire. However, the increasing area burned by fire in the western United States (Westerling et al. 2006) during recent decades, including wet productive forests of the Pacific Northwest (Reilly et al. 2017, Davis et al. 2017), drives concerns about the economic and societal risk of future wildfire. Resulting forest management activities (e.g., fire suppression, timber harvesting, and postfire salvage logging and planting) influence fire severity and recovery, with higher severity fire sometimes associated with younger forests (e.g., Zald and Dunn 2018). It has been suggested that the development of landscape management plans based partially on historical fire regimes could play a role in reducing risks to native species and ecological processes (Cissel et al. 1999), but it is unclear whether sufficient social license and economic capacity exist to support proposed management activities (Spies et al. 2010). Therefore, the process of recalibration to a new state or recovery to the prefire state depends on the amount of time since the fire, the prevalence and pattern of fire severity, and the management feedback loops, because they alter fuel characteristics and the resistance and resilience to the next fire (*sensu* Seidl et al. 2014).

Urban ecosystem: Central Arizona–Phoenix. The 2008 Great Recession and the accompanying housing market crash was a major social–ecological and economic disturbance to many residential areas in Central Arizona–Phoenix (supplemental figure S2). Many homes and other properties were abandoned because of rapid and dramatic declines in property values, mortgage foreclosures, and cessation of ongoing suburban development. In Phoenix, when yards are no longer being maintained with supplemental watering, plantings, and other care, rapid changes in plant community composition take place (Ripplinger et al. 2016). In desert cities, plant communities are water limited, and without supplemental watering, they may become depauperate as opposed to becoming overgrown with nonnative vegetation. Over the short term, the community shift associated with abandonment included a pulse of mostly native annual plants (e.g., weeds), whereas, in the long term, perennials were effectively replaced by annuals with low water requirements.

At the regional level, the loss of yard management transformed the effected neighborhoods from clusters of designed and managed yards to fallow, unmaintained landscapes. In some neighborhoods, a majority of the properties were vacated by force or abandoned in a short period of time. This set up a positive feedback of neighborhood neglect, where property values dropped even more rapidly as more homes and parcels became neglected and neighborhood social cohesion disappeared (Ripplinger et al. 2017). These human dimensions of disturbance then fed back to slow neighborhood recovery and reorganization or even encourage further abandonment and neighborhood decay. Once this positive feedback cycle was broken, the neighborhoods experienced gradual recovery of housing quality and real estate value. This return to prerecession landscape management levels is crucial for maintaining the relatively high levels of biodiversity in a desert city, and a healthy housing market is critical to larger economic recovery (Hope et al. 2003, Martin et al. 2004, Kinzig et al. 2005, Larson et al. 2009).

Subtropical coastal wetland: Florida coastal Everglades. The Everglades contains a mosaic of freshwater-to-marine coastal wetlands whose distribution on the landscape is shifting because of a changing balance of freshwater delivery and climate change (Childers et al. 2019). Decades of freshwater diversion and rapid sea-level rise have accelerated the expansion of coastal mangrove forests into freshwater marshes (Yao and Liu 2017). Where mangroves have not invaded freshwater marshes, saltwater intrusion is causing collapse of peat soils and elevation loss, creating a positive feedback to the driver (the relative sea-level rise rate; Wilson et al. 2019). The ecosystem is prone to multiple disturbances including fires, cold snaps, droughts, floods, and high-energy storms (Davis et al. 2019). We populated our framework with the latter; high-energy storms, including hurricanes represent a common disturbance in the Everglades that may determine social–ecological vulnerability to the shifting balance of fresh and marine water supplies (supplemental figure S3). Storms are agents of rapid change through their sustained high winds, marine water surges, and extreme rainfall that contribute to extensive flooding and change how the landscape is hydrologically connected to fresh and marine water supplies.

High-energy storms have an immediate impact on system properties including defoliation and canopy gaps (Danielson et al. 2017), increased delivery of the limiting nutrient phosphorus (Castañeda-Moya et al. 2010), increased fish recruitment (Boucek and Rehage 2013), increased sediment elevation through storm surge deposits (Smith et al. 2009), and export of soils as organic carbon through estuaries (Davis et al. 2004). Longer-term legacies include a reduced population age distribution of plants and animals often associated with landward recruitment and transgression, increased elevation because of the inorganic storm deposits, and increased upstream tidal transport of phosphorus (Castañeda-Moya et al. 2010, Barr et al. 2012, Danielson

et al. 2017). These legacies can increase net ecosystem productivity, landward expansion, and elevation of highly productive mangrove forests, reducing vulnerability to sea-level rise and saltwater intrusion via accelerated (Fourqurean and Rutten 2004, Ross et al. 2009, Smoak et al. 2013, Jiang et al. 2014).

High-energy storms increase flooding in urban and agricultural regions surrounding the Everglades, particularly during emergency floodwater management. Long-term water management and restoration are necessary to deliver freshwater flows throughout coastal wetlands to manage droughts and floods, prevent soil elevation loss, and reduce vulnerability to sea-level rise by fostering mangrove transgression (Wilson et al. 2018, Price et al. 2019). These changes may arise through increased public recognition of the ecosystem services provided by coastal mangrove forests (Jerath et al. 2016), including sediment, carbon, nutrient and water capture, as well as the attenuation of storm surges that reduces vulnerability of coastal ecosystems to sea-level rise and saltwater intrusion (Armitage et al. 2019, Tully et al. 2019). Long-term social–ecological feedback loops to tropical storms that result in net elevation gains are essential to building adaptive capacity of coastal ecosystems to rapid sea-level rise, a tenet that is testable with continued data collection and predictions of increasing storm intensity in the future (Walsh et al. 2016).

Temperate deciduous forest: Hubbard Brook Experimental Forest.

Disturbance research at Hubbard Brook has taken advantage of natural disturbance events such as ice storms, soil freezing events and windstorms and has also involved a series of whole-watershed experiments involving removal of vegetation by forest harvest (supplemental figure S4; Holmes and Likens 2016). The earliest experiment (1965) involved felling of all vegetation, which was left in place, followed by 3 years of herbicide application to inhibit regrowth. This long-term study of forest impacts on watershed ecology led to the development and advancement of fundamental theoretical paradigms in ecology—resilience, state change, and disturbance—as well as tested mechanisms of ecosystem-scale of recovery that emerge over decades. More recent events have included a large ice storm (January 1998) and a series of soil freezing events caused by a combination of low snow cover and an outbreak of cold air (Mitchell et al. 1996).

The watershed experiments at Hubbard Brook shed light on the mechanisms governing ecosystem recovery from vegetation removal and on the nature and extent of ecosystem resilience. Ideas about biotic control over the abiotic environment, in which the reestablishment of vegetation is essential to reducing the hydrologic extremes that drive nutrient loss, emerged from the 1965 experiment (Bormann and Likens 1979). The 1965 experiment also suggested a high capacity for resilience as vegetation, hydrology, and nutrient export returned to match reference watersheds on “normal” trajectories, despite the extreme nature of the treatment (Reiners et al. 2012, Likens 2013). The natural ice

storm of 1998 supported ideas about biotic control over the abiotic environment as increases or decreases in nitrogen export were associated with loss or recovery of the forest canopy (Houlton et al. 2003). Soil freezing disturbances also appear to be expressed through effects on plants, in this case by damage to roots that reduces plant uptake and leads to increased hydrologic losses of nitrogen (Tierney et al. 2001, Cleavitt et al. 2008, Campbell et al. 2014).

The disturbance experiments at Hubbard Brook have had significant human dimensions; most specifically in providing data and guidance for rotation times in forest management in the region. More generally, the long-term research group at Hubbard Brook functions as a nexus for scientists, managers, and stakeholders and to come together to discuss long-term change and management issues in the northern hardwood forest region (Driscoll et al. 2012).

The response to disturbance has been changing over the past 20 years at Hubbard Brook as soil freezing events (Judd et al. 2011) and experimental ice storms (Rustad and Campbell 2012) no longer appear to induce increases in hydrologic losses of nitrogen. These changes appear to be linked to a general nitrogen oligotrophication of the ecosystem at Hubbard Brook that may be driven by changes in atmospheric nitrogen deposition, increases in soil carbon flux associated with increased atmospheric carbon dioxide levels and soil deacidification or climate change (Groffman et al. 2018).

Desert grassland: Chihuahuan Desert ecosystem. In the American Southwest, periodic drought and livestock grazing have been part of the landscape for thousands of years (supplemental figure S5; Peters et al. 2015). However, in the northern Chihuahuan Desert, human decisions led to livestock overgrazing in the mid to late 1800s that combined with severe, multiyear drought resulting in high grass mortality and low herbaceous cover (Herbel and Gibbens 1996, Fredrickson et al. 1998). Shrubs such as honey mesquite that are resistant to grazing and dispersed by livestock expanded during and following drought. By the early 1900s, a savanna state existed consisting of a mixed grassland with scattered shrubs (Gibbens et al. 2005). As livestock grazing continued under periodic drought in the 1930s and 1950s, shrub expansion and grass loss continued that resulted in broadscale conversion of grasslands to shrublands throughout the northern Chihuahuan Desert that has persisted to present day (Buffington and Herbel 1965, Gibbens et al. 2005). Loss of perennial grasses on certain locations was possible with informed decisions about stocking rate (Peters et al. 2006, 2015). However, after a threshold of shrub and bare cover was reached then wind or water erosion became the dominant process that reinforced the competitive advantage of shrubs over grasses even if livestock grazing was removed (Peters et al. 2004). This model of grassland versus shrubland as alternative states driven by herbivory and drought is a broadscale model of desertification based on plant-scale processes (Schlesinger et al. 1990).

More recent studies have enriched this early model (modified from Peters et al. 2011) in two important ways. First, landscape-scale variation in woody plant encroachment involves multiple drivers and their mechanisms that are variable through time and space to interact with heterogeneity in system properties and lead to spatial variation in patterns in grass loss (Peters et al. 2006). Variability in precipitation, topography, distance to seed sources, and soil properties interact to affect patterns of plant-available water and seed availability to result in complex patterns in shrubs and grasses across the landscape even if these locations have similar disturbance regimes (McAuliffe 1994, Gibbens et al. 2005, Yao et al. 2006). Second, climatic regimes are changing to include precipitation pulses in the form of wet periods (i.e., sequences of 4–5 wet years) as another form of disturbance. These multiyear pulses in precipitation have resulted in perennial grass recovery in shrublands and a conversion back toward a savanna that is only possible with informed grazing management (Peters et al. 2012, Petrie et al. 2018). A future reset back to a grassland system may be possible if shrubs suffer mortality.

Temperate kelp forest: Santa Barbara coastal. Kelp forests and sandy beaches fringing the Southern California coast experience climate-driven disturbances that may be changing in frequency or intensity, such as destructive ocean storms and prolonged extreme temperatures (marine heat waves). Large storm-driven waves damage and remove the dominant foundation species, giant kelp (*Macrocystis pyrifera*), and overwhelm bottom-up (seawater nutrients) and top-down (sea urchin herbivory) controls of giant kelp biomass and production (supplemental figure S6; Cavanaugh et al. 2011, Reed et al. 2011, Bell et al. 2015). Long-term experiments and community surveys demonstrate that the interannual frequency of giant kelp disturbance outweighs year-to-year variation in the severity of kelp loss in structuring benthic biodiversity (Byrnes et al. 2011, Castorani et al. 2018). Repeated annual giant kelp loss—as could occur in a future with more frequent large storms—is associated with a doubling of smaller understory algae and sessile invertebrates but with 30%–61% lower biomass of many fish and shellfish (Castorani et al. 2018), probably because of impaired physical ecosystem engineering by giant kelp (Miller et al. 2015, 2018). Because large amounts of giant kelp production are cast onto shore as wrack, the loss of giant kelp forests cascades spatially to reduce organic matter subsidies to adjacent sandy beaches, thereby diminishing beach biodiversity and ecosystem function (Dugan et al. 2003, 2011, Schooler et al. 2017).

Giant kelp forests thrive in the cool, nutrient rich waters and are susceptible to prolonged disturbances arising from interannual variation in ocean climate. Between 2014 and 2016, large-scale ocean warming of unprecedented magnitude and duration (Di Lorenzo and Mantua 2016) caused monthly ocean temperature anomalies as high as 4.6 degrees Celsius in the northeast Pacific Ocean. Although massive

effects on kelp forests were anticipated, giant kelp and most associated taxa did not markedly decline within the Santa Barbara region (Reed et al. 2016). Instead, regional giant kelp biomass and most associated species remained within ranges observed during cooler years of the 34-year time series (Reed et al. 2016, Bell et al. 2017). However, in more southerly latitudes where warming was more intense and prolonged, several giant kelp populations crashed and failed to recover 2 years following the heat wave ended (Cavanaugh et al. 2019). Resilience of giant kelp to this exceptional warming was spatially variable, due in part to variation in dispersal and recruitment (Cavanaugh et al. 2019). The remarkable resilience of many giant kelp populations is due in part to their functioning as a metapopulation, in which neighboring populations rescue failing ones and promote recolonization following extirpation (Reed et al. 2006, Castorani et al. 2015, 2017). In Santa Barbara, sea urchins (the primary herbivores) and sea stars suffered high mortality because of warm-water associated diseases (Reed et al. 2016). The lack of consistent declines across the kelp forest community highlights the need for a mechanistic understanding of the processes that promote ecological resistance and resilience in the face of changing disturbance regimes. Long-term observations and experiments that encompass broad environmental conditions offer the best opportunity to understand and predict the future structure and function of coastal ecosystems.

Temperate barrier island: Virginia Coast Reserve. High energy storms, including nor'easters and hurricanes, are a common disturbance to Virginia Coast Reserve (VCR; supplemental figure S7). The shallow seaward slope of coastal barrier landscapes (typically below 0.1%) makes them particularly vulnerable to sea-level rise (i.e., approximately 5.4 millimeters per year; NOAA 2019) and storms (e.g., Day et al. 2008). Storm frequency has changed along the US Atlantic coast over the last century, with approximately 15 extra-tropical storms per year hitting the Virginia coast (Hayden and Hayden 2003). Large storms cause saltwater inundation, reduction in primary productivity of woody species (Johnson and Young 1992, Fernandes et al. 2018), and shoreline erosion or overwash on barrier islands (e.g., Wolner et al. 2013, Brantley et al. 2014, Walters and Kirwan 2016), leading to ecosystem state change through redistribution of sediment and subsequent changes in elevation or exposure (Zinnert et al. 2019). Elevation is an important determinant in vegetation cover (Young et al. 2011, Lentz et al. 2016), and vegetative cover type influences overall barrier island response to storms.

In barrier island uplands, vegetation influences sediment supply transfer processes by trapping and stabilizing sand (reviewed in Feagin et al. 2015). Interactions between vegetation cover and elevation play an important role in influencing sediment movement during a storm (Zinnert et al. 2017, Stallins and Corenblit 2018). Dune or swale vegetation creates feedback loops with island topography and

influences disturbance frequency and severity that interior communities experience (Stallins and Parker 2003, Stallins 2005, Miller et al. 2009). High dune ridges offer resistance to storm disturbance and minimize overwash frequency (Zinnert et al. 2019). Dune ridges enable establishment of salt sensitive woody vegetation by reducing abiotic disturbance (i.e., wind, salinity, overwash) to the interior island (Ehrenfeld 1990, Woods et al. 2019). Woody vegetation has been expanding across the VCR over the last 30 years because of warming winter temperatures and provides additional resistance to storm disturbance (Claudino-Sales et al. 2008, Arkema et al. 2013, US Army Corps of Engineers 2013, Zinnert et al. 2019).

Management decisions have preserved the VCR barrier islands in a natural state, allowing for possible migration with sea-level rise and the opportunity to understand barrier island ecological processes in the absence of direct intervention. Although woody expansion provides resistance to storm disturbance, over decadal time scales it appears to lower barrier island resilience in the VCR (Zinnert et al. 2019). By strongly resisting incursions of overwash, areas with high foredunes and extensive woody vegetation are more likely to block barrier island migration and erode over time with sea-level rise and storm events (Zinnert et al. 2019). Conversely, areas with lower dune elevation and less topographic relief do not support woody vegetation (Woods et al. 2019) and are more susceptible to overwash of sediments, migration of barrier island upland onto the marsh, and subsequent ecosystem state change because of changes in elevation (Zinnert et al. 2019). Long-term observations have enhanced our understanding of the interactions between ecology and physical processes in this coastal environment, provided conceptual frameworks that can be used to understand disturbance along coastlines, and enhance coastal management efforts.

Insights from operationalizing the revised conceptual framework

The operationalizing of a refined disturbance conceptual framework enabled us to address the three common challenges associated with disturbance ecology identified above and to undertake the four directives outlined by Turner (2010) across a wide range of disturbance regimes in diverse social–ecological systems. First, long-term ecological research has discovered the role of disturbance as a catalyst of rapid ecological change by providing baseline data on spatiotemporal dynamics of ecosystems, trajectories of change, and a basis of comparison for changing disturbance regimes (Kominoski et al. 2018). By disaggregating the disturbance processes, we found that ecosystem responses (or shifts) are neither fast nor slow (Gunderson and Holling 2002); rather, the disturbance process has both faster and slower-responding components that may positively or negatively reinforce predisturbance dynamics or trajectories. Second, although our revised conceptual framework consists of many boxes and arrows, it distinguishes the effects of prior

disturbances and their legacies on the effects of a particular disturbance event, thus allowing for evaluation of synergistic or antagonistic interactions over time and space. The ability to understand the role of these legacies will only increase with continued long-term data collection and experimental manipulations that capture new combinations of event types and system properties. Third, our framework explicitly integrates humans as both agents of and responders to disturbance. Finally, it recognizes that disturbance effects can change as the environment changes by adding a model reset or recalibration feedback loop to the system properties on which a subsequent disturbance may act. Below, we provide examples of how our conceptual framework has informed these four challenges.

Disturbance alters ecosystem vulnerability to presses. A common line of reasoning is that a disturbance (i.e., a pulse) can increase the vulnerability of an ecosystem to other agents of environmental change (e.g., other pulses or presses; Turner 2010). Although many theories of disturbance recognize that disturbance is something to which a system or organism adapts (i.e., Jentsch and White 2019), very few recognize the ability of disturbances to enhance resilience or reduce vulnerability. Some of our examples, however, showed just that. In the described coastal ecosystems, high energy storm disturbance can reduce vulnerability to sea-level rise. Where and when storms deposit sediments and nutrients, particularly behind vegetation traps, elevation gains allow for encroachment of salt-resistant and highly productive woody species that resist storms and further build elevation relative to sea-level rise. In temperate forests, canopy disturbance from ice storms or tree fall increases light, water, and nutrient availability that fosters recovery and does not necessarily create an ecosystem state with increased vulnerability to further disturbance. By describing disturbance recovery, reorganizational processes, and the feedback loops to human decisions and actions, we can evaluate the role of complex processes that can result in both positive and negative responses and feedback loops (even within the same ecosystem) to other ongoing social–environmental drivers.

Spatial heterogeneity in disturbance interactions. The Grimm and colleagues (2017) framework deliberately characterized the disturbance process according to the event itself, its effect relative to existing system state or dynamics, and social–ecological responses. These three features recognize that disturbances are not acting in a vacuum but instead on a spatially complex template that has been influenced by prior disturbance (Pickett et al. 2017). In our refinement of this framework, we describe spatial heterogeneity not only as a driver of disturbance outcomes but also as a response. From the temperate coniferous forest, we have identified how fire effects both depended on and helped to develop the patchiness of fuels and forest succession in the landscape, although timber harvesting alters those patterns. In our

urban ecosystem, the change in regional ability to provide an external subsidy (water) strongly decreased the response of biodiversity to economic recession at much smaller scales of the neighborhood and yard level. In the desert grassland, disturbance effects were highly scale dependent, and proximity to shrubland or grassland patches determined the trajectory of ecosystem structure following a shift in precipitation. Similarly, in temperate kelp forests, regional variation in physical disturbance interacts with landscape-scale differences in metapopulation dynamics to determine whether a foundation species went locally or regionally extinct. The temperate barrier island system evaluated in the present article showed how the effect of tropical storms on sea-level rise vulnerability was modified by vegetation and topographic legacies of prior storms; woody vegetation attenuates storm surge sediments, whereas low-elevation marshes behind dunes may erode rather than build elevation after a storm. Spatial heterogeneity was one of the more difficult features of the disturbance process to quantify, but our multidimensional framework qualitatively depicted its importance in ways that motivate landscape-scale empirical, experimental, or modeling approaches.

Social-ecological disturbance feedback loops. Although the LTER sites incorporated in these case studies represent a large range of human-environment interactions, they all showed evidence of strong human feedback loops across social, ecological, and technological axes. Social factors in the urban ecosystem drove ecological responses (i.e., yard plant biodiversity) to drought, which in turn influenced local socioeconomic resilience to larger-scale economic change. Climate and land use change may alter fire frequency in temperate coniferous forests, generating management tradeoffs between laws relevant to species of special concern inhabiting old-growth forest with fire risk management. Such tradeoffs are also obvious drivers of storm-disturbance effects in South Florida, where decisions to move floodwater to the ocean via canals to protect urban and agricultural lands may threaten endangered species reliant on dry conditions (Pearlstone et al. 2015). In the temperate kelp forest system, human-caused climatic changes that may increase the frequency, intensity, duration, and extent of marine heat waves are likely to impair the resistance of giant kelp to these and other disturbances and to affect coastal communities that rely on kelp forests for tourism and fisheries. In the temperate barrier island system, recognition of mechanisms by which storms may increase or decrease vulnerability of low-lying areas to future storms depending on vegetation cover type may inspire technological or infrastructural interventions such as jetties and sediment barriers, green infrastructure, or active sediment delivery to offset these effects. In the temperate deciduous forest, societal efforts to reduce sulfur and nitrogen deposition from the atmosphere, along with increases in atmospheric carbon dioxide have had profound effects on soil resources that reduce hydrologic losses of nutrients following disturbance (a good

thing), but may slow vegetation regrowth and biotic control of the abiotic environment following disturbance (Groffman et al. 2018, Weitzman et al. 2019). The desert grassland system framework captured a social system feedback broken by ecosystem hysteresis; past mismanagement leading to overgrazing increased susceptibility to drought-driven state change but hysteresis in the shrubland state prevented return to grasslands even when livestock grazing was reduced. Future climatic changes that include multiple, sequential wet years may have the potential to recover perennial grasses under managed livestock grazing and shift the system back toward the historic grassland state. Recognition of the possibility of hysteretic properties of ecosystems is a critical component of conveyance of science into adaptive management of disturbance.

Interactions of disturbance and rapid global change. Peters and colleagues (2011) anticipated that disturbance regimes in LTER sites shift with changes in global environmental drivers. A research strategy that disaggregates disturbance processes may advance our understanding of disturbance-ecosystem interactions, particularly when conditions fall outside the historical range of variability. The case studies described in the present article contain disturbance elements that have no past analogue but from which we have gained new insight as follows. The coastal barrier island LTER site reviewed is experiencing unprecedented (for the period of record) rates of sea-level rise, and this is enhancing resilience by the sediment-building effects of storms in areas with low woody vegetative cover. Although wet productive coniferous forests around the Andrews Forest do not appear to be a high priority for forest restoration intended to reestablish historical fire regimes (DeMeo et al. 2018), observed and projected increases in area burned associated with changing climate could alter the frequency of large fires (Davis et al. 2017). In the desert grassland system, drought periodicity is changing, and this will interact with livestock management to determine the probability of the return of grassland ecosystems. In our urban ecosystem, socioeconomic factors may alter the effectiveness of yard management feedback loops to climate at the local scale. Ongoing changes in atmospheric chemistry (nitrogen, sulfur, carbon dioxide) will affect both the response to and the recovery from disturbance at the temperate deciduous forest site. These interpretations of interactions between the slower presses of climate change and socioeconomic change with event-driven disturbance pulses were aided by combining disturbance narratives with graphical models of both the changing disturbance regime and the framework of disturbance process interactions.

Conclusions

The lack of an operationalizable theoretical framework has limited the development of a general and synthetic understanding of social-ecological disturbance across diverse ecosystems undergoing environmental changes. We refined

the conceptual framework for social–ecological disturbance offered by Grimm and colleagues (2017) by compartmentalizing processes, drivers, and feedback loops across social and ecological dimensions. By using the framework to depict and describe disturbance processes at seven LTER sites, we were able to accommodate both antagonistic and synergistic interactions among disturbances, facilitate understanding of the role of spatial heterogeneity in driving disturbance response, underscore the importance of feedback loops between social and ecological agents of change, and reveal how consequences and drivers of disturbance were likely to change as the environment changes. Application of this compartmentalized framework may allow users to improve expectations of system vulnerability to ongoing environmental changes and better inform management of vulnerability to disturbance. Application of the framework to social–ecological systems that vary in governance structures (e.g., tribal, democracy, oligarchy, monarchy, authoritarian, totalitarian) may provide additional insight into the social–ecological feedback loops in the framework. In addition, future application of this framework across ecosystems with even longer data series capturing multiple event–ecosystem state interactions, should profoundly advance our understanding of social–ecological feedback loops to disturbance processes underlying long-term change.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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